A TIME-BUDGET STUDY OF THE SOUTH ISLAND ROBIN
PETROICA AUSTRALIS AUSTRALIS AT KOWHAI BUSH, KAIKOURA

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ABSTRACT

I timed the activities of individually colour-banded South Island Robins *Petroica australis australis* of known age at Kowhai Bush, Kaikoura (August 1976 to December 1978) and on Outer Chetwode Island, Pelorus Sound (April to June 1978) to establish and investigate their time-budgets and diurnal patterns of behaviours. The number of Robins present in the Kowhai Bush study area gradually declined from a peak of about 100 in January 1977 to 37 in July 1978. Probably, about 120 Robins were present on Outer Chetwode Island during my visits there (Flack and Lloyd 1978).

The birds seemed to be active only during the day, and no data on sleeping and roosting were collected. Generally, each behaviour included several activities: for example, body-maintenance behaviour was made up of stretching, beak-wiping, body-shaking, scratching, preening, bathing, anting and sunning. Many activities were timed separately and descriptions of them are given. To determine the proportion of time Robins devoted to a behaviour, the time they spent in the various activities making up the behaviour were combined.

Throughout the year Robins foraged for more than half the daylight hours. It was evident that foraging to find enough food to meet their maintenance requirements was their first priority. Once this need had been met, extra time was devoted to body-maintenance and resting. The behaviours of lowest priority were those associated with reproduction.

In the non-breeding season (January to July inclusive), adult males and adult females foraged least of all just before starting to moult (December and January), spending about 55% of observation time on feeding. Over the year they foraged most in July, 90-94% of their time. The shortest day and lowest monthly mean temperature occurred in June, but both factors increased little to July. Since the Robins devoted more time to foraging during the course of autumn (April and May) and winter (June and July), they spent gradually less time in resting and body-maintenance. Adults spent the least time in partner-interactions, territorial defence and vocalizing when moulting (January to March). These behaviours increased as a proportion of their time-budgets thereafter.

From January to June, both immature males and immature females foraged more and spent less time on body-maintenance and resting than did adult males and adult females respectively. Furthermore, from January

to April, immature males sang less than did adult males, but in June and July the reverse was true.

In the breeding season (August to December inclusive), the time-budgets of males were determined to a large extent by the number of trips with food per hour they made to their mates and/or progeny; the higher the rate of food-trips the more time males foraged. When rearing nestlings, males made an average of five food-trips per hour to their young and foraged for 83.3% of observation time, significantly greater for both factors than at any other stage of the breeding cycle. Paired males foraged least of all during the nest-site selection stage (60.8%), but this value was significantly higher than that for bachelors (57.4%).

As only females built nests, incubated and brooded, their time-budgets were greatly influenced by the stage of the breeding cycle they were engaged in. They foraged most when tending juveniles (82.0%). In contrast to their partners, females raising nestlings foraged for only 42.6% of time because they spent 46.7% of their time brooding. Females foraged least of all in the incubation stage (12.9%) when they incubated for about 80% of their time.

In general, the results of this time-budget study support the findings of investigators into the time- and energy-budgets for other species. Without a change in food availability or energy content per food item, when birds require more energy they spend more time foraging. Winter was the season when Robins spent almost all their time in behaviours associated with self-maintenance, particularly foraging. At that time of year they devoted less time to behaviours associated with reproduction than they did during summer and autumn. It seems that Robins began breeding as soon as the environmental conditions enabled them, in the daylight hours available, to meet the energy costs of self-maintenance and breeding at the same time.

Other investigators have shown that flights and yolk formation require large energy inputs to sustain. In support of this finding, female Robins that build nests and form yolks simultaneously, foraged for as much of their time as possible and had their food intake supplemented by that provided by their partners. Similarly, parent birds feeding nestlings or juveniles devoted most of their time to foraging. The moult, a process known to be of considerable energetic cost to birds, was undertaken by Robins at the most favourable time of year for self-maintenance and they stopped breeding in order to do so. Thus, when moulting, they spent a minimum of time meeting their self-maintenance requirements and so were able to devote a large proportion of their time to foraging in order to find enough food to meet the energy costs of feather replacement.

PART 1

CHAPTER ONE

INTRODUCTION

The South Island Robin, *Petroica australis australis* (Sparrman 1788) (Muscicapidae: Muscicapinae) is a medium-sized passerine of 32-40 g and about 185 mm in length. It has a distinctive yellowish-white breast, an erectile white frontal spot, a pale white bar on the underside of the wings, with the rest of the plumage being slate-grey to black. A slight plumage dimorphism exists between the sexes, females being lighter coloured than males (Falla *et al.* 1966, Flack in prep., Fleming 1950). The irides are black, the relatively long tarsi and feet brownish-black, and the soles yellow.

The South Island Robin was first collected at Dusky Sound by Sparrman and Forster in 1773. Sparrman placed the species in the genus *Turdus*. Both generic and specific names underwent a number of changes until the revision by Fleming (1950).

The bird inhabits a variety of forest types (introduced *Pinus*, manuka-kanuka, coastal broadleaf, beech, podocarp and forests involving associations of these types), at all altitudes almost to the treeline. South Island Robins (hereafter referred to as Robins) occur in forests in Marlborough, Nelson, Westland, western Otago, Southland, Fiordland and on some islands in the Marlborough Sounds. Only localised populations remain in Canterbury and eastern Otago (Bull *et al.* 1978, Fleming 1950), and throughout the South Island, Robins may be absent from areas of, apparently, suitable habitat (Fleming 1950).

The species' present distribution is a relic of its former range (Fleming 1950, Potts 1870). Many factors probably caused its disappearance from some areas, the most obvious being the clearing of forests by man. Several introduced mammalian predators take Robins, their eggs and nestlings (Flack and Lloyd 1978, Moors 1975, 1976). In addition, introduced avian diseases and competition for food with introduced birds may have contributed to the reduction in range (Hay 1975). A low rate of dispersal between Robin populations where areas of open country separate them is a reason given for their patchy distribution (Flack 1979). Transfers of Robins to suitable habitat have been successful, so their distribution by this method may be increased in the future (Flack 1975b, 1978).

As a consequence of its confiding nature and sedentariness, the Robin has received more attention than most New Zealand passerines. Anderson (1926) and Moncrieff (1932) gave brief accounts of general habits and Richdale (1941) described breeding by a pair in captivity. As well as giving a detailed taxonomic account of the genus *Petroica* in New Zealand, Fleming (1950) described some aspects of the species' biology. Soper (1976) recorded some activities of nesting Robins, while Alspach (1973) wrote of their territorial behaviour. Hay (1975) investigated the vocal behaviour of *Petroica australis* and compared it with other *Petroica* species. An intensive six year study of the Robin at Kowhai Bush, Kaikoura was carried out by Dr J.A.D. Flack of the Wildlife Service (Flack 1973, 1975a, 1976a and b, 1978, 1979, Flack and Lloyd 1978). Less detailed studies of the species by Flack were also undertaken on populations inhabiting three islands in the Marlborough Sounds (Allports, Motuara and Outer Chetwode).

A time-budget study of the Robin population at Kowhai Bush seemed a suitable thesis study for the following reasons. First, such a study seemed timely and appropriate. It would build on the results from previous studies. Second, the Robins were individually colour-banded, of known-age and the sexes were dimorphic, this enabling me to obtain comparative information on various categories of Robins (e.g. adult male, adult female, immature male, immature female and bachelor). Another colour-banded population, on Outer Chetwode Island, had several features that differed from those of the mainland population (Flack 1976b) and promised interesting comparisons. Third, the bird's sedentariness meant they could be readily found, and their approachable nature made detailed observations at close range possible. These South Island Robins do not retreat when a person appears, as is more usual of northern hemisphere passerines: on the contrary the Kowhai Bush birds tend to be attracted to a person so that detailed observations at close range without concealment are easy. In addition, the male Robin's habit of regularly feeding his mate once nest-building began and until the nestlings hatched, made nest finding fairly easy. It was believed that no such long-term study of the use of time by the different categories and sexes of a passerine had previously been attempted.

A time-budget presents an analysis of the time an animal spends in performing each of the behaviours that make up its repertoire. The data are gathered by recording the proportion of time the members of a population devote to each behaviour, and recording the intensity of these behaviours (e.g. the number of foraging movements per minute). Early studies involved noting the timing of feeding periods (Beer 1961, Lees 1948). By dividing the day into several equal parts and comparing the proportion of time spent feeding in each, maximum and minimum periods were determined. Such evidence from birds suggested the existence of an ordered daily pattern of activity and prompted the investigation of diurnal rhythms. Palmgren (1949), using caged birds, noted a bimodal pattern of activity, but as daylength increased to the summer maximum, a polyphasic rhythm developed so that the birds had several periods of activity and sleep rather than just one active period as they had under short daylength regimes. Aschoff (1960) and Palmgren (1949) found that caged birds in continuous light showed a marked diurnal pattern of activity denoting that this was endogenously controlled. Thus, these early studies established that 'time' was an important factor in the ecology of an animal.

From the results of some time-budget studies it has been assumed that time is an important limiting factor regulating populations, either as a consequence of the death of individuals or by preventing others from breeding. For example, several workers have shown that recently fledged birds were less successful foragers than were adults, and that the former had to forage for longer to obtain their food needs (Buckley and Buckley 1974, Groves 1978, Morrison *et al.* 1978, Recher and Recher 1969). That time is an important resource for such inexperienced foragers was demonstrated by Heppleston (1971) for juvenile Oystercatchers *Haematopus ostralegus*. Under extreme environmental conditions the juveniles feeding at lower rates than adults were unable to compensate adequately for any food deficiency incurred such that losses of first-year birds accounted for 77% of the winter mortality.

With regard to time being a factor limiting breeding for some species, Schartz and Zimmerman (1971) found that breeding male Dickcissels *Spiza americana* were forced by physiological heat stress, caused by very high ambient temperatures, to rest more. To spend more time resting and maintain the time devoted to foraging in order to find sufficient food for self-maintenance needs, the Dickcissels were forced to suspend their reproductive activities. Similarly, Verbeek (1972) concluded from his time-budget study of Yellow-billed Magpies *Pica nuttalli* that breeding could not commence at an earlier date than it did because there was insufficient time available. Before breeding, 60% of the day was spent in foraging for self-maintenance by both sexes. The female was responsible for all incubation and during this stage the male provided the female with almost all her food. Males foraged for almost 80% of the day during the incubation stage. Therefore, before breeding, the male would have insufficient time to find enough food for the pair's needs in the daylight time.

The apportionment of time, as well as energy and matter, determines how an animal adjusts to the complexities of its environment, and therefore provides considerable information about its ecological niche (Pianka 1974: 201). The quantitative information provided by time-budgets can also yield information on the roles of the sexes in reproduction (Ryan and Dinsmore 1979) and about many aspects of a species' behaviour. Furthermore, once available, a time-budget opens up further avenues for study. For instance, it provides a base for the calculation of a detailed energy-budget. Determining a species' energy-budget became possible with the advent of suitable oxygen-measuring equipment and the use of a very amenable research bird, the hummingbird. Because of the hummingbird's ability to hover in a confined space, and since its nectar food could be readily supplied in measured amounts of known calorific value, the hummingbird featured prominently in the determination of energy-budgets (Pearson 1954, Stiles 1971, Wolf and Hainsworth 1971). Now it has become possible using doubly-labelled water to estimate the daily energy expenditure of free-ranging vertebrates (Utter and LeFebvre 1973, Hails and Bryant 1979).

Although, over the last 20 years, many time-budget studies of birds have been made, only two studies, to my knowledge, have provided an annual time-budget for a species (Verbeek 1972, Wright 1978). However, in neither study could particular birds be identified nor could the sexes be always distinguished. All other time-budget studies were continued for only parts of annual cycles.

In this study, I was readily able to sex and age the Robins and I continued the field-work for two and a half years. The aim of my study was to describe quantitatively the Robin's use of time (the proportion of time spent in each behaviour) and to determine how this varied in various categories of Robins, months of the year, stages of the breeding cycle and periods of the day. Because of the limited time available it was not possible to determine why the birds spent as much time as they did in a particular behaviour, or why their involvement in it changed. In particular, I was unable to weigh the birds regularly to correlate their behaviour with their physical condition or to study quantitatively the food supply available to them.

It was hoped to answer the following questions:-

1. Were certain behaviours more common than others, and was there any "order of priority" in their use? Did such an order differ with the various categories of Robins and if so, what were possible explanations for such orderings?
2. How did the monthly time-budgets (the proportion of observation time for one month that the birds devoted to each behaviour) differ from month to month outside the breeding season (January-July) for each of the categories of Robins? Were there significant differences in time-budgets between members of the various categories in the same month?
3. Was there a recognisable sequence of behaviours in the course of the day outside the breeding season? If so, did these sequences vary according to the category of Robin involved? Did any such diurnal pattern change for different times in the non-breeding season?
4. For each stage of the breeding cycle, what were the monthly and total breeding season time-budgets (time-budgets determined from the combined data recorded over the entire breeding season) for male and female Robins? Did the time-budgets and diurnal patterns of behaviour (a comparison of the proportion of time the birds devoted to a behaviour for each of six equal-lengthed day-periods) change from one breeding stage to the next? Furthermore, how did the monthly budgets for bachelors (unpaired adult males) differ from those for breeding males?
5. Did any factors, such as the Robin's behaviour, annual pattern of mortality, and timing of breeding and the moult, help to explain changes in their monthly and diurnal time-budgets?

This thesis has four parts. Most chapters contain sections entitled introduction, results, discussion and summary. Some chapters contain a methods section where methods specific to the work in the chapter are described.

Part 1, chapters 1-3: this part contains this introduction, and a description of the study areas and general methods.

Part 2, chapters 4-8: contain detailed descriptions of each activity and which activities were combined as a "behaviour". Time data for specific activities are also given and discussed.

Part 3, chapters 9-12: contain the monthly and diurnal time-budgets for the various categories of Robins during the non-breeding season.

Part 4, chapters 13-18: contain the time-budgets for bachelor and breeding Robins.

Following the chapters is a general summary and discussion. The appendices include a table of the graphed values for each time-budget figured in the text.

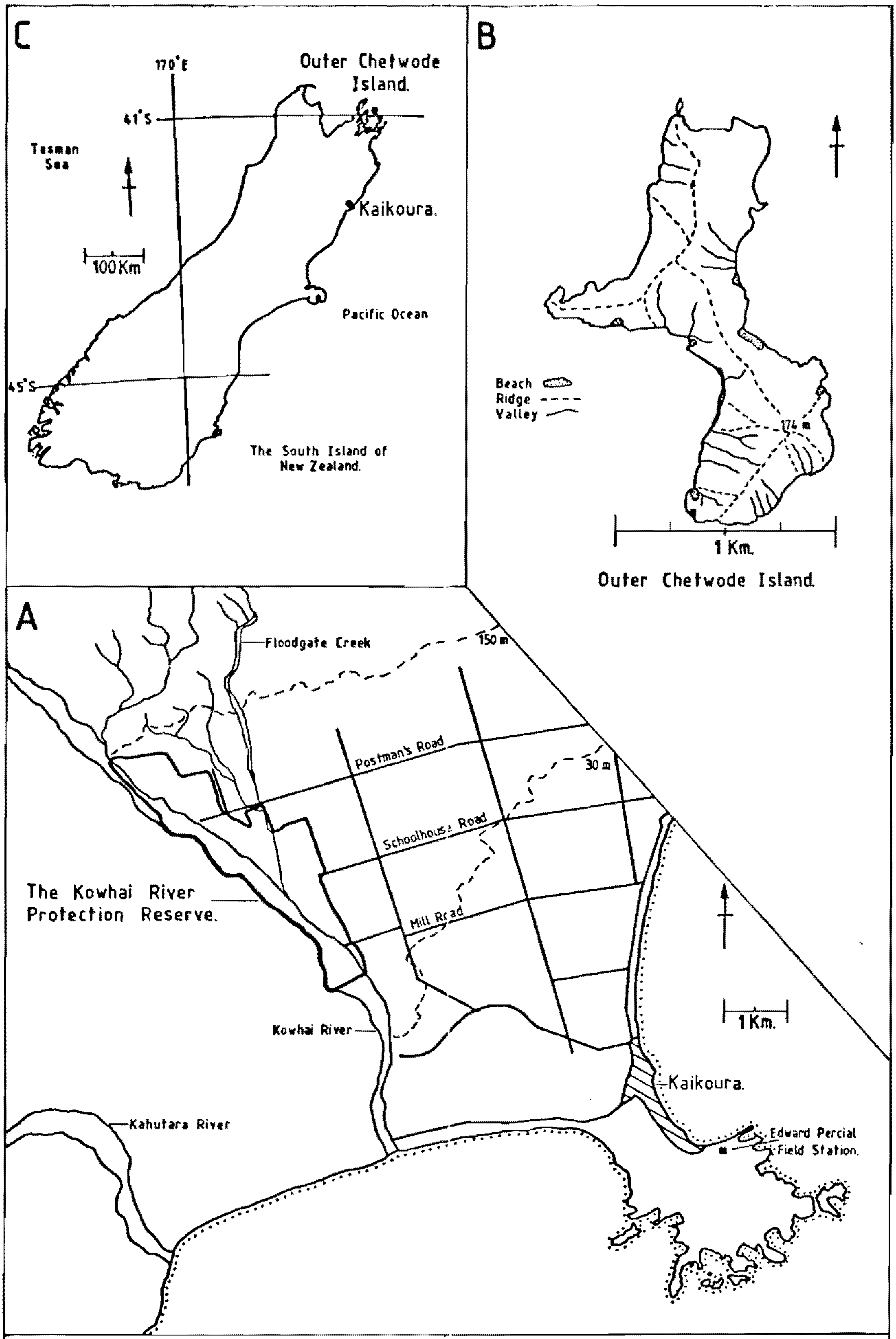


Figure 2.1 Maps of the study areas, the Kowhai River Protection Reserve (A) and Outer Chetwode Island (B), and a map of the South Island (C) showing the locations of the study areas.

CHAPTER TWO

STUDY AREAS

2.1. Kowhai Bush

2.1.1. Introduction

The main study area was within Kowhai Bush (42°23' S, 173°37' E; NZMS 1 S49 895 953; Fig. 2.1), part of the Marlborough Catchment Board's Kowhai River Protection Reserve. Kowhai Bush, rising from 60 to 150 m a.s.l., is a narrow strip of forest along the north-eastern edge of the Kowhai River covering about 240 ha and situated a few kilometres north-west of the Kaikoura township (Fig. 2.1). The forest is mainly bounded by farmland and riverbed, but there is a narrow connection to forest on the slopes of Mount Fyffe. The study area, outlined in Figure 2.2, included all Robin territories in Kowhai Bush, except for a few coastwards of Floodgate Creek and some at the north-west end. Robins were also present on the south-west side of the Kowhai River and on the lower slopes of Mount Fyffe.

Most of the following information about the history, geology, hydrology, meteorology and vegetation of Kowhai Bush was obtained from Flack and Flack (1976), Gill (1980), Hunt (1977, 1978) and Hunt and Gill (1979). In 1866, Kowhai Bush was gazetted as a reserve and was managed by the Kowhai River Board. However, since 1967 it has been controlled by the Marlborough Catchment Board and prescriptions for its management were incorporated into a flood control, drainage and erosion control scheme for the Kaikoura region. Kowhai Bush was divided into two zones, a 'Protection Zone' and a 'Secondary Protection Zone' (Fig. 2.2). The Protection Zone was re-fenced in 1978 to protect it from grazing stock. The forest within this zone consists of a flood-induced mosaic of successional stages often dominated by kanuka *Leptospermum ericoides* and having a dense understorey. The Secondary Protection Zone, which is leased for grazing, contains scattered native trees. Grazing by stock restricts the ground cover to grasses, herbs and bracken *Pteridium aquilinum* var. *esculentum*.

The catchment of the Kowhai River consists of basement rocks of greywacke and argillite which are extremely contorted and folded (Chandra 1968). On exposure to weathering they shatter supplying scree to the river. Since European settlement the natural erosion has been hastened because of the loss of much of the native vegetation by fire and the

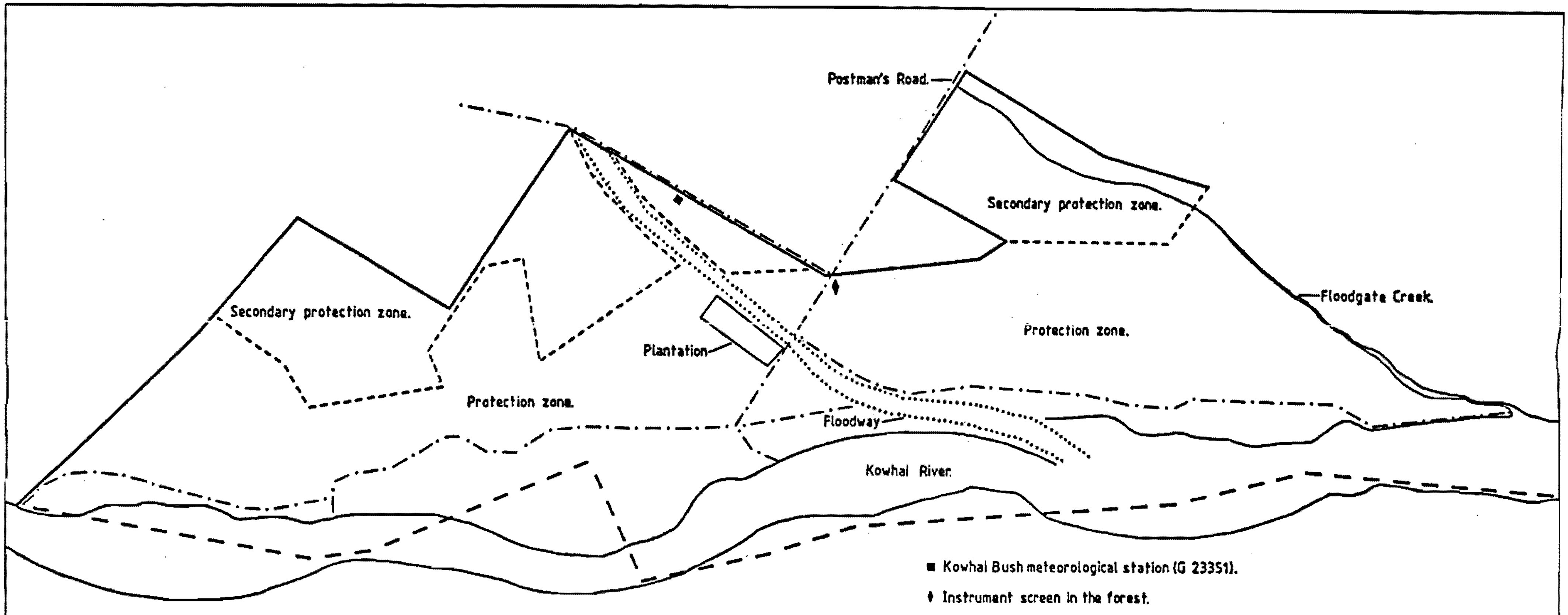


Figure 2.2 Kowhai Bush: the Kowhai River Protection Reserve from its northwestern limit to Floodgate Creek.

grazing and browsing of wild and domestic mammals. This has led to the erosion of the underlying soils exposing the rock to weathering with the result that large quantities of gravel are carried into the riverbed. Where the steep mountain gradients join the relatively flat land of the Kaikoura Plains, the sudden loss of stream energy results in the deposition of vast quantities of gravel. Gravel has been deposited such that the Kowhai River flows on top of alluvial fans above the level of the surrounding forest and farmland. Before stopbanks were erected, intense rainstorms and consequent high river flows resulted in water flowing down the sides of the alluvial fans flooding portions of Kowhai Bush and in some cases destroying areas of vegetation (Gaynor 1974). The size of particles deposited in the bush during a flood ranged from fine silt to large boulders.

2.1.2. Vegetation

Dobson (1979) found that plant diversity increased with increasing fineness of the soil. Thus, the mosaic of plant communities within Kowhai Bush was determined to a large extent by soil characteristics which in turn depend on the action of floods. Which community has developed in a particular area of Kowhai Bush probably depends on several factors: the time since the area was last flooded, the nature of the soil, the drainage and the micro-climate.

On exposed shingle close to the riverbed *Buddleia davidii, Coriaria sarmentosa* and *C. arborea* are the predominant invaders. Where existing vegetation is cleared, but soil remains, *Ulex europaeus, Cytisus scoparius, C. monspessulanus, Digitalis purpurea*, thistles, grasses and herbs grow. Many of these species are also present on stabilised areas of riverbed and persist in the forest. Both manuka *Leptospermum scoparium* and kanuka invade the early stages of the succession, but manuka persists only in dry areas where the soil is poor. Kanuka competitively excludes it in the areas of fertile soil (Burrows 1973) because the kanuka seedlings are more tolerant of shade and root competition (Burrell 1965). Kanuka becomes the dominant species of the community forming a canopy 6-12 m high. Beneath the canopy many broadleaf species germinate and eventually grow to share the canopy. These include *Dodonaea viscosa, Melicytus ramiflorus* and *Acacia dealbata* at an early stage, followed by *Carpodetus serratus, Pittosporum tenuifolium, P. eugenioides* and *Griselinia littoralis*. *Cordyline australis,* *Pseudopanax arboreus, Myoporum laetum* and *Sophora microphylla* (kowhai) appea later. *Coprosma* spp. and *Rubus* spp. are abundant in the understorey and much of the ground is covered by *Uncinia* spp., ferns and *Astelia fragrans*.

An area undisturbed by flooding for many years and known as the "old forest" represents the most advanced stage of succession at Kowhai Bush. It is dominated by broadleaf species and contains some large examples of kowhai and kanuka. The few examples of *Podocarpus hallii* and *P. spicatus* found in this part of the forest are possibly a remnant of the once widespread podocarp forests which were favoured by the warmer, wetter climates of the past (Holloway 1953). Next to the riverbed and beside the stopbanks *Populus* spp. and *Salix fragilis* have been planted for flood control.

2.1.3. Vertebrates

The density and diversity of native passerines at Kowhai Bush is high by New Zealand standards with seven species being abundant year round. These are the Rifleman *Acanthisitta chloris*, Brown Creeper *Finschia novaeseelandiae*, Grey Warbler *Gerygone igata*, South Island Fantail *Rhipidura fuliginosa*, South Island Robin, Silvereye *Zosterops lateralis* and Bellbird *Anthornis melanura*. Occasionally seen in the forest are the Australasian Harrier *Circus approximans*, New Zealand Falcon *Falco novaeseelandiae*, New Zealand Pigeon *Hemiphaga novaeseelandiae*, Shining Cuckoo *Chrysococcyx lucidus*, Morepork *Ninox novaeseelandiae*, New Zealand Kingfisher *Halcyon sancta*, Yellow-breasted Tit *Petroica m. macrocephala*, and Tui *Prosthemadera novaeseelandiae*. Eleven introduced species are also commonly seen in Kowhai Bush (see Hunt and Gill 1979).

Eleven species of mammals, all introduced, frequent the study area. Four of these mammals are probably responsible for most of the predations of birds' eggs and nestlings. Two are rodents (*Rattus rattus* and *Mus musculus*) and two mustelids (*Mustela erminea* and *M. nivalis*). These predators are sufficiently agile to be able to climb to bird nests (Moors 1976). Flack and Lloyd (1978) also considered that *Mustela putorius, Felis catus* and *Trichosurus vulpecula* occasionally preyed upon eggs and nestlings in Kowhai Bush. Other mammals present are *Erinaceus europaeus, Lepus capensis, Oryctolagus cuniculus* and *Cervus elaphus*.

2.1.4. Climate

The climate of Kowhai Bush is warm-temperate with moderate winters and very warm summers. Dry Foehn winds from the north-west sometimes produce day temperatures above 30°C. The other predominant winds of the district are cool, wet southerlies and north-easterlies. A change in wind direction during summer from north-west to south-east may cause the temperature to drop by about 20°C in an hour. Rainfall on the Kaikoura Peninsula is heaviest in autumn and least in spring (data from the Kaikoura Meteorological Office, Ministry of Transport; 30 years of records). Generally, the rainfall is evenly distributed throughout the year, but sometimes it varies erratically. Mean annual rainfall on the Peninsula is 865 mm compared with 1,441 mm at the foot of the Seaward Kaikouras (Hunt and Gill 1979). The coldest month is July and the warmest February. During the study, snow fell at Kowhai Bush a few times, but only once accumulated, remaining for a day or two in areas unshaded by the canopy. Frosts are frequent during late autumn and winter (about 40 per year; Thomson and MacArthur 1969), but never penetrate beneath the canopy.

In March 1977 Mr B.D. Lloyd of the Wildlife Service set up a meteorological station (Kowhai Bush, G 23351) next to the Bush in the Secondary Protection Zone (Fig. 2.2). Instruments present were a standard Octapent rain gauge, a Lambrecht recording rain gauge, and an instrument screen housing wet and dry bulb thermometers, maximum and minimum thermometers and a thermohydrograph. These provided a continuous record of rainfall (mm), percentage humidity and ambient temperature (°C). The station was maintained from 1 April 1977 to 31 December 1978. From March to October 1978 I operated a thermograph in an instrument screen within Kowhai Bush (Fig. 2.2).

Daily mean temperatures were determined by halving the sum of the maximum and minimum temperatures of each day. The daily mean temperatures for a month were averaged to provide the monthly mean temperature. The same procedure was used to calculate the monthly mean humidity. For some months an incomplete daily record was obtained because the thermohydrograph malfunctioned.

Meteorological records for the duration of the study are presented in Table 2.1. Records from the Kaikoura meteorological station, G 23471, are provided as a comparison with those obtained from the Kowhai Bush station. The monthly mean temperatures, total rainfall and the

Table 2.1. Some meteorological records for Kowhai Bush (station G 23351) and Kaikoura (station G 23471) from August 1976 to December 1978.

	Kaikoura			Kowhai Bush			Within the forest
Year and month	Mean temp. (°C)	Total rainfall (mm)	Hours of sunshine	Mean temp. (°C)	Total rainfall (mm)	Mean humidity (%)	Mean temp. (°C)
1976							
A	7.8	70.7	125.0				
S	8.5	96.2	111.4				
O	10.3	156.0	164.4				
N	10.8	66.2	144.2				
D	14.8	121.3	169.5				
1977							
J	14.8	103.5	226.4				
F	15.5	47.0	218.0				
M	14.7	13.6	171.3				
A	13.5	28.0	179.9	13.1	40.3	75	
M	9.3	91.6	141.3	8.7	106.7	78	
J	8.1	117.9	96.5	7.6	99.6	79	
J	7.2	196.8	86.8	7.1	279.1	84	
A	7.7	163.2	117.2	7.6	188.7	80	
S	7.4	125.7	123.8	6.8	146.0	78	
O	11.1	58.0	242.5	10.1	71.5	-	
N	12.6	36.7	250.6	11.4	80.5	-	
D	14.7	40.0	243.6	13.4	33.5	-	
1978							
J	16.8	14.8	214.2	17.1	32.0	-	
F	17.4	57.2	249.1	16.8	73.0	-	
M	15.9	35.6	195.5	15.5	80.5	73	
A	14.4	400.7	113.6	14.1	468.0	85	
M	10.7	96.2	97.0	10.2	157.9	78	9.4
J	6.9	190.0	69.8	6.7	323.0	84	6.0
J	8.3	150.2	122.2	8.1	295.5	83	7.0
A	9.3	91.4	201.7	9.0	103.0	73	7.7
S	9.6	115.9	135.7	-	174.5	82	8.9
O	11.1	34.8	231.1	10.5	84.0	77	10.0
N	13.3	31.9	227.6	13.3	45.5	73	
D	15.1	32.8	203.8	14.6	60.9	83	

change in these from month to month showed similar trends at the two stations. However, Kowhai Bush usually received a higher rainfall and a slightly lower mean temperature than was recorded at Kaikoura. The main features to note from the records are:

1. The decreased temperature in September 1977 compared with that of the previous month.

2. The lower monthly rainfalls and higher mean temperatures from December 1977 to March 1978 compared with those of the same period of the previous year. Totals and averages for station G 23471 are: 285.4 mm and 15.0°C for 1976-77 compared with 147.6 mm and 16.2°C for 1977-78. During the 1977-78 summer, the Kaikoura district experienced one of the driest periods on record. The drought ended when 468 mm of rain fell almost continuously over a ten day period in April 1978.

3. Monthly mean temperatures in the forest were generally a degree lower than those at station G 23351. The forest tended to lower extreme temperatures, particularly the maximums.

2.2. Outer Chetwode Island

Under permit from the Marlborough Sounds Maritime Park Board, three one-week visits (6-13 April, 15-22 May and 6-12 June 1978) were made to Outer Chetwode Island (Te Kakaho) at the head of Pelorus Sound (40°55' S, 174°05' E; Fig. 2.1). The island is part of the Marlborough Sounds Maritime Park and is a flora and fauna reserve. It lies on a north-south axis and rises to 174 m (Fig. 2.1). From a ridge running along the centre and length of the island, the land slopes steeply to the sea usually ending in cliffs. Few beaches occur around the coast. V-shaped valleys run almost directly to the shore. Beneath the forest was a covering of soil and litter, but in some places the Permian greywacke was exposed forming areas of scree. One valley contained a small stream.

Until about 1920 Outer Chetwode Island was farmed with sheep and the vegetation was burnt periodically (Marlborough Sounds Maritime Park Board files). A concrete sheep-dip was the only evidence of this past venture.

A variety of vegetation types is present on the island, probably reflecting the various stages of regeneration since farming, as well as soil depth and the degree of exposure to the weather. A few steep, exposed hillsides and small areas of the ridge tops are covered in grasses. Many other slopes have a dense covering of *Phormium cookianum* or *Pteridium aquilinum* var. *esculentum* interspersed with small areas of low-growing shrubs and herbaceous species. Most of the forest is in the sheltered valleys. At the south-east end of the island are four valleys containing dense stands of *Dysoxylum spectabile* (Kohekohe). These form a closed canopy 5-10 m high under which all that grows are a few species of ferns. This vegetation may not have been burnt during farming of the island and may represent the original forest for these sites. Elsewhere forest consists of pure stands of manuka with little or no undergrowth, or a mixture of manuka, *Pseudopanax arboreus, Dodonaea viscosa, Melicytus ramiflorus, Olearia paniculata* and kohekohe.

Within the forest a variety of native birds is present at an overall density that seemed to be greater than at Kowhai Bush. Common species included Blue Penguin *Eudyptula minor*, Western Weka *Gallirallus australis* (transferred onto the island; Kinsky 1970), Yellow-crowned Parakeet *Cyanoramphus auriceps*, South Island Robin, Fantail, Silvereye, Bellbird and Tui. Other native species occasionally seen were the Australasian Harrier, Morepork, New Zealand Kingfisher, New Zealand Pipit *Anthus novaeseelandiae* and Grey Warbler. As well eight species of introduced birds, all passerines, were present.

Except for several New Zealand fur seals *Arctocephalus forsteri* at the northern tip of the island, no mammals were seen nor was any evidence of their presence found.

CHAPTER THREE

GENERAL METHODS

3.1. Terminology

As most pairs began nesting in August, the breeding season was defined as beginning on 1 August and continuing until 31 December, although a few pairs were still feeding juveniles in late February. The breeding season was arbitrarily divided into three portions, which can be approximately correlated with three successive breeding cycles for pairs that succeeded in rearing their first two broods, and began a third:

Early - August, September
Middle - October, November
Late - December.

The rest of the year was termed the non-breeding season and was arbitrarily divided into three parts:

Summer - January, February, March
Autumn - April, May
Winter - June, July.

The system of dividing the bush into layers or storeys, for recording the positions of feeding Robins, was that described by Atkinson (1966):

Canopy: The uppermost storey of tree crowns unshaded by other crowns.
Upper understorey: A storey of plant crowns (> 2 m high) shaded by the canopy.
Lower understorey: A storey of shrubs, tree ferns, etc., from 0.3-2.0 m in height shaded by the canopy.
Ground storey: The lowermost storey consisting of plants with growing points situated less than 0.3 m above the ground. This also included the ground surface and any stones and dead plant material upon it such as litter and rotting logs.

Twigs had diameters of less than 1.5 cm, while those of branches were 1.5 to 10.0 cm. Trunks (diameter > 10 cm) were any stems of trees and shrubs that were vertical or nearly so, so that Robins had to cling to them rather than perch on them.

Four basic feather postures were distinguished, the naming and description of which follows Morris (1956):

Sleeked - feathers are fully depressed against the body, giving it a slim appearance.

Relaxed - feathers are neither depressed nor erected. The body shape is intermediate between slim and rounded.

Fluffed - feathers are erected, but only partially, giving the body a very rounded appearance, with a smooth, unbroken outline.

Ruffled - feathers are fully erected and the body, although rounded, has a ragged appearance with a broken outline.

The nomenclature of the New Zealand birds mentioned in this thesis follow the "Annotated Checklist of the Birds of New Zealand", (Kinsky 1970).

3.2. Banding

Metal serial bands (size B, butt-ended) and colour bands (size C, butt-ended) were placed on all nestlings at about 13 days of age as part of the National Banding Scheme controlled by the Wildlife Service, Department of Internal Affairs. This banding programme was a continuation of the study begun by Dr J.A.D. Flack in 1971 and enabled individual Robins to be recognised after fledging. Robins which immigrated into the study area were caught using a clap-trap (Flack 1973) or mist net and were banded.

3.3. Identification of Robins by age, sex and status

Robins were colour-banded on the left leg with an individual combination and on the right with a year combination so that those banded as nestlings could be aged as well as individually identified. Phenotypic and behavioural characters were used to recognise sex and some age classes. Juveniles were Robins that had left the nest and were dependent upon parental care. They could be distinguished by their streaked feathers and few, if any, white breast feathers. Immature Robins were defined as those independent of parental care, a status attained about four weeks after leaving the nest. Their immature status, for the convenience of this study, ended when breeding began, although Flack (1979) described an occasion when a male showed breeding activity at four and a half months of age. Initially, immature Robins were readily distinguished by their streaked crown feathers and a small area of white breast feathers. By March the growth of more contour feathers made most immatures indistinguishable from adults, except that some had shaft lines on the crown feathers.

Adults tended to have more white on the breast and abdomen with a darker lemon yellow colouring just after the moult than did immature birds, but this colouring faded to white by the end of winter. Females were smaller (Flack in prep., Fleming 1950), had less yellow on the breast and abdomen, and were brown-grey on the dorsum in contrast to the male's black-grey dorsum. Some females were difficult to distinguish from males by plumage colour unless they were together (Flack in prep.), especially when both members of a pair were immature. However, behaviour during partner-interactions indicated the sex of such individuals; males usually dominated their mates, the latter adopted characteristic appeasement and submissive postures.

I was unable to define whether a male was paired or not before May because unpaired females, especially immatures, tended to move from one territory to another. The presence of an unpaired female on a territory at this time did not indicate that she had formed a pair bond with the male. Bachelors (unpaired adult males) could be recognised after April because they spent much time singing from high vantage points in their territories. This regular singing was not seen from paired males, and bachelors on acquiring a mate abruptly and markedly reduced the time they sang. Only adult male bachelors were observed for time-budget information because immature male bachelors occurred infrequently. Therefore, the five categories into which the Robins were divided during the non-breeding season were adult males, adult females, bachelors, immature males and immature females.

The Robin's breeding cycle involved seven stages:

1. Nest-site selection - a variable period during which the male tried to attract the female into nest sites using characteristic calls and wing movements. The female sometimes responded by entering the sites. Occasionally she made a few visits with nest material to a nest site, but then left and was enticed by her mate to other sites.

2. Nest building - this stage began when the female made repeated visits to a site carrying building material and carried out "nest-shaping"

movements. Completion of the nest was defined as occurring when the bird made fewer than one trip per hour carrying material to the nest.

3. Prelaying - this stage began with the completion of the nest and finished the day before the first egg was laid.

4. Laying - included those days on which an egg was laid and when incubation attentiveness was less than 50%.

5. Incubation - day one of this stage was the first day the female spent more than 50% of her time incubating. This stage culminated with the hatching of the first egg.

6. Nestling-rearing stage - from the hatching of the first egg and until the last nestling had left the nest.

7. Juvenile-rearing stage - from the time the nestlings left the nest until they became independent of parental care. The length of this stage varied with the sex of the parent Robin. For example, often the male continued to feed the juveniles while the female commenced the next breeding cycle. She was involved in stages two to five while the male fed their progeny from the previous breeding cycle.

Only two dead adult Robins were found during the two and a half years of this study. Therefore, to determine Robin mortality, it was inferred from the disappearance of a Robin from the study area that the individual had died. Adults in Kowhai Bush were very sedentary, very few adults that had lived in the study area were subsequently found during censuses outside it. Thus, the disappearance of an adult seemed a reasonable indication that it had died, but because some immatures tended to disperse considerable distances, such an assumption could not be made with the same degree of confidence.

3.4. Day-periods

To determine whether diurnal patterns of Robin activity occurred and to make observations during different months comparable, daylight hours were arbitrarily divided into six equal periods (Verner 1965). The limits of daylength were taken as sunrise and sunset. Robins were active in twilight and so the few observations made at these times were amalgamated with data for day-periods 1 and 6. Mean daylength and day-period length were determined for each month from official sunrise and sunset information ("The Air Almanac", United States of America Government

Printing Office (1976)), (Table 3.1).

Table 3.1. Monthly mean daylength and day-period length (h).

Month	Mean daylength	Mean day-period length
January	14.9	2.5
February	13.8	2.3
March	12.4	2.1
April	10.9	1.8
May	9.7	1.6
June	9.1	1.5
July	9.3	1.6
August	10.4	1.7
September	11.8	2.0
October	13.3	2.2
November	14.6	2.4
December	15.3	2.6

3.5. General observation procedures

Time-budget studies of avian species have generally involved caged birds (Palmgren 1949) or sedentary birds in open habitats (Gibson 1978, Verbeek 1972, Verner 1965, Wakeley 1974, Wright 1978). Such observations, necessitating the use of binoculars and telescopes from hides were not possible or desirable for a study of the Robin. It inhabits dense bush and spends long periods feeding on the ground and under the ground-storey plants. Therefore, to observe and time the behaviour of Robins it was necessary to follow them closely as they moved about their territories. Such a procedure was followed by Austin (1976), Root (1967), Smith (1977) and Walsberg (1978) with other species.

Robins are attracted to any disturbance or noise in their territories. This is part of the Robin's normal hunting behaviour since they follow cows and sheep to feed on any disturbed invertebrates. Consequently, my presence may have influenced their behaviour, the most likely effect being to increase the frequency of partner-interactions and territorial disputes between neighbouring Robins, although I believe my influence was minor.

To facilitate accurate identification of the Robins and to enhance finding their nests, Robins at Kowhai Bush were rewarded by disturbing a small area of litter to provide food whenever they moved towards Wildlife Service personnel (Flack pers. comm.). Initially, to overcome the Robins' habit of associating food with people, I moved about with the birds on several occasions without feeding them until they became oblivious of my presence. Repeated observations showed that they resumed normal activities after a short investigatory period of about three minutes. Root (1967) used a similar method to "tame" the Blue-gray Gnatcatcher *Polioptila caerulea* which enabled him to approach to within 10 metres of this wary species for critical observations of foraging. Similarly, Post (1974) found that Seaside Sparrows *Ammospiza maritima* became accustomed to him being within five metres away as they foraged.

Robins whose behaviour was influenced by my presence and/or movement near them were not timed. Such occurrences were uncommon during the non-breeding season, but sometimes nest-building females and adults tending nestlings or newly fledged juveniles behaved "unnaturally" and therefore were ignored. Immature Robins, which were very inquisitive initially, were habituated to my presence by following them about their territories several times without recording their behaviour. There was considerable variation from bird to bird in the time taken for habituation.

Time-budget observations began in June 1976 and were completed by the end of December 1978. The first two months' data were discarded because I had not distinguished some similar-appearing behaviours: for example, scanning and resting. No timed observations were made in rain or when the vegetation was very wet. During the non-breeding season I endeavoured to obtain a minimum of 50 hours per month of timed observations equally divided among the various sexual and status categories of Robins and the six day-periods. For example, in a month the five Robin categories were each timed for ten hours. The ten hours per Robin category was divided between the six day-periods so that adult males were timed for 1.7 hours each day-period per month. Throughout the breeding season, 80 to 100 hours of timed observations were obtained each month, and included some made while watching Robin behaviour at nest sites. A strict policy to obtain a minimum number of hours of observations of Robins involved in each breeding-cycle stage was not possible because some stages were not represented or were present for only a short time during some months.

Before an observation of a Robin began, its band combination, sex, the territory name and the New Zealand Standard time (12 hours ahead of Greenwich Mean Time) were recorded. Each Robin was watched for one hour at the most so as not to over-emphasise the behaviour of any particular bird and so as many individuals as possible could be timed each month. Behaviour was timed using a Lemania stopwatch and the elapsed time for each behaviour was written into a note-book as it occurred. The duration of momentary activities (less than five seconds) was often estimated rather than timed.

Another commonly used method of determing a species' time-budget is to record the type of activity being undertaken by an individual at set intervals of time (Gibson 1978, Wakeley 1974, Wright 1978). I did not use this "frequency of activities" method because usually only one Robin was in sight at a time, compared with the situation when watching a flocking species where the activities of many individuals can be scored over a short period. Furthermore, scoring the frequency of each type of activity assumes that the data are directly representative of the proportion of time birds devoted to each activity for the period of observation. However, particular activities that are seldom given may be over- or underestimated in a time-budget by this method.

Timing the duration of each behaviour of a Robin was found adequate for recording all types of behaviours, except foraging rates. Foraging-rate observations involved recording the number of pecks (successful or not), and hops and steps per minute on three substrates (ground, branches, trunks), the number of wing-flicks, the number and estimated distance of flights, and the substrate on which the bird landed. At the same time, the duration of each behaviour was timed. Details were spoken into a portable cassette taperecorder.

To obtain representative observations, each Robin in the population was searched for and watched each month. This procedure was combined with a monthly census. During the non-breeding season most birds were observed at least three times per month. However, during the breeding season it was necessary to find some individuals more often in order to obtain sufficient information about birds involved in stages of the breeding cycle that lasted only a few days (prelaying and laying stages).

Observations at the nest site were made while sitting about seven metres away. Experience has shown that Robins tolerate a considerable amount of disturbance near the nest without deserting. Soper (1976) erected a platform for his cameras close to an incubating pair and found that the birds took little notice. Moors (1977) set up and operated an 8 mm movie camera two to five metres from nests to film predators taking eggs or nestlings. The camera system involved several hours of work near the nest and resulted in equipment being placed within five centimetres of the nest. Over the 1976 breeding season, four nests were observed in the above manner without any desertions occurring. Flack (in prep.) also found that Robins were "usually extremely tolerant of people around their nests", quickly returning to their normal routine after the initial alarm and display.

For a detailed description of the activities which were timed as part of the various behaviours, except resting, see the methods section of chapters four to eight. Robins were timed as resting when they assumed the resting posture. The head was withdrawn onto the body, the contour feathers fluffed, the tail slightly depressed and the legs flexed. Occasionally birds sat on a branch rather than stood on it. Usually, the bird perched on one leg with the other tucked into its feathers. Sometimes birds closed their eyelids while resting, but only briefly. Invariably, Robins rested where there was shelter from above. Some head movements and shifting of position took place and much of the resting time preceded pellet casting (Powlesland 1979).

3.6. Computer analysis and statistics

After each day's observations, the time each bird had spent in various behaviours was tallied and the summaries entered onto computer sheets for card punching. Once punched, the information was analysed to determine the time-budgets of the various age and sex categories of Robins for each month and day-period. The time Robins spent in each behaviour was calculated as a percentage of the total time they were observed, but in the text it is shortened to "the percentage (proportion) of time".

The data were analysed using the sub-program "Breakdown" from "SPSS V7" (Statistical Package for the Social Sciences, version seven). Using the "variance test for homogeneity of the binomial distribution" (Snedecor and Cochran 1967, p. 240), statistical differences between time-budgets were tested. Chi-squared values at the 0.5% probability level for seven degrees of freedom is 20.3. To test statistically the difference between the percentage of time two categories of Robins, or one category of Robin for two sample times, devoted to a behaviour, the method of "testing the equality of two percentages" (Sokal and Rohlf 1969, p. 608) was used. The values plotted in each of the time-budget figures are given in appendices so that anyone wanting to analyse them in other ways may do so.

3.7. Abbreviations and symbols

Behaviours	Abbreviations
Foraging	F.
Above-ground gleaning	Ab.G.
Ground gleaning	G.G.
Vegetation gleaning	V.G.
Scanning	S.
Flycatching	Fl.
Hawking	H.
Food-storing	Fst.
Vocalizations	V.
Full song	Ful.
Sub-song	Sub.
Downscale	Dsc.
Chuck	Chk.
Body-maintenance	Bm.
Resting	R.
Partner-interactions	P.
Territorial defence	Td.
Interspecific interactions	Ie.
Nest-site selection	Nss.
Nest-building	Nb.
Prelaying	Pre.
Laying	Lay.
Incubation	Inc.
Feeding progeny	Fp.
Brooding	Brd.
Nest sanitation	Ns.

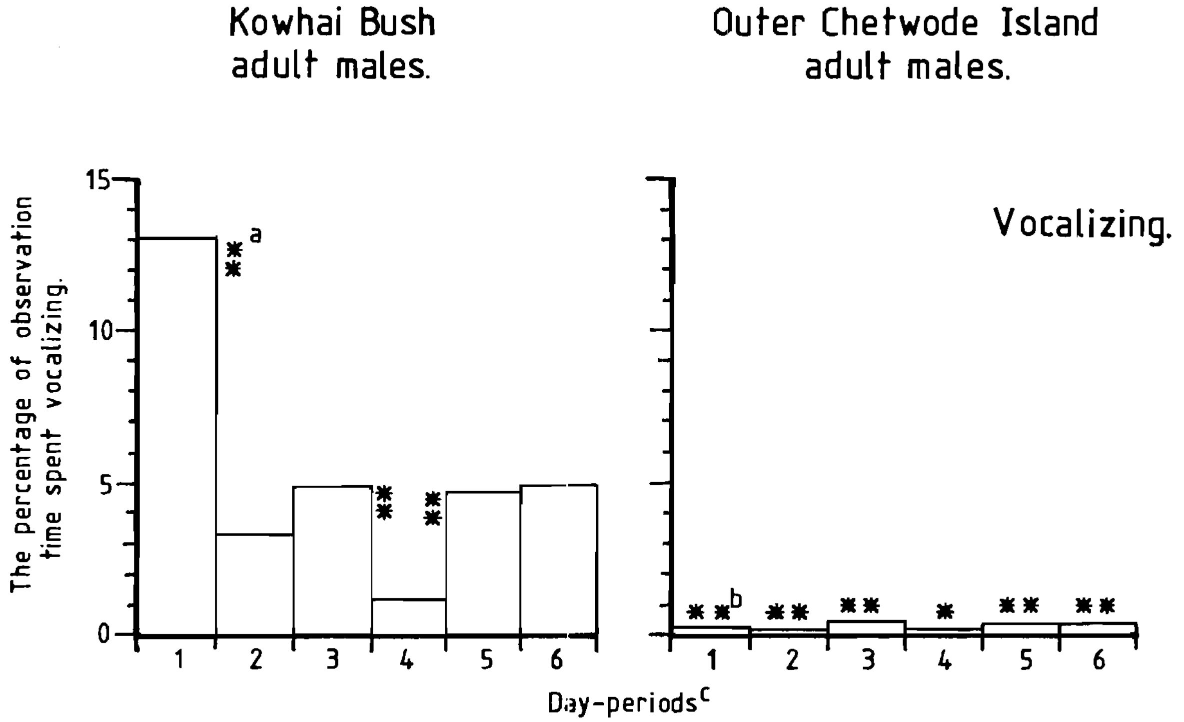


Figure 3.1 The diurnal pattern of vocalizing for adult male Robins at Kowhai Bush and Outer Chetwode Island.

[a] Asterisks placed at the side of a column denote a significant difference between the percentage of time spent on the behaviour in the adjacent day-period sample.

[b] Asterisks at the top of a column shows a significant difference between the percentage of time spent in that behaviour for the day-period by the two populations.

[c] The division of the day-light hours into six equal-lengthed parts.

Age and sex classes	Symbols
Adult male	◆————◆
Adult female	◊—— · ——◊
Bachelor	●— — — —●
Immature male	▩—— ——▩
Immature female	□·—·—·—□

On the figures showing time-budgets and diurnal patterns of behaviours, significant differences between two percentages is represented by asterisks or crosses: * or + = $P < 0.05$, ** or ++ = $P < 0.01$. Asterisks and crosses placed at the side of a column (a, Fig. 3.1) denote a significant difference between the percentage of observation time spent on the behaviour in the two adjacent monthly or day-period samples. For example, in Figure 3.1 the asterisks show that for the Kowhai Bush males the percentage of time they vocalized decreased significantly from day-period 1 to 2 and day-period 3 to 4 ($P < 0.01$). From day-period 4 to 5 the percentage of time spent vocalizing increased significantly ($P < 0.01$), but from day-periods 2 to 3 and 5 to 6 no significant change arose. No significant changes in the proportion of time spent vocalizing by Outer Chetwode Island males from one day-period to the next was found.

Asterisks and crosses at the top of a column denotes a significant difference between the percentage of time spent in that behaviour, for the month or day-period, by different populations or the same population during different seasons. For example, Figure 3.1 (b) shows that for each day-period the Outer Chetwode Island birds sang significantly less than did their Kowhai Bush counterparts. During day-period 4 the level of significance was $P < 0.05$, but for the other day-periods it was $P < 0.01$.

PART 2

DESCRIPTIONS OF THE BEHAVIOURS OF THE SOUTH ISLAND ROBIN

CHAPTER FOUR

FORAGING BEHAVIOUR

4.1. Introduction

The Robin is very suitable for detailed observations of diet and foraging behaviour because of its approachable nature and habit of hunting for food mainly on the bush floor. However, only brief comments on feeding are contained in the literature. Both Oliver (1955) and Falla *et al.* (1966) commented that Robins spent much of their time hopping over the forest floor taking mainly earthworms and insects.

A five-year study by Flack (1973) on the Robins at Kowhai Bush revealed that the population there was almost wholly insectivorous with only occasional instances of berry eating. Flack (in prep.) reports most hunting took place on or near the ground, but extended periods of searching at higher levels also occur. He describes Robins as having a range of hunting methods including hawking and skilled flycatching. Activities associated with foraging include wing- and tail-flicking, and foot-trembling.

The present study aimed at elucidating the Robin's foraging methods, feeding stations, and prey-handling and eating activities. The proportion of the total foraging time spent in each activity was recorded. The effect of Robin age, season, and time of day on foraging methods are described including movement and peck rates. In subsequent chapters dealing with time-budgets, time birds spent using the various foraging methods is pooled as "foraging behaviour".

4.2. Methods and terminology

From August 1976 to July 1978 inclusive, Robins were followed individually and the amount of time each bird spent using the various foraging methods, feeding stations and height regions were recorded.

Foraging behaviour may be subdivided in the following way:

1. Gleaning, which is defined as the "search for prey not in flight by birds not on the wing" (Croxall 1977), was the main method of locating prey. Different kinds of gleaning were distinguished based on the substrate where it occurred. Ground gleaning (G.G.) involved Robins searching while hopping and stepping over soil, litter and rotting logs.

The time spent while the birds stood on the ground and took prey from low growing vegetation was also included in this category. Vegetation gleaning (V.G.) involved birds standing on plants, both living and dead, to search plant surfaces at any height above 0.1 metres high. While on the ground Robins reached prey on vegetation from ground level to that about 0.1 metres high. Thus, only those birds foraging from vegetation and perched over 0.1 metres from the ground were considered to be gleaning from vegetation.

2. Scanning (S.) involved a Robin perching at a suitable vantage point and looking for prey. Perches commonly used included limbs, branches and boulders, but if these were not available Robins clung vertically to trunks and stems. If no prey were sighted, the birds usually flew to another perch a few metres away and repeated the scan. The movement between perches was timed as scanning behaviour. Scanning Robins could be distinguished from resting ones because the former had their necks extended and their heads frequently turned. Furthermore, both feet were used to grip the perch and their plumage was relaxed. An exception arose if a foot was withdrawn into the plumage when the bird was infected by bird pox (Flack 1973). Occasionally, scanning birds hopped about on the perch or stretched up to gain a better view. Resting birds, on the other hand, typically squatted motionless with the plumage slightly fluffed, a foot withdrawn into the plumage, the head drawn down on to the breast, and with the eyes sometimes closed.

3. Flycatching (F.) was the attempted capture of flying prey by a bird on the wing.

4. Hawking (H.) or flight gleaning (Pinkowski 1977) was defined as the attempted capture of prey not in flight, by a bird on the wing. The bird flies to vegetation after finding prey and remains in flight to capture it. The bird may flutter briefly while inspecting the prey, but never does so before locating it; this sets hawking apart from hovering. Robins were never seen to hover while searching for prey. Usually prey was hawked from trunks, leaves and terminal shoots on which Robins would have had difficulty in perching, but hawking also included time spent taking prey from spider webs and taking caterpillars suspended on silken threads.

The data were analysed to see whether the various foraging methods were used to the same extent at various times of the day. To simplify this analysis, the little time spent hawking and flycatching was combined

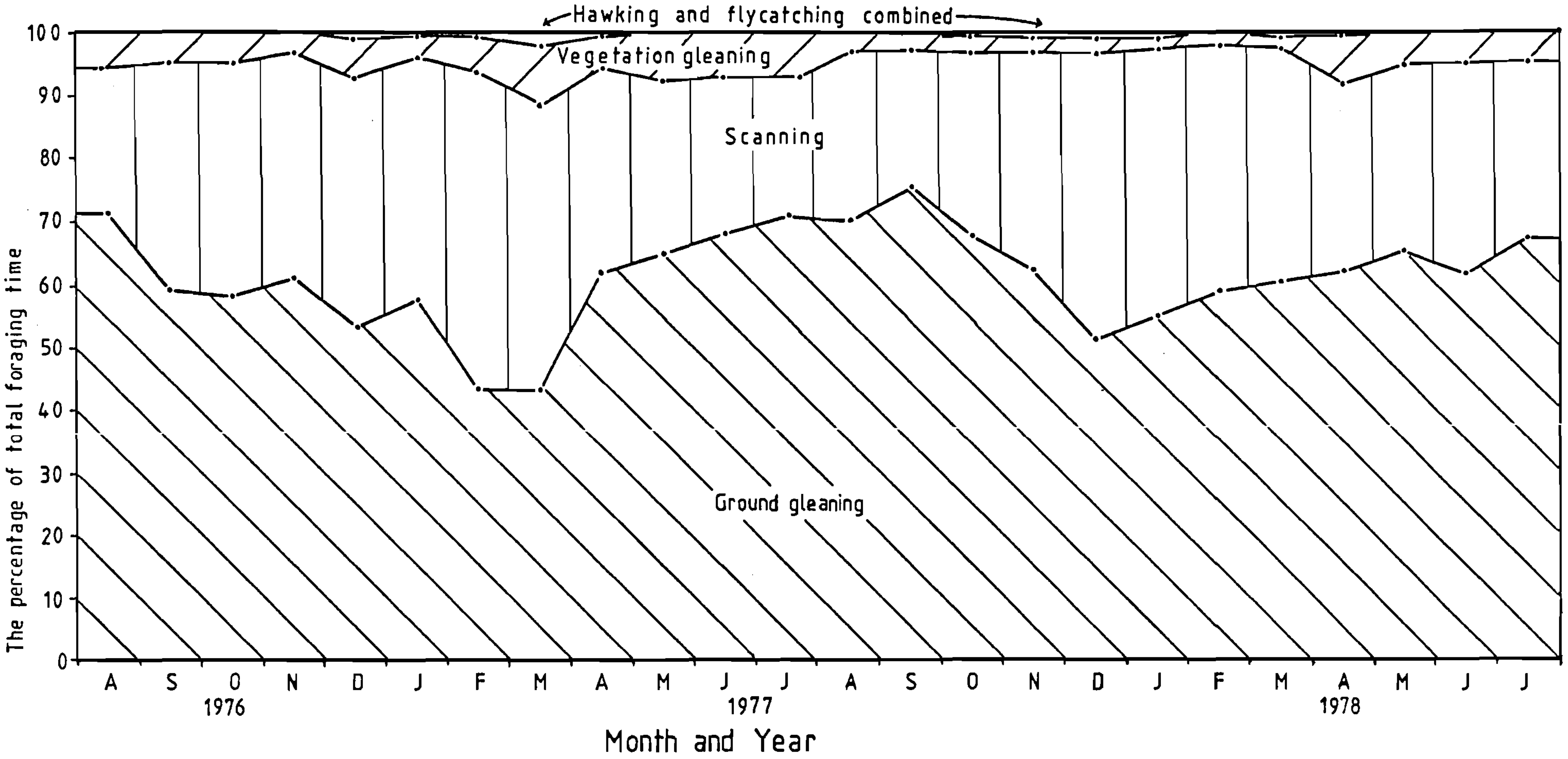


Figure 4·1 The monthly percentage of foraging time Robins used five foraging methods from August 1976 to July 1978. See Appendix 1 for the graphed values.

with that spent in vegetation gleaning and called above-ground gleaning (Ab.G.).

Gleaning among vegetation was subdivided into five categories to denote the feeding stations searched for prey:

1. Searching a branch, limb or among vines while standing on the same type of vegetation (B-B, branch to branch).
2. Searching a trunk while standing on a branch, limb or vine (T-B, trunk to branch).
3. Searching a trunk while clinging to it (T-T, trunk to trunk).
4. Searching the top of a decaying stump (S-S, stump to stump).
5. Searching foliage and twigs while standing on it (F-F, foliage to foliage).

From April 1977 till July 1978 records were kept of the time Robins spent gleaning among vegetation at various heights above 0.1 metres high. Height intervals were of half a metre from 0.1 to 5.1 metres, above which all observations were grouped. The height that a bird gleaned among vegetation was recorded and the time spent in each region noted. See Section 3.5 (p. 20) for a description of the method used to record movement and peck rates.

During the 1978 breeding season, male Robins whose mates were incubating were timed to determine what proportion of their foraging time was spent in searching, handling and eating activities. Robins were timed as involved in handling activity when killing and dismembering prey items greater than 5 mm long. Many small prey (< 5 mm) were also picked up and swallowed.

4.3. Results

4.3.1. Foraging methods

The proportion of foraging time Robins devoted to the five foraging methods is shown in Figure 4.1 and Appendix 1. Overall, 61.3% of foraging time was devoted to ground gleaning, 33.8% to scanning, 4.5% to vegetation gleaning, 0.3% to hawking and 0.1% to flycatching from 923 hours of observation of foraging Robins. More than 50% of foraging time was spent gleaning from the ground, except in February and March 1977. The data for vegetation gleaning showed no consistent pattern of seasonal variation: from April to July in both 1977 and 1978 the birds spent a large proportion of time vegetation gleaning, but they also spent a

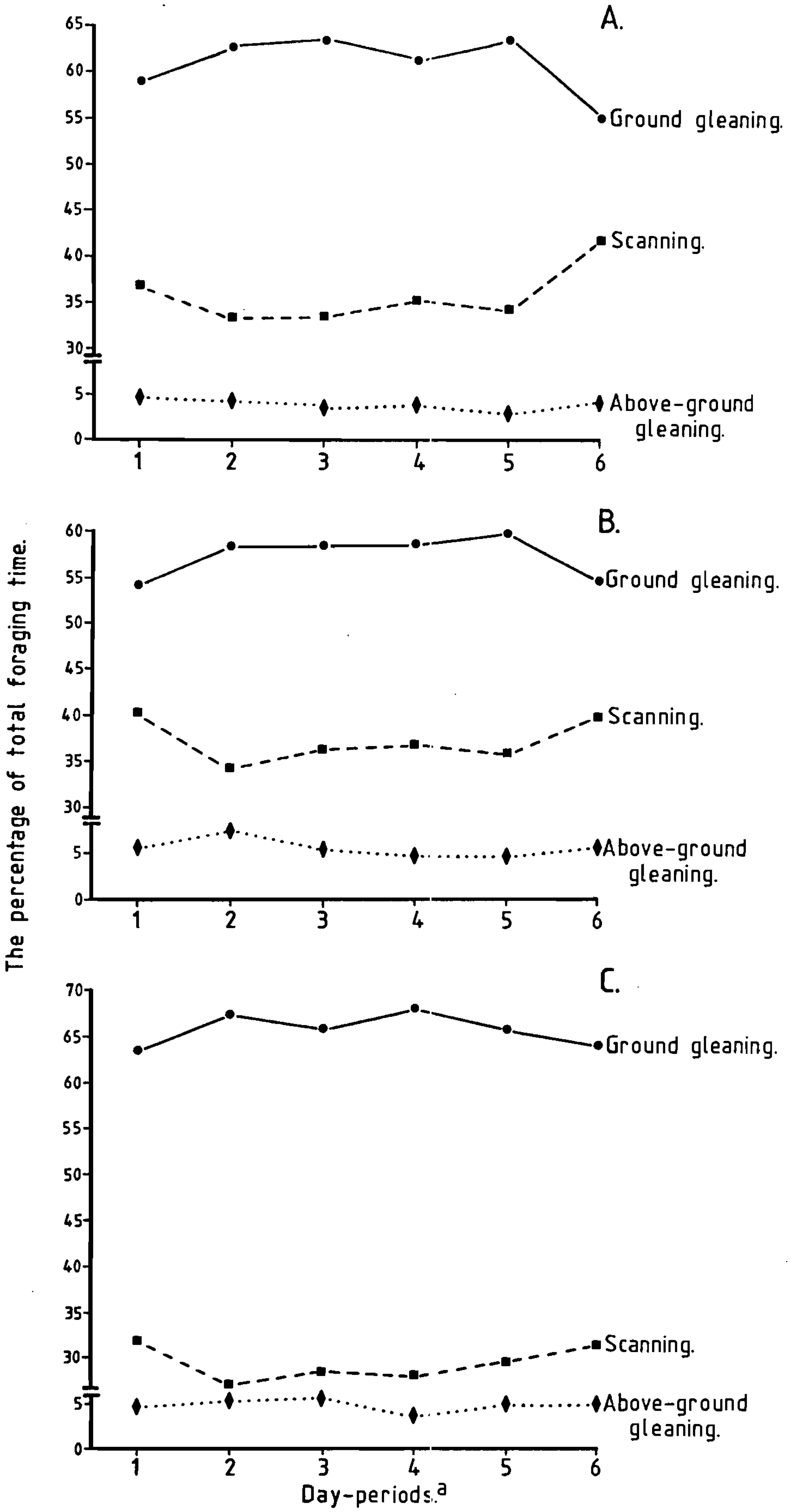


Figure 4.2 The diurnal patterns of three foraging methods used by:

A. Adults in the breeding season (1976+1977 data).

B. Adults in the non-breeding season (1977+1978 data).

C. Immatures in the non-breeding season (1977+1978 data).

[a] The division of the daylight hours into six day-periods of equal length.

considerable proportion of time using the same foraging method during the spring of 1976 and summer of 1977. Scanning, hawking and flycatching all showed peaks during the summer months.

A comparison of the proportion of foraging time male Robins of two populations spent using the various foraging methods is given in Table 4.1. Observations at Outer Chetwode Island made during April, May and June 1978 were amalgamated and compared with those from Kowhai Bush during the same months. Males from both populations used a similar proportion of foraging time gleaning from the ground, hawking and flycatching. However, the Outer Chetwode Island males spent significantly more time scanning ($P < 0.01$), and less time vegetation gleaning ($P < 0.01$) than did the Kowhai Bush males.

Table 4.1. A comparison of the proportion of total foraging time that adult male Robins from Kowhai Bush and Outer Chetwode Island spent on five foraging methods during April, May and June 1978.

	Foraging methods					
	Ground gleaning	Vegetation gleaning	Scanning	Hawking	Flycatching	Total foraging time (h)
Kowhai Bush:	55.59	4.58	39.60	0.21	0.02	37.1
Outer Chetwode Is:	55.41	0.67	43.76	0.14	0.02	57.4

Adult and immature Robins spent different proportions of foraging time using the various foraging methods (Table 4.2). Their time-budgets of foraging behaviour for the same year were significantly different ($P < 0.01$). Both age groups spent a similar time vegetation gleaning and flycatching, but adults devoted a greater percentage of foraging time to scanning and hawking than did immatures. Immatures preferred to forage on the ground.

The diurnal patterns of ground gleaning, scanning and above-ground gleaning were similar for adults in both the breeding and non-breeding seasons (Figs 4.2 A and B). Ground gleaning represented a relatively constant percentage of foraging time from mid-morning to mid-afternoon inclusive, but was used less in the early morning and late afternoon. With scanning the reverse was true. The time spent gleaning above the

Table 4.2. The proportion of time spent by adult and immature Robins at Kowhai Bush using five foraging methods during the non-breeding seasons (January to July).

	Foraging methods					
	Ground gleaning	Vegetation gleaning	Scanning	Hawking	Fly-catching	Total foraging time (h)
Adult						
1977:	56.59	6.76	36.09	0.48	0.08	211.9
1978:	58.14	3.65	37.92	0.25	0.04	183.3
Immature						
1977:	64.94	6.77	28.03	0.17	0.09	81.1
1978:	66.02	3.73	29.97	0.22	0.06	162.7

ground was fairly constant throughout the day, although a slight increase was found during mid-morning and late afternoon.

For both age classes of Robins the diurnal pattern for each foraging method was similar (Figs 4.2 B and C).

4.3.2. Feeding stations and foraging height

Robins spent most time gleaning from branches (39.5%) and trunks (37.97 + 20.27 = 58.2%) of trees when vegetation gleaning (Table 4.3).

Table 4.3. The proportion of time Robins at Kowhai Bush spent gleaning from five feeding stations on vegetation.

Feeding stations[a]					
B-B	T-B	T-T	S-S	F-F	Total foraging time (h)
39.47	37.97	20.27	2.01	0.28	19.8

[a] B-B = branch to branch, T-B = trunk to branch, T-T = trunk to trunk, S-S = stump to stump, F-F = foliage to foliage

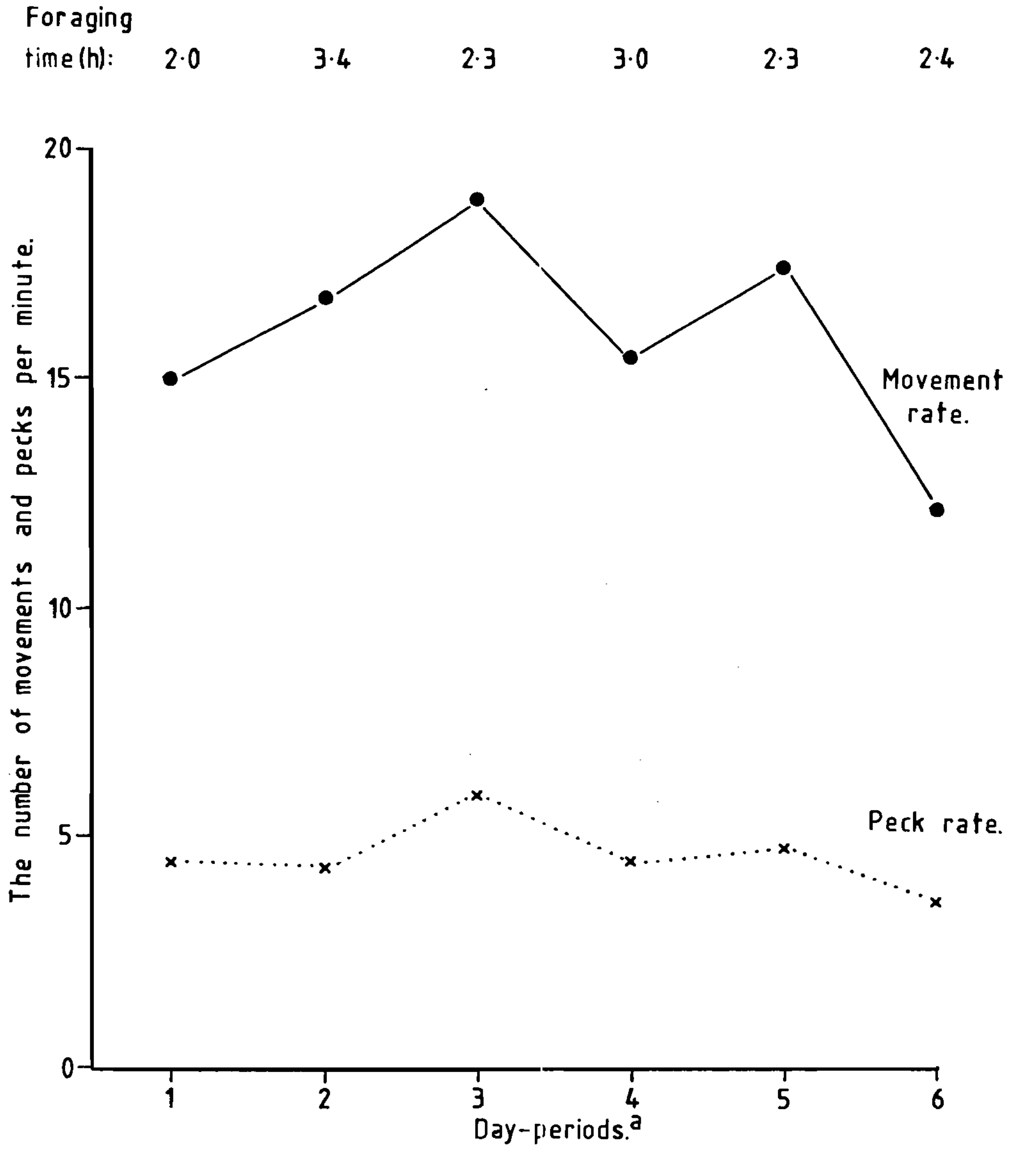


Figure 4·3 The diurnal patterns of movement and peck rates (number per minute) for foraging male Robins involved in the incubation stage during the 1978 breeding season.

[a] The division of the daylight hours into six equal-lengthed day-periods.

Little time was spent gleaning from decaying tree stumps or amongst foliage and twigs. About 70% of time when gleaning amongst vegetation was spent within two metres of the ground (Table 4.4). Little time was spent foraging above four metres even though the bush was up to 7-12 metres high. Although the heights of scanning perches were not measured, they seemed to be similar to those for vegetation gleaning. Therefore, 90% of the Robin's foraging time was spent on the ground and within two metres of it.

Table 4.4. The proportion of time Robins at Kowhai Bush spent on vegetation gleaning at various heights.

	Height (m)											Total vegetation gleaning time (h)
	0.1–0.6	0.7–1.1	1.2–1.6	1.7–2.1	2.2–2.6	2.7–3.1	3.2–3.6	3.7–4.1	4.2–4.6	4.7–5.1	>5.1	
%:	23.8	13.8	18.4	15.1	9.0	7.2	4.6	3.7	1.8	1.8	1.6	29.1

4.3.3. Movement and peck rates

Robins foraged most actively during winter when their movement and peck rates were fastest (Table 4.5). The rates of movement gradually decreased from a peak in July to a low in March. Similary, the rate of pecking decreased through the breeding season, but rose again during February and March.

Peck and movement rates of foraging male Robins in the breeding season showed similar diurnal patterns (Fig. 4.3). The rates increased through the morning to peak just before noon. The rates then declined to dawn levels in early afternoon, rose slightly during mid-afternoon, before declining again to their lowest levels just before sunset.

4.3.4. Searching activity

During the incubation stage of the breeding cycle, male Robins spent 93.7% (n = 12.8 h) of their foraging time searching for prey. They were never seen to systematically turn over an area of litter as Blackbirds

Table 4.5. The movement and peck rates (number/min.) of foraging Robins.

Month	Status of Robins	Observation time (h)	Rate of movement	Moves/mean daylength	Rate of pecking	Pecks/mean daylength
June	Adult	1.1	18.24	9923	8.82	4798
July	"	0.5	18.81	10533	9.00	5040
Aug.	Males feeding an incubating female	4.0	16.58	10296	5.32	3304
Sep.	"	4.7	17.39	12295	4.45	3146
Oct.	"	3.4	17.24	13740	4.56	3634
Nov.	"	0.8	13.04	11397	3.75	3278
Dec.	"	2.5	11.86	10887	3.43	3149
Feb.	Adult	1.9	10.75	8923	6.12	5090
Mar.	"	1.4	10.72	7950	4.24	3150

Turdus merula and wekas *Gallirallus* spp. do, but seemed to rely largely on sight to find prey. Searching activity involved Robins hopping and stepping over litter and vegetation, or scanning from a vantage point. It seemed that litter and bark were only moved aside to retrieve prey that were seen to retreat underneath them.

Special movements of the feet, wings and tail seemed to stimulate prey to move and to enhance their detection. Flack (1973) and Soper (1976) noted foot-trembling by Robins. One foot was placed on the ground slightly forward of the other and vibrated up and down rapidly. This foot movement took the form of either a continuous action or discrete pulses with the two feet being used alternately. On dry litter a distinct rustle could be heard as the Robin's foot vibrated upon it. All foraging Robins foot-trembled and some juveniles were seen making these movements when only twelve days out of the nest.

Wing- and tail-flicking also seemed to flush prey. Wing-flicking "is the quick extension and replacement of the hand and primary feathers out to either side of the body" (Horwich 1965). The tail was similarly flexed to form a fan and sometimes cocked up and down. However, few individuals tail-flicked, but all wing-flicked. The speed of wing-flicking was very rapid with several flicks in quick succession after which the bird made a few hops before repeating the action. During 20.3

hours of foraging observations, Robins averaged one wing-flick every 51 seconds.

Nearly 88% of movements made during searches for food involved hopping and stepping, the rest were flights (Table 4.6). The greatest proportion of hops and steps occurred on the ground, with only a few made on trunks. Sixty-six percent of flights ended with Robins landing on branches compared with 30% ending on the ground (Table 4.6). Ninety percent of flights made by foraging Robins were over distances of less than six metres. Because most flights lasted only a few seconds, timing them with a stopwatch was inaccurate. However, I judged that Robins took about one second to fly a metre and by multiplying by the number of metres flown, I estimated that nearly eight percent of foraging time was spent flying.

Table 4.6. The percentage of movements and pecks by Robins at three feeding stations.

	—Feeding stations—			Total pecks or movements observed
	Ground	Branches	Trunks	
Hops and steps:	86	13	1	16438
Flights:	30	66	4	2289
Pecks:	94	2	4	6083

4.3.5. Handling and eating activities

The time Robins took to kill, dismember and eat prey depended on the prey's size and defensive actions. Of 12.8 hours of foraging time Robins spent 6.3% in handling and eating activities.

Small items (< 5 mm long) were swallowed whole and seemed to be killed merely by being crushed between the mandibles. Large invertebrates were killed by quick stabbing and pinching movements (mandibulation) of the beak. Once the prey was subdued sufficiently, it was carried to a protected place for breaking into smaller portions. Such places were on the ground and under vegetation giving seclusion from other birds. Male Robins occasionally took food from their mates during the non-breeding season.

Dismemberment of prey involved smashing it against a log or the ground. Prey were grasped in the middle or at one end and swung from side to side with a downwards and sideways movement of the head. This action was repeated until a portion broke off that was small enough to swallow. Sometimes caterpillars found above ground-level were broken up on a branch. Table 4.7 shows the mean time taken to kill, dismember and eat some common prey animals. The large amount of time spent by Robins dealing with slugs, snails and large earthworms is a reflection of their bulk and sliminess. Before being broken up, slimy prey were thoroughly rubbed on a log or over the ground to remove most of the slime that may otherwise have fouled the Robin's plumage. Lepidopterous larvae were vigorously bashed until macerated. Many berries were broken up even when they seemed to be small enough to be swallowed whole. This apparently separated the indigestible seeds from the fleshy exocarp, although some seeds were ingested (Powlesland 1979).

Table 4.7. The time taken by Robins to kill, dismember and eat some prey animals[a].

Animals and their length	N	Time in minutes		
		Time	Range	S.D.
Amphipsalta zelandica (cicada) 3-4 cm	27	2.2	1.0-4.0	0.71
Earthworm < 4 cm	16	0.3	0.0-0.9	0.06
Earthworm 4-14 cm	13	1.3	0.4-2.4	0.32
Earthworm > 14 cm	14	6.0	3.4-13.6	11.81
Stick-insect 8-15 cm	25	1.8	0.4-4.6	1.32
Slug 2-4 cm	14	2.5	0.4-4.8	1.46
Snail 1.5-3.0 cm	3	5.1	4.6-5.5	0.17
Hemideina femorata (tree weta) 3.5-5.0 cm	10	5.0	2.8-8.4	3.45

[a] Appendix 2 describes the large prey animals and their seasonal occurrence in the Robin's diet.

Few invertebrates could deter Robin attacks. Ground beetles (*Megadromus* and *Mecodema* spp.) were usually ignored, presumably because they emit an "acrid, pungent and offensive smell when disturbed" (Sharell 1971) and have strong exoskeletons. However, on three occasions these beetles were seen being eaten. Two instances involved *Megadromus wallacei* being taken by the same Robin which ate only the viscera. Stick-insects occasionally deterred attacking Robins by waving their long spiny legs. Similarly, tree wetas (*Hemideina femorata*) were able to ward off Robins by raising their large spiny legs. Their vigorous thrashing movements, accompanied by a rasping noise, and the animals strong exoskeleton, combined to deter some Robins, especially immature individuals, from killing tree wetas.

Robins have a recognisable behaviour associated with catching soil-burrowing prey, such as earthworms, a behaviour consisting of a "head-cock" and "beak-pounce" (Heppner 1965). When a Robin sighted a likely hole it stood still while cocking its head from side to side. If prey was seen the bird straightened its head and jumped forward with both feet off the ground, thrusting its beak into the soil with considerable speed and force. Repeated beak-pounces were seen when prey retreated out of reach or when an earthworm broke in two leaving a portion in the hole.

4.4. Discussion

4.4.1. Seasonal and diurnal patterns of foraging methods

As noted by Falla *et al.* (1966) and Oliver (1955), Robins spend much of their foraging time on the ground. However, they are versatile hunters as prey are caught by a variety of methods which vary with the structure of the habitat and type of prey available (Flack in prep.).

During winter when the soil was moist, Robins spent most of their foraging time gleaning on the ground. Gleaning from vegetation became more important in winter than in the other seasons. Food was searched for in crevices, fissures, holes, among dead foliage and tangles of vines, and at branch and trunk axils where debris collected. The rough-barked surfaces of trees are important places for insect larvae and pupae to overwinter (MacLellan 1959). Thus, the coarse-textured and flaky bark of kanuka provided many opportunities for Robins to find over-wintering and sheltering invertebrates. Scanning, hawking and flycatching activities diminished during the course of winter, presumably because aerial and arboreal invertebrates were then less numerous and inactive because of lower ambient temperatures. Similarly, South Island Fantails fed more frequently on the ground and in the lower understorey in winter compared with the other seasons (Ude Shankar 1977).

A marked change arose in the proportions of time devoted to the various hunting methods from the winter-spring situation to that of summer. The proportion of time spent scanning, hawking and flycatching increased with the presence of large numbers of aerial and arboreal invertebrates. During late November and throughout December swarms of March flies *Philia negrostigma* (Bibionidae) were present which the Robins caught by hawking and flycatching. Cicadas, which emerged in January and remained in great profusion until mid-March, were also caught by hawking and flycatching. Caterpillars were hawked from terminal shoots, and a variety of invertebrates, especially moths, were hawked from trunks. During late summer berries were often taken by hawking as the slender twigs on which they grew did not support a Robin's weight. To some extent the increased time spent scanning and hawking during summer was forced upon the Robins. Low rainfall and dry soil conditions meant few prey were active in the upper soil and litter so that the birds had to turn to arboreal prey. More time was spent flycatching in summer than at other times of the year, presumably because the favourable weather (warm and calm) enabled insects to fly.

For adult Robins, the diurnal pattern of three foraging methods showed similar trends during the breeding and non-breeding seasons. Scanning peaked in the early morning and late afternoon for two reasons. First, while Robins avoided open areas, they did venture into sparsely vegetated areas during twilight. Many of their territories bordered on to relatively open habitat, such as the edges of the Kowhai River riverbed and grazed parkland covered with scattered trees and a sparse ground cover or pasture. The foraging styles of Robins venturing into these areas were made up almost entirely of scanning with brief flights to the ground to catch and eat prey; foraging behaviour similar to that of the Yellow-breasted Tit (Falla *et al.* 1966), Pied Tit *Petroica macrocephala toitoi* (Gibb 1961) and Eastern Bluebird *Sialia sialis* (Pinkowski 1977). Possibly in the low light intensities at dawn and dusk the Robin's dull plumage afforded them some protection from competitors and predators, so enabling them to use open areas. Kacelnik (1979) found that captive Great Tits were less efficient foragers in light intensities comparable with those that occur for a one and a half hour period after sunrise. Therefore, it is likely that Robins, which spent much time foraging on the ground, would also be less successful foragers in the forest at dawn and dusk. Perhaps by venturing out into open habitat, Robins were able to spend a greater proportion of the day foraging profitably.

Second, Robins within the bush spent more time scanning in the early morning and late afternoon, possibly to find prey which were active at dawn and dusk. Invertebrates damaged during the night, those that had failed to conceal themselves adequately before dawn, and those that became active just before sunrise (e.g. cicadas) would have been most vulnerable in the early morning. Scanning would enable the greatest area of territory to be searched quickly. Furthermore, it would have brought the Robins to a level where they were most likely to encounter moths, prey they catch in flight in the evening (Flack 1973).

4.4.2. Influence of habitat and age on the foraging style of Robins

Adult male Robins on Outer Chetwode Island spent more foraging time scanning, and less time gleaning among vegetation and hawking than did adult males at Kowhai Bush. This result I attributed to habitat differences. Robins on the island were observed in open gullies which had few ground storey and lower understorey plants, and where coarse-barked trees were uncommon. Therefore, opportunities for vegetation gleaning and hawking were probably fewer on the island than at Kowhai Bush. A comparison of hunting behaviour between populations could therefore be misleading unless the structure of the habitats was taken into account. Similarly, Brownsmith (1977) found that the type of habitat used by Starlings *Sturnus vulgaris* affected their feeding pattern.

The reason why immature Robins spent more time gleaning over the ground and flycatching compared to adults at Kowhai Bush ($P < 0.05$) was not obvious. Perhaps they were less proficient at finding arboreal prey by scanning than were adults. Scanning may not have been profitable in relation to effort expended by immature Robins, but may have been so for adults. Wakeley (1978) found that the time Ferruginous Hawks *Buteo regalis* devoted to four hunting methods was not related to their success ratio (successful strikes per total strikes) nor to their capture rates (capture per unit time), but was positively related to the number of captures they made per unit of energy expended.

The diurnal patterns of foraging methods used by adult and immature Robins during the non-breeding season were similar even though immatures scanned less than adults ($P < 0.01$). The peaks of scanning in the early morning and late afternoon were less for immature Robins than for adults, probably because immatures ventured less into open habitats.

4.4.3. Feeding stations

Little time was spent moving over or through twigs and foliage, perhaps because Robins were too heavy and lacked the precise agility and balance of smaller birds. Although capable of clinging to coarse-textured trunks, they preferred to forage from trunks while perched on a branch. Robins seldom moved up a trunk by clinging to it in the manner of Riflemen (pers. obs.), but usually hopped from branch to branch.

In general, the number of crevices, holes and bark furrows in tree trunks decreases with height up trunks (Travis 1977). This may have been why Robins carried out much of their gleaning from vegetation within two metres of the ground. Behavioural intolerance of open spaces meant that Robins rarely ventured up into the canopy to glean. Another reason is that Robins were very wary of Bellbirds, Magpies *Gymnorhina tibicen*, New Zealand Kingfishers and Australasian Harriers whose presence often caused them to give alarm calls and to flee into the lower understorey vegetation.

These morphological and behavioural features of the South Island Robin contributed to it spending 90% of its foraging time on the ground and within two metres of it. In this respect, it is notable that of 43 observations of foraging North Island Robins, 93% involved birds on the ground or within three metres of it (Gravatt 1971).

4.4.4. Movement and peck rates

Foraging male Robins decreased their rate of movement from July to March, although the number of moves per day per month increased to October and then declined mainly because of changes in hunting style and daylength. Since nearly 88% of all movements were hops and steps, and most of these movements took place on the ground, to a large extent the movement rates reflect the amount of ground gleaning undertaken. Gleaning from the ground as a proportion of the foraging time was highest in winter and spring, as too were the movement rates. The proportion of time spent scanning gradually increased to a peak in March. Scanning involved mostly patient watching with few movements so a low average movement rate resulted during the summer months. Although daylength was longest in December, the number of moves per day only increased until October. Possibly the number of moves per day declined after October because daylength was then longer and not all the time available was required to find sufficient food to meet their requirements.

Peck rates and the number of pecks per day averaged for each month showed similar trends to movement rates. The highest rates occurred in winter and the rates gradually decreased as the breeding season progressed, but rose sharply in February and March when moulting took place. Peck rates reflect the time spent ground gleaning because about 95% of all pecks were made by Robins foraging on the ground. Peck rates probably also varied according to prey size. During winter, a lot of very small items were eaten, but time taken to eat them was not recorded as handling time because they were eaten so quickly. Later in the season larger prey were caught and the many pecks that were required to kill and dismember them were visible and so were timed separately as handling time. The sudden rise in peck rates during February and March presumably was related to the Robin's increased food requirements during the moult. It was not determined whether the increased peck rate was related to increased consumption of small prey, although this may have been the case. Gibb (1956) found that Rock Pipits *Anthus spinoletta* also fed most rapidly in mid-winter. Because Robins used the greatest number of pecks per day during the winter months, they were presumably eating most prey, including quite small items.

Male Robins had a bimodal diurnal pattern of movement and peck rates. Although a large proportion of foraging time was spent ground gleaning in the late morning and mid-afternoon, and would have produced high peck and movement rates, other factors could have influenced these results. Some poikilothermic invertebrates are most active when diurnal temperatures are highest and could be most available to the Robins then. The high rates during the mid-afternoon possibly resulted from hunger after the lull of feeding activity around midday and the need to build up food reserves before the night fast.

The decrease in both peck and movement rates during the early afternoon was not wholly related to the slight increase in scanning at that time. The lower rates around midday may have been also related to an increased resting then. Palmgren (1949) found that for a variety of caged passerines their rate of activity (jumps/h) showed peaks of activity in the morning and evening and a state of relative rest in the afternoon. Caged Chaffinches *Fringilla coelebs* kept in isolation under constant conditions, exhibited similar diurnal rhythms of activity, the rhythm apparently being controlled endogenously (Aschoff 1967). Similarly, several studies of wild avian populations have shown an increased proportion of individuals resting or sleeping at midday:- Northern Shovelers *Anas clypeata* (Afton 1979), Gadwalls *A. strepera* (Dwyer 1975), Herring Gulls *Larus argentatus* (Galusha and Amlaner 1978), Yellow-billed Magpies *Pica nuttalli* (Verbeek 1972) and male Long-billed Marsh Wrens *Telmatodytes palustris* (Verner 1965). Therefore, it is likely that the lower movement and peck rates of Robins in the early afternoon arose because the birds slowed their foraging activity before resting.

4.4.5. Searching activity

The searching activity of Robins at Kowhai Bush differed from that of the North Island subspecies *Petroica australis longipes* because Gravatt (1971) described the latter as raking the litter with its beak and turning over leaves to disturb small animals. Generally, South Island Robins only moved aside litter or bark to capture prey seen retreating under them.

Foot-trembling by several *Petroica* species has been reported. Hobbs (1954) observed the behaviour in Flame Robins *P. phoenica* feeding near Deniliquin, Australia. Best (1975) noted that Black Tits *P. macrocephala dannefaerdi* quivered one leg up and down rapidly. Similarly, Kearton (1979) found that Yellow-breasted Tits occasionally foot-trembled on branches. Sparks (1961), making reference to feeding shorebirds, hypothesised that foot movements were adopted "to exploit the properties of intertidal muddy sand, in order to expose or incite movement in cryptic invertebrates of the intertidal zone". Thus, foot-trembling by Robins may have been to stimulate movement from hidden prey by transmitting vibrations.

Much controversy exists on the role played by wing movements during the feeding of passerines: for example, wing-flashing in Mockingbirds *Mimus polyglottos* (Hailman 1960, Horwich 1965). Wing-flashing is the extension of the wings up to about an 85° angle to the horizontal and completely extending the remiges. Thus, this movement consists of a prolonged extension without any hesitations until the wings are quickly brought down to the sides. Hailman (1960) considered that the flashing of white wing patches startled insect prey into revealing themselves. However, Horwich (1965) noted that 69% of all observations of wing-flashing by Mockingbirds were associated with a situation in which birds showed escape tendencies or ambivalent behaviours, such as slight fear or uneasiness. Wing-flicking by Robins often took place at sites that could have concealed predators and so could represent a flight intention movement. However, they were never given in a crouched stance as though preparatory for flight. Ude Shankar (1977) studied the tail fanning, flicking and flashing of foraging South Island Fantails and concluded that these movements provided maximum thrust during take off and balance while hopping about on branches and the ground. However, Warham (1956) suggested that the wing and tail-flicking of Willy Wagtails *Rhipidura leucophrys* were made to scare "camouflaged prey into revealing flight or movement." Prey startling by Robin wing movements would seem to be enhanced by the flashing of a narrow pale band on the underside of the wings. Wing-flicking was seen only from foraging birds, and then usually while they were near or under overhanging vegetation. These wing movements did not seem to be used for balance since both wings were moved equally out from the body and at the same angle to it. Birds afflicted by bird pox moved about with one foot tucked into their plumage, and balanced by flapping both wings asymmetrically.

As would be expected of a bird that spends much of its foraging time on the ground, most of its movements were hops and steps. Scanning involved Robins making frequent short flights from perch to perch so that most foraging flights ended on branches, with few ending on the ground and trunks where prey items were usually captured. This behaviour was also true of Black Robins *Petroica traversi* (Flack MS). Although most pecks were made by Robins foraging on the ground, this may not indicate the effectiveness of pecking in capturing prey. Most pecks made while Robins were on branches and trunks seemed to be at prey, whereas some made while they were on the ground included pecks to move litter aside and to probe into the soil to catch retreating animals. More pecking occurred on trunks than on branches because branches were less furrowed (Travis 1977) and so were poorer sources of food.

4.5. Summary

Overall, 61.3% of Robin foraging time was spent ground gleaning, 33.8% scanning, 4.5% gleaning amongst vegetation, 0.3% hawking and 0.1% flycatching. Gleaning over the ground predominated in winter and early spring when the soil was moist. The time spent scanning, hawking and flycatching all peaked during the summer months when large numbers of aerial and arboreal invertebrates were present. No consistent seasonal trend in the proportion of time spent vegetation gleaning was evident.

Male Robins at Kowhai Bush and Outer Chetwode Island spent significantly different proportions of time scanning and vegetation gleaning, probably as a consequence of habitat differences. Likewise, adult and immature Robins at Kowhai Bush spent different proportions of foraging time using the various foraging methods. Immatures preferred to forage on the ground, while adults spent more time scanning and hawking.

The diurnal patterns of ground gleaning, scanning and above-ground gleaning were similar for adults in the breeding and non-breeding seasons, as were the diurnal patterns of these foraging methods for adult and immature Robins in the non-breeding season. A smaller percentage of foraging time was spent ground gleaning in the early morning and late afternoon, than for the rest of the day; the reverse was true of scanning. This was largely a consequence of the birds foraging in relatively open habitats during twilight conditions where they spent much time scanning, with only brief moments on the ground to catch and eat prey.

Ninety percent of the Robins foraging time was spent on the ground and within two metres of it. Robins seemed to lack the precise agility and balance of smaller birds, and were possibly too heavy to search for prey while moving among twigs and foliage. Ninety-eight percent of time spent searching among vegetation involved Robins hunting over branches and trunks.

Movement rates of foraging Robins were highest in winter and lowest in summer. Similarly, peck rates were highest in winter, decreased during the course of the breeding season, but rose while the birds were moulting. Since most movements and pecks occurred while they were ground gleaning, the high movement and peck rates in winter probably reflect the combination of two factors; the greater proportion of time spent ground gleaning then than during the other seasons, and the many small prey items eaten in winter. The diurnal patterns of peck and movement rates of foraging male Robins in the breeding season were similar, with the peak rates occurring during the late morning and mid-afternoon, and the slowest rates around dawn and dusk.

Most foraging time was spent searching (93.7%). Robins relied largely on their keen sight to find prey, but also seemed to stimulate prey movement by foot-trembling and tail- and wing-flicking.

Most movements of foraging Robins were hops and steps (88%), the rest being flights. About 8% of foraging time was spent flying, mainly from branch to branch from which the surrounding ground and vegetation surfaces were scanned for prey. Almost all pecks were made while Robins were foraging on the ground, very few were directed at prey on branches and trunks.

Robins spent 6.3% of their foraging time killing, dismembering and eating prey. Since few prey were able to deter Robin attacks and were quickly subdued, most of this time was spent either wiping the slime off some species (slugs, snails and large earthworms) or dismembering those that had hard exoskeletons (cicadas, wetas and stick-insects).

CHAPTER FIVE

FOOD-STORING BEHAVIOUR

5.1. Introduction

A variety of birds store food, especially birds of prey, shrikes and owls (Angel 1969, Balgooyen 1976, Collins 1976, Collopy 1977, Cope and Barber 1978, Dunn *et al.* 1976, Greaves 1968, Mueller 1974). Applegate (1977) saw a male Loggerhead Shrike *Lanius ludovicianus* storing prey by impaling it on thorns, and Durango (1951) observed similar behaviour in the Red-backed Shrike *L. collurio*. Goodwin (1951) and Chettleburgh (1952) described nut burying by Jays *Garrulus glandarius*, and Purchas (1975) saw Rooks *Corvus frugilegus* hiding nuts. Swanberg (1951) described nut hoarding by Thick-billed Nutcrackers *Nucifraga caryocatactes* and Haftorn (1953, 1956a, b, c, 1974) gave detailed accounts of storing of seeds and invertebrates by several *Parus* species. Food storing by Robins has been recorded by several observers (Falla *et al.* 1966, Flack in prep., Fleming 1950, Moncrieff 1932, Richdale 1941, Soper 1976). During this study, Robins at Kowhai Bush and Outer Chetwode Island were often seen storing invertebrates.

A description of food-storing behaviour, the types of invertebrates stored, the time taken to store an item, as well as the height and nature of the store site is given here. The diurnal pattern of storing and retrieving food is described. The description of food-storing behaviour in subsequent chapters will only deal with the percentage of time various categories of Robins devoted to this behaviour at different times of the year and day.

5.2. Methods

For the purpose of timing, food-storing behaviour started when a Robin carrying food flew off in search of a store site and finished when the bird departed after depositing the item. Food-storing behaviour was timed separately from other behaviours throughout the study, but from March to July 1977 and January to July 1978, data about the prey stored, store sites and recovery of food were also recorded. Retrieval of stored food was not seen often and when it was I was sometimes unsure whether cached or new prey was involved, so retrieval behaviour was timed as foraging. Repeated visits were made to store sites to determine the time and day food was retrieved. Since observations were distributed more or less equally throughout the day during the non-breeding season, the possibility of biassing the temporal distribution of storing behaviour was minimized. Therefore, I consider Figure 5.1 to be a representative sample of the time of day in which Robins stored and retrieved prey.

5.3. Description of food-storing behaviour

Although Robins ate invertebrates and berries, they were seen to store only the former. Prey were stored whole or in portions and singly at different sites. Prey items too large to be carried in flight were broken up before being stored. Before being cached, most prey were killed by mandibulation and slamming against a hard object more vigorously than when eaten immediately. However, on a few occasions prey, especially earthworms, were still writhing when stored so that some fell from the sites. Similarly, Haftorn (1953) found that Crested Tits *Parus cristatus* sometimes stored prey still capable of movement.

Various sites were used as food stores, with branch-trunk axils being the commonest. Stump ends, and holes and crevices in branches and trunks were also used. Ample suitable sites were apparently available or Robins were not very selective because most prey were stored within ten metres of the place where they were killed and broken up. Soper (1976) described Robins storing food in "larders", as though such sites were repeatedly used. This was not the case at Kowhai Bush where I found no evidence that sites were used more than once. Also, a Robin sometimes foraged beyond its territory during autumn and surplus food was not brought back into the territory to be put in larders, but was stored very near where it was found.

No effort was made to hide stored prey by covering it with bark or lichen, as is done by Boreal Chickadees *Parus hudsonicus* (Haftorn 1974). Stored items of Robins were often visible from above. They were placed in sites and not forced in between two surfaces. Nor did it appear to be held in place by saliva produced by the bird (Haftorn 1953) or any similar method. Often stored prey adhered to the site because fluids that had issued from the prey's wounds had coagulated.

Male Robins dominated their mates so that before a female cached food she often moved out of his sight. However, cases were seen where either sex immediately consumed the food stored by its partner. Occasionally,

Table 5.1. The number of different foods observed to be stored by Robins in the non-breeding season (January to July).

	Months													
	1977					1978								
	M	A	M	J	J	J	F	M	A	M	J	J	Total	%
Earthworm	1	12	8	8	20		1	7	17	36	45	33	188	69.8
Slug	1	2	1	3	2				1	1	4	2	17	6.3
Stick-insect			2	2					1	4	3	2	14	5.2
Cicada	2						6	2			1*		11	4.1
Beetle larvae			5	3	1				1				10	3.7
Tree weta				1							4	2	7	2.6
Ground weta		2	1	1	1						2		7	2.6
Snail		1	1	1	1							1	5	1.9
Caterpillar					1			1				2	4	1.5
Flatworm				1						2			3	1.1
Spider		1											1	0.4
Fly		1											1	0.4
Cockroach					1								1	0.4
Total	4	19	18	21	26		7	10	20	43	59	42	269	

*A nymph

Table 5.2. A comparison of the mean height of storage sites and vegetation-gleaning sites.

	Mean height (m)	Range (m)	S.D.	N
Storage site:	2.8	0.3-8.0	1.5	293
Vegetation-gleaning site:	1.4	0.1-8.0	1.1	500

($t = 14.3$ for 792 d.f., $P < 0.05$)

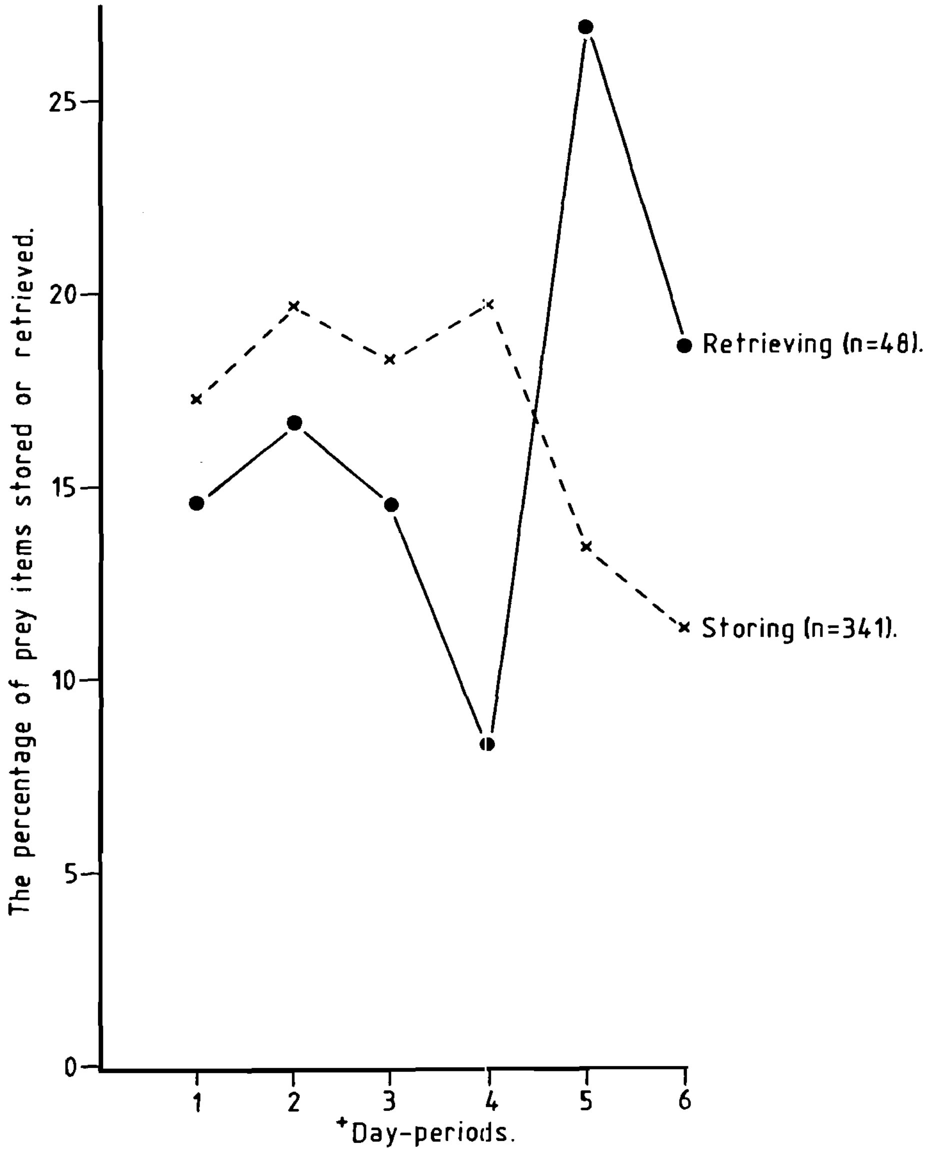


Figure 5·1 The diurnal rhythm of the storing and retrieving of prey by Robins.

+ The division of the daylight hours into six day-periods of equal length.

instead of eating the stored food, the partner transferred it to a new site. Such behaviour has also been observed in tits (Gibb 1960, Haftorn 1974) and Rooks (Kallander *in* Andersson and Krebs 1978).

5.4. Results

Food storing was seen during most months of this study, but it took place most frequently from April to July. Table 5.1 summarises the types and frequency of food stored each month. Nearly 70% of cached items were earthworms which were stored mainly during autumn and winter. Cicadas were the main food items cached during summer. The mean height of store sites (n = 293) was 2.85 m, with a range from 0.3 to 8.0 m. The mean height that prey were stored was significantly greater than the mean height at which Robins gleaned from vegetation (Table 5.2). Of 340 caching operations, the average time taken was 24 seconds, varying from four seconds to two and a half minutes, although storage rarely took more than a minute. Of 40 stored items, 58% had disappeared, presumably retrieved, the same day they were stored.

Figure 5.1 shows the diurnal pattern of storing and retrieving food. Although both activities occurred throughout the day, Robins tended to store food more often in the morning and retrieve it mainly in the late afternoon.

5.5. Discussion

Earthworms were stored most often, which probably reflects their frequency in the diet during the non-breeding season. It is not known whether Robins selectively stored particular prey species. Collopy (1977) found that the relative proportions of prey types cached corresponded directly with the relative proportion captured by female American Kestrels *Falco sparverius*.

Unidentified native earthworms were present in Kowhai Bush and were captured occasionally by Robins. Many were 10 mm in diameter with an average length of about 200 mm. Such large prey were never eaten completely, possibly because the bird's proventriculus was not capable of holding so much food. The excess was stored. Thus, for the Robin, stored food seemed to be surplus to their immediate requirements. Robins spent more time storing food during the course of the non-breeding season

(Fig. 10.5, p. 154), even though fewer hours were spent foraging per day (Fig. 10.3, p. 152). I presume that Robins foraged less per day in June and July (winter) than previously because of the shorter daylengths and not because food was more abundant. Therefore, as well as storing surplus food, it is possible that Robins stored at least some food as a source for consumption when food found by hunting did not meet their maintenance requirements. However, it is also possible that this result was a consequence of prey, particularly earthworms, being more available in winter than previously.

Haftorn (1956c) found that the Willow Tit's *Parus atricapillus* storing areas corresponded to their feeding areas, but that Boreal Chickadees stored food at a level lower than where they foraged (Haftorn 1974). The mean height of food-storage sites of Robins was higher than that at which they gleaned from vegetation, but within the height range that they fed. Suitable sites for caching food in are probably infrequent higher in the canopy and this possibly limits the height of storage sites. Furthermore, the more open nature of the canopy may make these sites more susceptible to potential cache robbers, such as Brown Creepers, Bellbirds and *Turdus* species. Robins showed a high degree of interspecific territoriality (Flack 1976a), especially around their caches, but I never saw other species taking stored food.

Crested Tits usually took 30-50 seconds to find, kill and store an item (Haftorn 1953) and Boreal Chickadees took about 40 seconds (Haftorn 1974) to collect and hoard insect larvae. Although collection times of items were not recorded for the Robin, the mean time of 24 seconds taken by them to store an item is a similar time to that for other species. By comparison, Gibb (1960) described tits as spending a long time looking for places in which to store their food and investigated many trial places before deciding on one that was suitable. Thus, these birds may have spent longer in this activity than Robins because the latter usually stored prey in the first site they visited.

Storage of food by Robins was a short-term process lasting only a few days at most, compared with several months for Rooks (Purchas 1975) and tits (Haftorn 1956c). Hoarding of invertebrates by tits in England (Gibb 1960) and Norway (Haftorn 1953) for retrieval in winter was presumably feasible because the food would have been preserved by natural freezing in the colder climate (Roberts 1979). At Kowhai Bush stored items quickly decomposed even in winter. Several items seen in cache sites after four days may have been rejected because of their state of decay. However, dried earthworms were occasionally retrieved and eaten so that some food was acceptable after several days.

Robins tended to store and retrieve prey throughout the day, but with less storing and more retrieving late in the day. Crested Tits (Haftorn 1953), Thick-billed Nutcrackers (Swanberg 1951) and Jays (Chettleburgh 1952) all displayed a diurnal pattern of food storage with the intensity rising in the morning, reaching a peak about midday, and declining afterwards. Collopy (1977) found that female American Kestrels tended to store prey throughout the day, but retrieved it in the late afternoon. He concluded that such behaviour "may dampen daily variation in food availability for the diurnal-hunting Kestrel." This may also be a reason for food storage by Robins.

After storing food, Robins usually began hunting again unless an unusually large prey item was caught, partially eaten and the rest stored. When this was the case, storing was followed by preening and resting. By hunting throughout the day Robins could increase their food consumption by storing prey whenever an excess was captured. Late in the day they probably had to capture enough prey to meet their immediate physiological requirements as well as to sustain them during the night. Consequently, they tended to consume more of the prey captured in the late afternoon and recovered stored prey as well (Fig. 5.1). Also, some prey stored the previous day was available in the early morning to provide a quick source of food after the long night fast at a time when invertebrates were likely to be least active and therefore more difficult to detect.

Many species depend upon their ability to relocate stored food for survival and reproduction. Thick-billed Nutcrackers (Swanberg 1951) and Clark's Nutcrackers *Nucifraga columbiana* (Bock *et al.* 1973) both stored hazelnuts for consumption during winter and spring and for feeding to their young. Haftorn (1956c) showed that a Willow Tit population in Norway relied to a very great extent on stored food in the winter months. In Norwegian spruce forest, Haftorn (1953) concluded that up to about 60% of the food of Crested Tits in mid-winter consisted of stored seeds. Similarly, Robins found their stored food readily. On one occasion the mate of an incubating female collected food from five different sites in quick succession before taking all of it to her.

There are several reasons why storing food was advantageous to Robins. By not having a crop the amount of food they could ingest at a time was limited. Hoarding any surplus enabled them to eat it later, saving energy and time by not having to search for and capture prey when they were less readily available. Because of their highly territorial nature against conspecifics, except their mates, and several avian species the chances of other birds pirating their caches were low. By hunting again after caching, Robins may take advantage of temporary abundances of prey for consumption when prey is scarce. Small birds, such as Robins, have a high metabolic requirement which takes about 90% of the day in winter to satisfy (Figs 10.2 p. 150, 10.3 p. 152, 11.1 p. 189 and 11.2 p. 191). Therefore, during periods of adverse weather stored food could aid survival.

Although caching was not seen frequently during the breeding season because males fed most surplus prey to their mates and young, males were observed gathering stored food to feed their mates, especially during the first nesting cycle. At that time of year (August-September) long nights, cool temperatures and frequent inclement weather may sometimes prevent males maintaining a steady supply of food to the female, which she relied on for maximum attentiveness to the eggs and young nestlings. The proportion of eggs and nestlings abandoned was much higher early in the breeding season than afterwards. Presumably, nesting success would have been lower still early in the season if males had not taken advantage of temporary abundances of prey and used these sources to feed the females when prey was less readily available. Applegate (1977) found a similar situation in the Loggerhead Shrike where the female relied on her mate's hoarded food to maintain the degree of attentiveness necessary for successful incubation and brooding. Robins were the first passerines to begin breeding each year in Kowhai Bush and this may have been partly a consequence of the advantages conferred by storing food.

The Robin and its environment show some of the characteristics given by Roberts (1979) that have led to the evolution of food-storing in birds. Robins have generalized diets and foraging repertoires. In addition, they are strongly territorial against neighbouring Robins as well as some of the other avian species that inhabit the same area of forest. This trait helps storers to retain possession of stored items. Furthermore, Roberts considered that the environment should have seasonal pulses of durable particulate food items, followed by periods of relative food scarcity. These last two factors were not very evident in this study on a seasonal basis. However, it is possible that during the course of the day such changes in prey availability did occur. This may explain why the behaviour is present in Robins, even though they feed on invertebrates which decompose rapidly when stored. Since, perhaps for the Robin the periods of food abundance and scarcity take place over several hours, and at most a few days, the evolution of this trait would not be prevented by the relatively quick decomposition of invertebrates compared with seeds that remain edible months after being stored.

5.6. Summary

A description is given of the food-storing behaviour of the South Island Robin. They stored whole or portions of invertebrate prey. Nearly 70% of cached items were earthworms. Most items were stored in sites close to where they were found, often branch-trunk axils. Particular store sites were not used more than once and no attempt was made to conceal prey by covering it. Storing of food took place in most months of the year, but most frequently in autumn and winter. The average time taken to store an item was 24 seconds. The mean height of store sites (2.85 m) was significantly higher than the mean height at which Robins gleaned from vegetation (1.49 m). Robins tended to store food most often in the morning and retrieved it mainly after mid-afternoon. Most items were retrieved within three days. Stored food seemed to be surplus to the Robin's immediate requirements. However, time-budget results suggested that they stored prey when not satiated, as a source of readily available food for use during periods of food scarcity.

CHAPTER SIX

VOCALIZING BEHAVIOUR

6.1. Introduction

Early observers of the Robin were impressed by its loud song and ability to sustain it for many minutes. Potts (*in* Oliver 1955) wrote - "This bird as a songster is perhaps unequalled by any native warbler and we think scarcely surpassed by any of the woodland melodists of the old country." Moncrieff (1932) also noted the loudness of the song and wrote that the birds often used "chucking" calls. Calls associated with feeding the young were described by Soper (1976), who also mentioned an alarm note without defining it. Alspach (1973) described five types of Robin calls from birds studied in Mount Aspiring National Park. However, it was not until Hay's study (1975) that the species' full repertoire was described. Using sound spectrograms of songs and calls, Hay was able to distinguish full song, sub-song, and eighteen recognisable calls. Flack (1973, in prep.) and Hay (1975) described the context in which the songs and calls were given and noted the annual and diurnal cycle of some, but without quantitative information.

A quantitative description of the proportion of time Robins spent giving four vocalizations; full song, sub-song, "downscale" calls, and "chuck" calls, is given in this chapter. The description includes the proportion of time Robins devoted to each vocalization at different times of the year, periods of the day, and stages of the breeding cycle. In subsequent chapters, dealing with time-budgets, the time Robins spent giving the four types of songs and calls will be combined and described as "vocalization" behaviour.

6.2. Methods

Vocalizations were timed to the nearest second using a stopwatch. The time Robins spent giving short calls (< 3 sec.) was estimated as their brevity made timing with a stopwatch inaccurate. Each bout of full song involved several bursts separated by brief pauses. When measuring full song, the length of each burst was noted. The times for all bursts in a song were totalled to obtain song-bout length. To determine the incidence of full song and the "downscale" call on a wider basis than that based on the few birds followed each day, I noted whether these two vocalizations were heard during a period encompassing two minutes on either side of the hour each hour I was in the field.

Since the "downscale" call lasted only three to four seconds, I thought I may have underestimated its frequency by noting its occurrence over such a short period as four minutes. As a check I counted every "downscale" heard and compared the results of the two methods. Over several months both methods showed the same trend in the frequency of "downscales" and so the latter method was discontinued.

Robins gave full song from perches at all heights ranging from those low in the understorey to those high in the tallest trees in their territories. An estimate of the perch height from which full song was delivered was made.

Calls and phrases that were associated with a particular behaviour were timed as a portion of that activity and not as a vocalization. For example, both sexes gave phrases of song when trying to locate juveniles to feed them. These "feeding phrases" (Hay 1975) were not timed as such, but as feeding-progeny behaviour.

6.3. Glossary (From Hay 1975)

Call	Any syllable or series of syllables which subserve a specific communicatory function.
Frequency	Acoustic term meaning pitch. Measured in Hz. (cycles/ second).
Phrase	Any of a series of sound patterns, each comprising a series of identical syllables. The start or finish of a phrase is determined by a change to another phrase comprising a series of a different syllable type.
Song	A ritualized, relatively stereotyped vocalization given generally by male birds in breeding condition, primarily as a mate attraction and territorial signal.
Sub-song	A quiet, non-stereotyped form of song.
Syllable	A vocalization which will produce a continuous black marking on a sonagram.

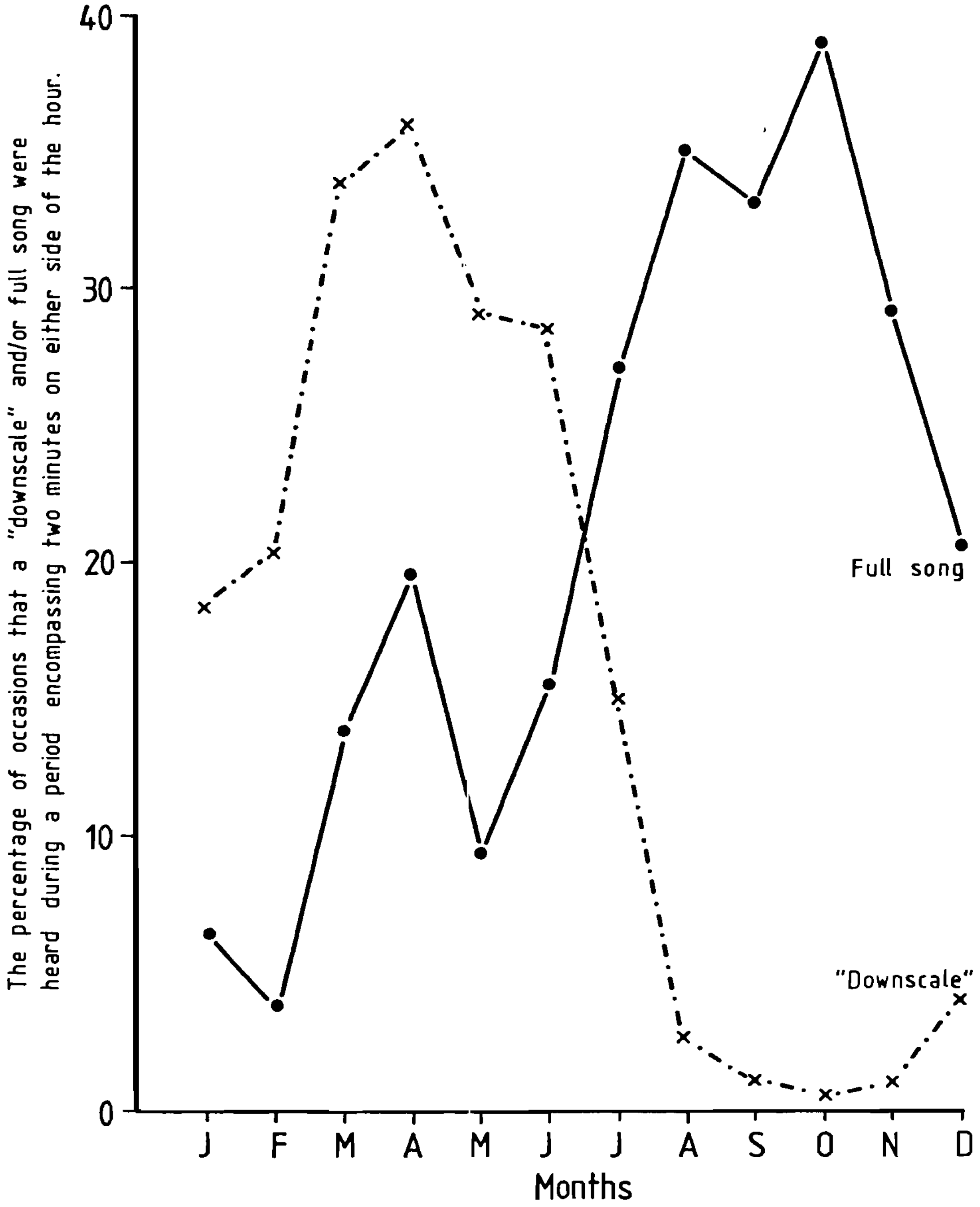


Figure 6.1 The annual cycle of full song and "downscale" calls given by Robins during a four minute period encompassing two minutes on either side of the hour. The results are for data collected from August 1976 to July 1978.

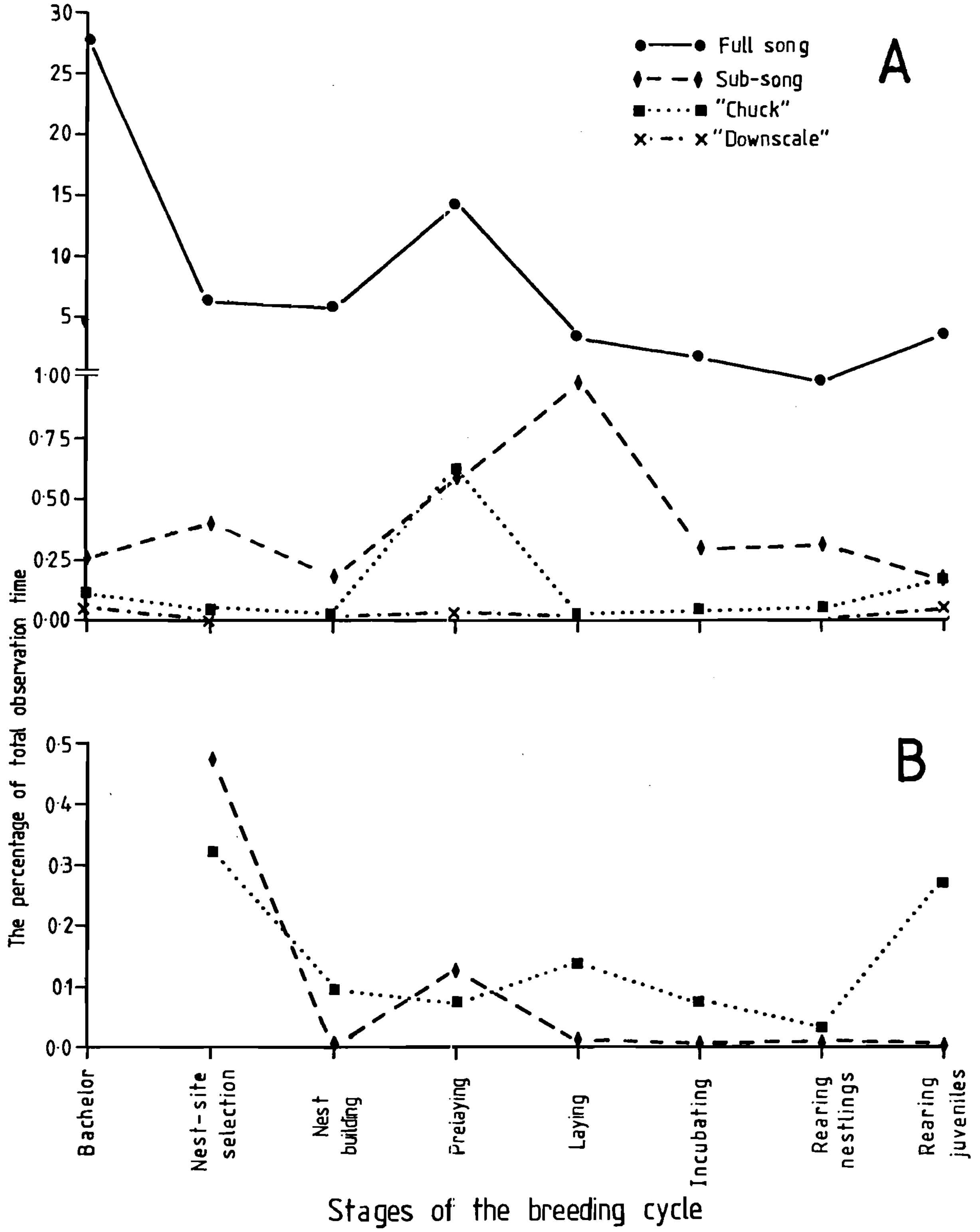


Figure 6·2 The percentage of observation time that male [A] and female [B] Robins spent giving four types of vocalizations during the stages of the breeding cycle.

The results were from the combined observations made during the 1976,1977 and 1978 breeding seasons.

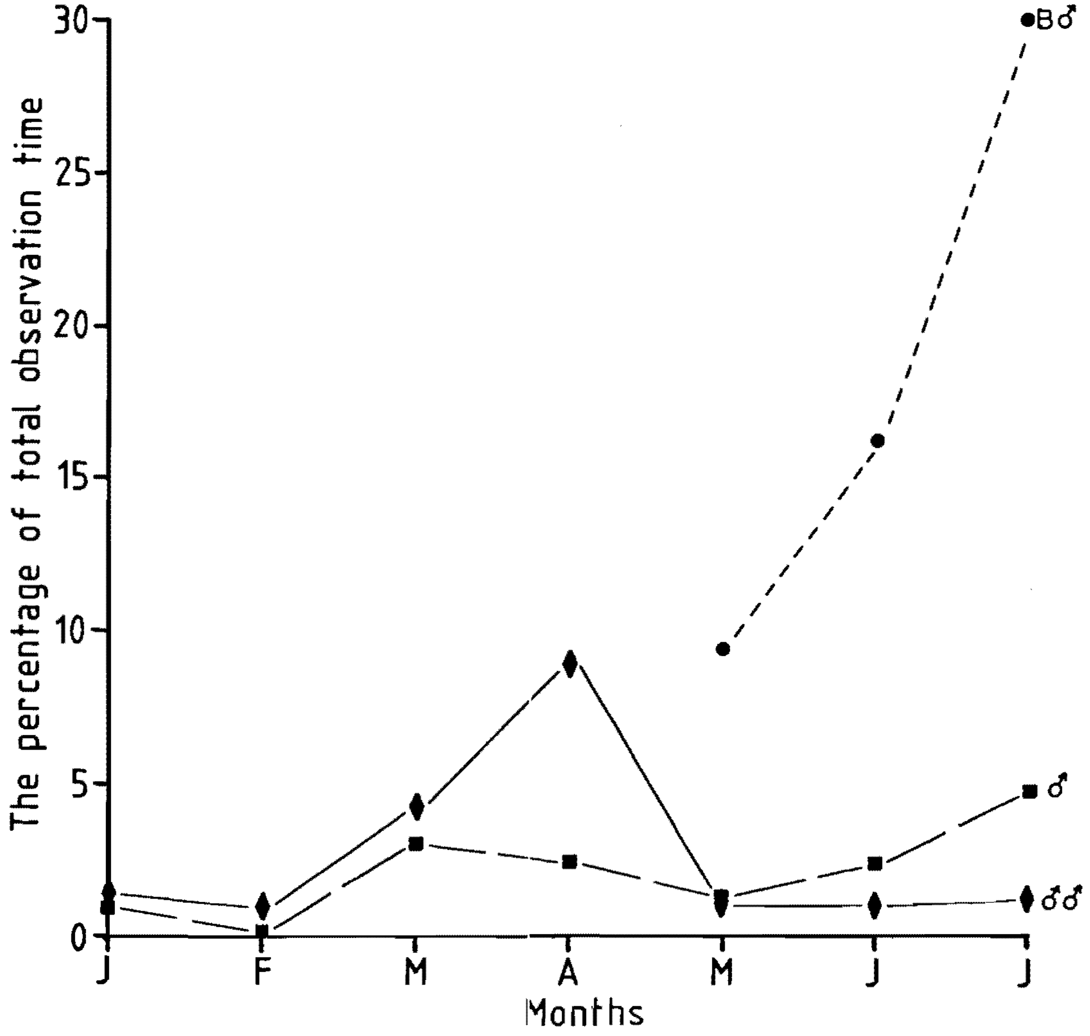


Figure 6·3 The monthly percentage of observation time that male Robins gave full song during the non-breeding season.

♂♂ - adult males, ♂ - immature males, B♂ - bachelors.

6.4. Results

6.4.1. Full song

"Full song is typically a series of phrases, each consisting of a number of identical syllables uttered in a non-random sequence" conforming to a third-order Markov chain (Hay 1975). Hay (1975) identified 114 syllable types for the Kowhai Bush population, but individual males had a repertoire of 19 to 36.

Females were never heard in full song (Table 6.1). Full song was heard during all months (Fig. 6.1), but was less frequently heard in January and February when the moult took place. After March, when most males had renewed their feathers, except for some primaries and secondaries, the frequency of full song increased gradually until May. During May the frequency declined, but afterwards increased again reaching a peak in October.

Table 6.1. The percentage of observation time that Robins spent giving four types of vocalizations in the non-breeding season.

	Vocalizations				
Status of Robins	Full song	Sub-song	"Down-scale"	"Chuck"	Observation time (h)
Adult male	2.97	0.74	0.13	0.18	256.0
Immature male	2.17	0.35	0.12	0.17	120.2
Adult female	-	0.09	0.03	0.05	193.2
Immature female	-	0.11	0.03	0.09	150.2

In the breeding season, the proportion of time spent singing varied according to the stage of the breeding cycle males had reached (Fig. 6.2A). Bachelors, with no involvement in breeding, sang more than did paired males at any stage ($P < 0.01$). Breeding males sang most often during the prelaying stage, but only infrequently once the nest contained eggs or nestlings.

Outside the breeding season, adult males spent more time singing than did immature males ($P < 0.05$) (Table 6.1). However, from Figure 6.3 it is apparent that adult males spent significantly more time singing than did immature males in February and April, but significantly less in

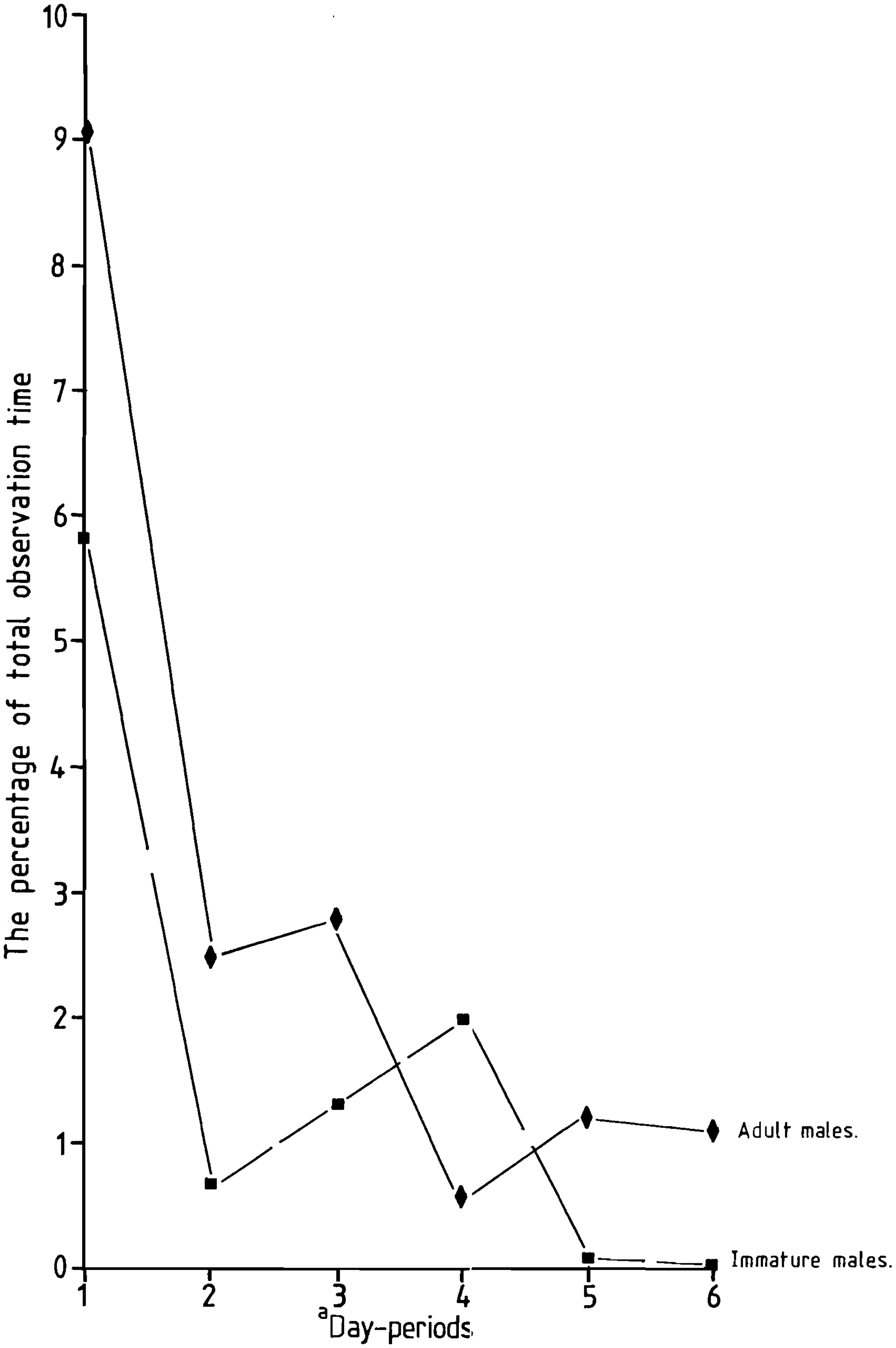


Figure 6·4 The diurnal patterns of full song given by male Robins during the non-breeding season.

[a]The division of the daylight hours into six equal-lengthed day-periods.

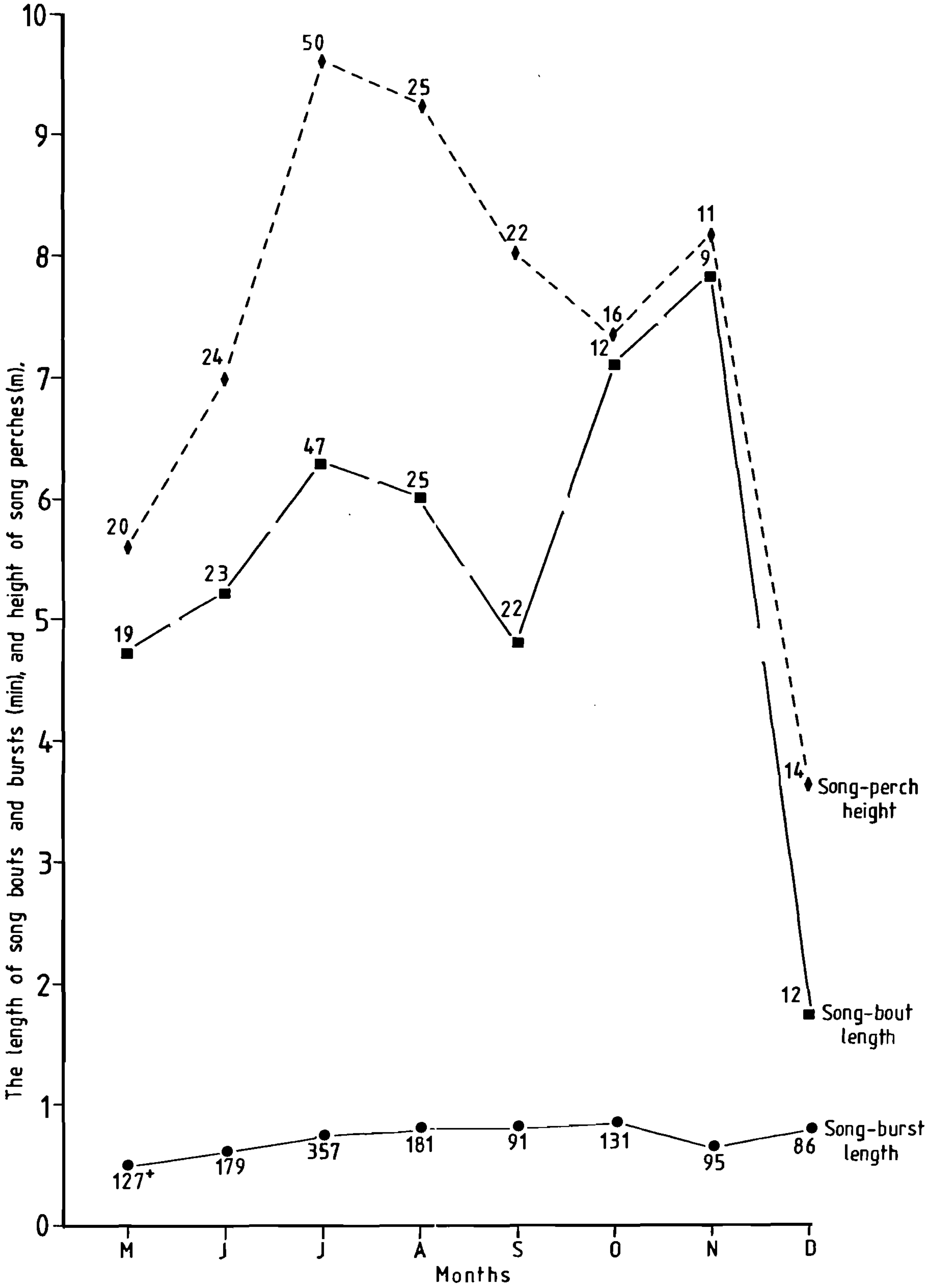


Figure 6.5 The monthly mean lengths of song-bouts and song-bursts, and mean heights of song-perches for bachelors. The results presented were from observations made from May to December 1977 and May to July 1978.

+ Figures indicate samples sizes.

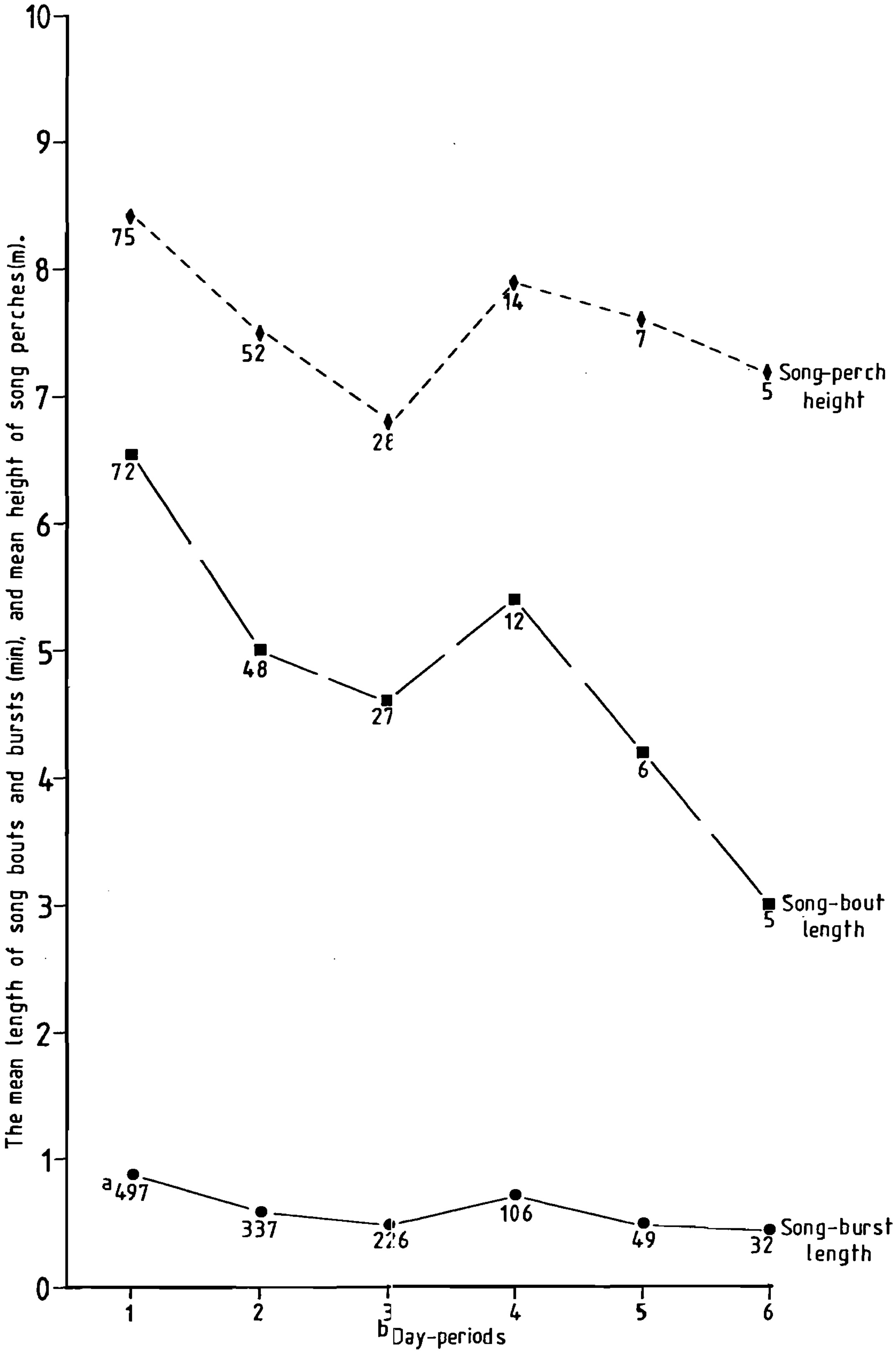


Figure 6.6 The diurnal patterns of song-bout and song-burst length (min), and song-perch height (m) for bachelors. The results were for the pooled data from observations made during May to December 1977 and May to July 1978.

[a] Figures indicate sample sizes.

[b] The division of the daylight hours into six equal-lengthed day-periods.

June and July. Both categories of paired males (adult and immature) spent significantly less time singing than did bachelors after April (Fig. 6.3).

On a diurnal basis, the time spent singing in the non-breeding season was highest during the early morning (Fig. 6.4), with a significant decrease in mid-morning recorded for both categories of males. For each day-period the two categories of males spent significantly different percentages of time singing. Adult males sang more than did immature males during all day-periods, except in the early afternoon.

Because bachelors sang frequently (about 55 songs of 4.7 minutes duration per day during the 1977 breeding season), their songs were timed to compare mean song-bout and burst lengths and the mean height of song perches on a monthly (Fig. 6.5) and diurnal basis (Fig. 6.6). The monthly changes in mean song-burst length were not significantly different (Fig. 6.5). Mean song-bout length increased to July, declined during August and September, then increased until November. None of these monthly changes were statistically significant, but songs sung in December were shorter ($P < 0.001$) than were those of the previous month (Fig. 6.5). The monthly mean height of song perches used by bachelor Robins increased to July, significantly ($P < 0.01$) so from June to July, then declined until October. From November to December mean song-perch height decreased significantly ($P < 0.001$) (Fig. 6.5).

The same diurnal trends were apparent for mean song-bout and burst lengths and mean song-perch heights (Fig. 6.6). The three variables were greatest in the early morning, with a gradual decline during the course of the day, except for an increase in the early afternoon. From one day-period to the next, song-perch height did not change significantly. Song-bout length decreased from the early morning to mid-morning ($P < 0.05$), as did song-burst length, and the latter increased during the early afternoon ($P < 0.01$).

6.4.2. "Downscale" call

The "downscale" call was a series of very loud "chucks" (syllables with a short period and a large frequency range) descending in frequency which started in rapid succession and finished slowly (Flack in prep.). Because of the rather constant length of this call (three to four seconds) regardless of the sex and status of the caller, the differing amounts of

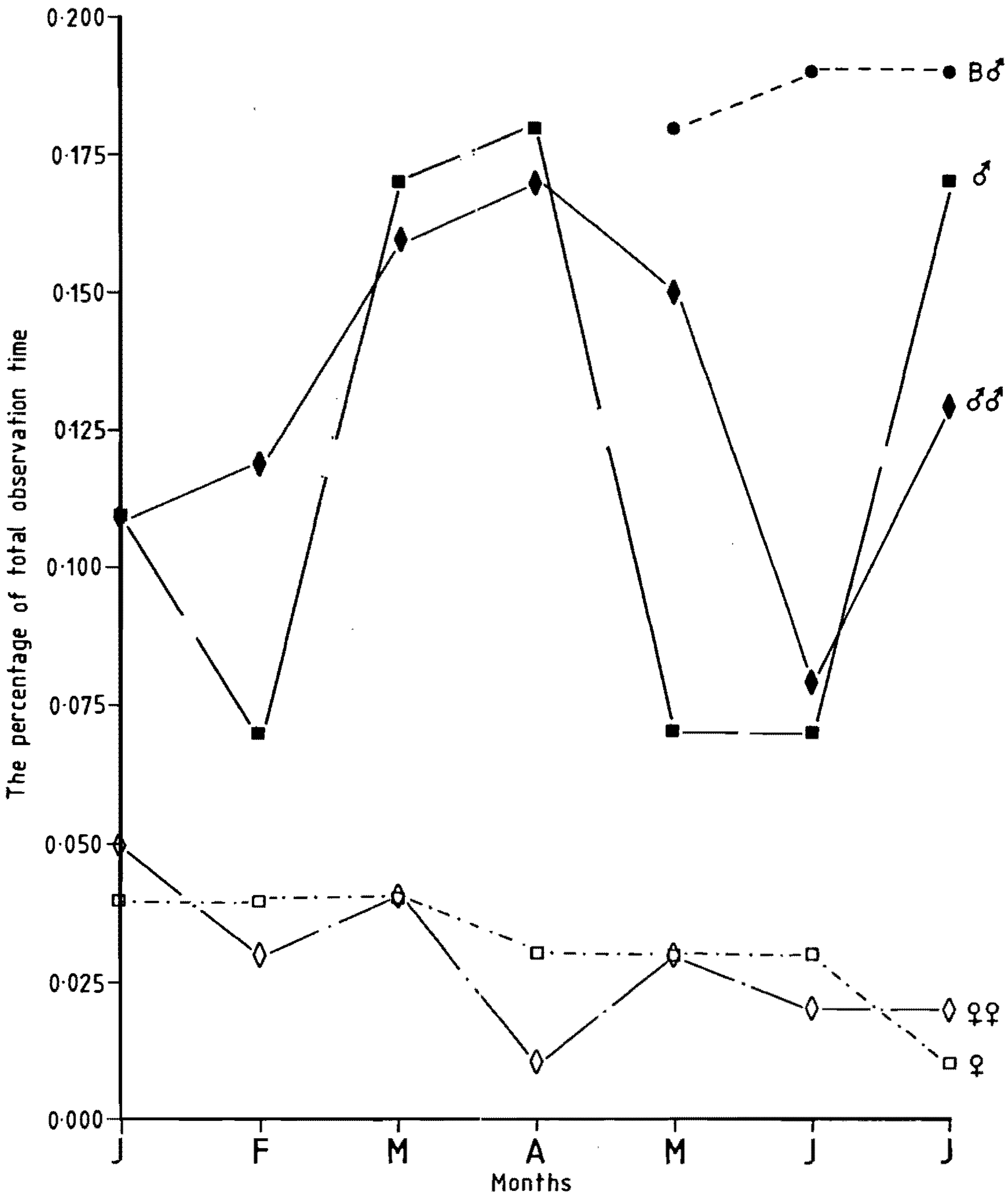


Figure 6·7 The percentage of monthly observation time five categories of Robins spent "downscale" calling during the non-breeding season.

♂♂ - adult males, ♂ - immature males, B♂ - bachelors
♀♀ - adult females, ♀ - immature females.

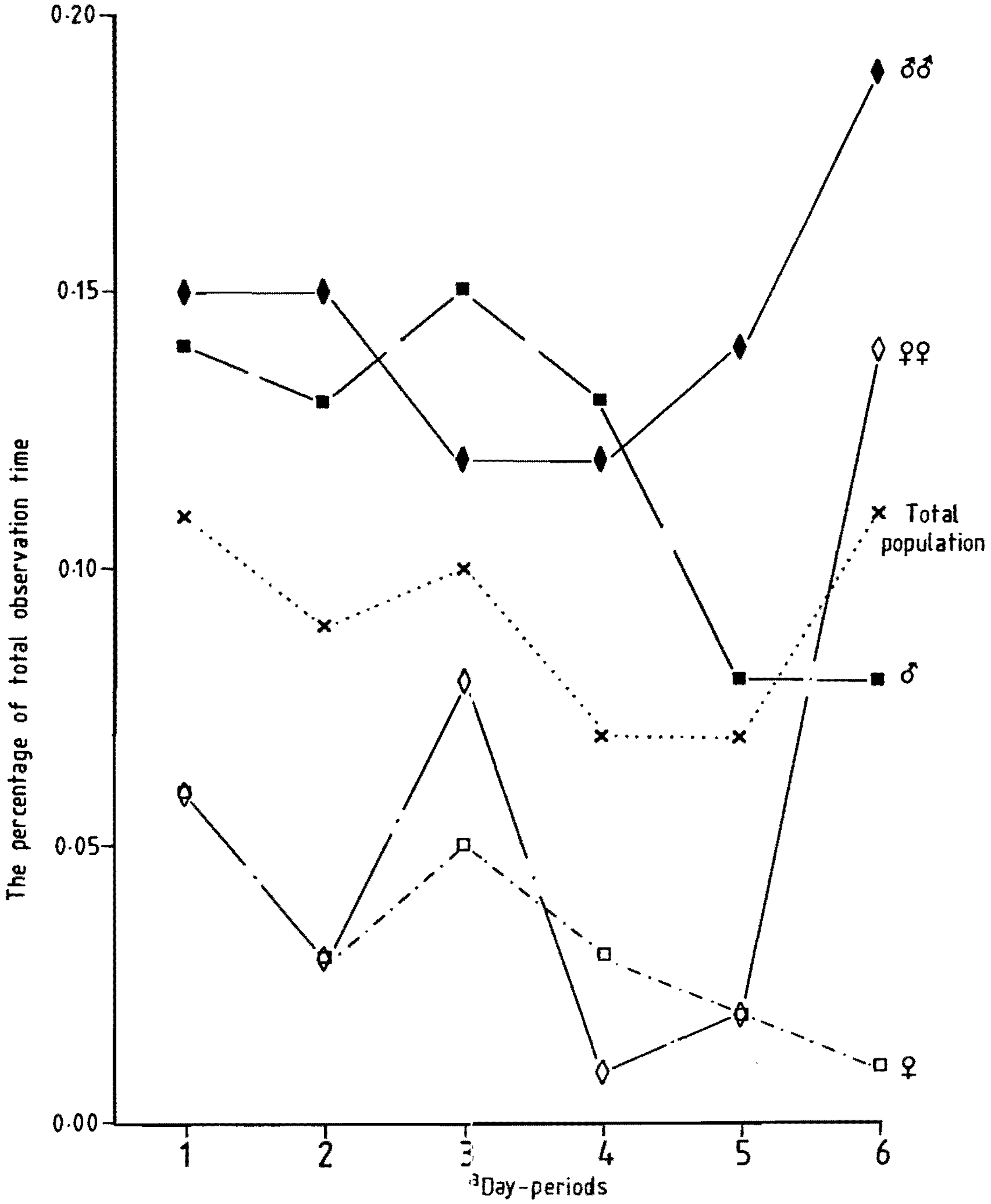


Figure 6·8 The diurnal patterns of the "downscale" call given by four categories of Robins and the total population during the non-breeding season.

♂♂ - adult males, ♂ - immature males,

♀♀ - adult females, ♀ - immature females.

ªThe division of the daylight hours into six equal-lengthed day-periods.

time devoted to it on a monthly and a diurnal basis were a good indication of its frequency. As also noted by Hay (1975), "downscales" were usually given by solitary birds, were never repeated immediately, but were given several times per hour.

For 24% of the 273 times "downscales" were heard, the partner responded with a "downscale" and/or moved towards its mate; a partner-interaction (Section 8.3.1, p. 115). Sometimes the female "chucked" in response to her mate's "downscale". Twenty-seven percent of occasions involved an intraspecific reaction: either a neighbour responded to the "downscale" by moving towards the caller or gave an answering call, a "downscale" was given while a neighbour was singing, or the call was given by a Robin engaged in a boundary dispute. Of the remaining occasions (49%), "downscales" did not seem to elicit a response, nor were they caused by any obvious stimuli.

"Downscales" were heard most frequently outside the breeding season (Fig. 6.1). During the breeding season they mainly came from bachelor (Fig. 6.2A) and juvenile Robins. Paired males occasionally gave these calls during the early and late stages of the breeding cycle (Fig. 6.2A), but females used it so rarely that it accounted for less than 0.01% of their time-budget.

Table 6.1 shows that there was little difference in the time devoted to "downscale" calling by males of the two age classes. The same is true of the two classes of females. However, males spent more time calling than did females ($P < 0.05$). Month by month during the non-breeding season, adult and immature Robins of the same sex spent statistically similar proportions of time giving "downscale" calls (Fig. 6.7). Females spent gradually less time calling, but males increased the frequency of calling until April, called infrequently in May and June, and then increased the frequency just before breeding. Combined data of the two age categories for each sex, excluding bachelors, showed that males spent significantly more time calling than did females in April and July. From May to July, bachelors spent a similar time calling in contrast to paired males (Fig. 6.7).

Figure 6.8 shows the diurnal pattern of "downscale" calling by Robins outside the breeding season. Statistically there was no difference in the percentage of time spent calling per day-period when data for the immature sexes were compared. The same is true of the two sexes of adult Robins. Furthermore, when the results for the adult birds were

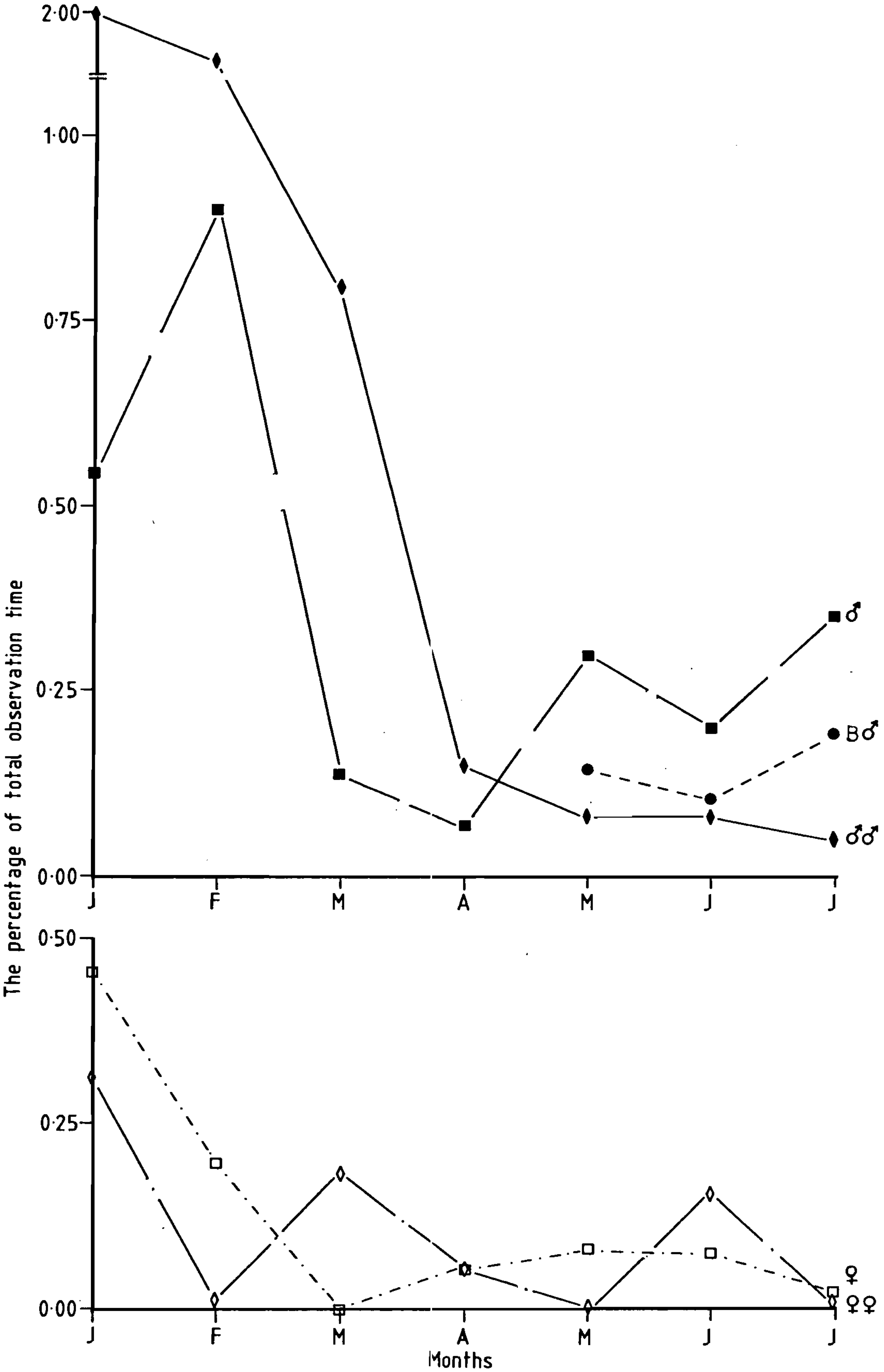


Figure 6·9 The percentage of monthly observation time Robins spent giving sub-song during the non-breeding season.

♂♂ - adult males, ♂ - immature males, B♂ - bachelors
♀♀ - adult females, ♀ - immature females.

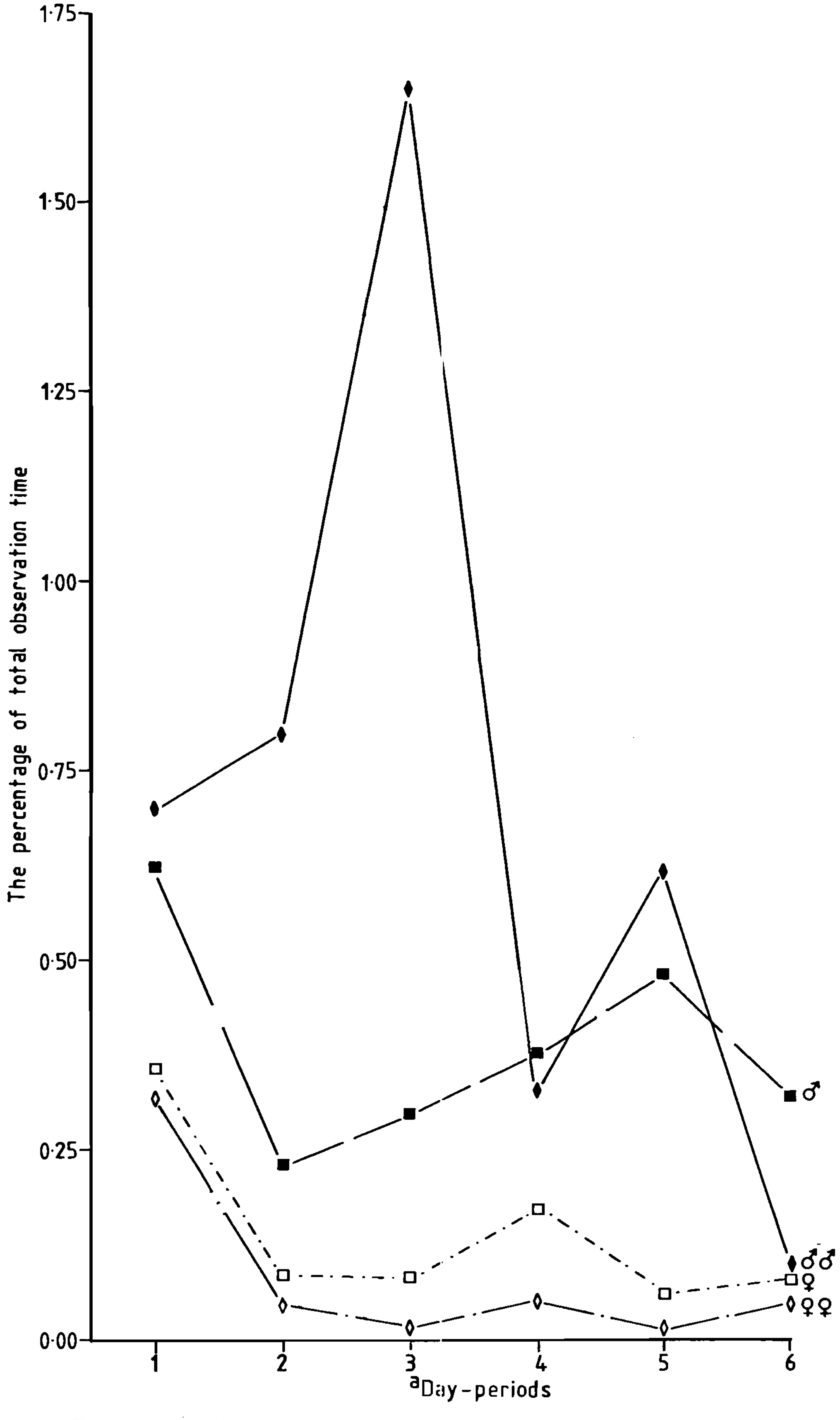


Figure 6·10 The diurnal patterns of sub-song given by four categories of Robins during the non-breeding season.

♂♂- adult males, ♂-immature males,

♀♀- adult females, ♀-immature females.

^{a}The division of the day-light hours into six equal-lengthed day-periods.

pooled and compared with those for the immatures, no difference in the proportion of time devoted to "downscale" calling was present for the same day-period. Therefore, data for all Robin categories were combined for each day-period to give the points labelled "total population" in Figure 6.8. No significant change in the percentage of time spent on "downscale" calling from one day-period to the next was apparent for the "total population" data. The frequency of calling was highest at the start and end of the day, and lowest during the early and mid-afternoon.

6.4.3. Sub-song

Early observers of Robins made no mention of sub-song, probably because of its very low volume. Hay (1975) defined it as "a quiet, non-stereotyped form of song", because the syllables and phrases were given randomly, in contrast to their ordered arrangement in full song. Sub-song was usually sung quietly by solitary birds and so it did not seem to be directed at another individual.

Males were rarely heard to produce sub-song when breeding, except while involved in the prelaying and laying stages (Fig. 6.2A). For females, the time spent giving sub-song during the breeding cycle differed from that for males (Fig. 6.2B), being greatest when selecting a nest-site.

Table 6.1 shows that during the non-breeding season adult males spent more time giving sub-song than did immature males ($P < 0.05$). Both age classes of female Robins spent similar percentages of time in this activity, but less than did immature and adult males ($P < 0.05$). For all categories of Robins, the proportion of time devoted to sub-song was greatest during the months of the moult (Fig. 6.9). As a portion of their time-budgets, sub-song fell to a low level by April. By the start of breeding, adult paired Robins and immature females spent even less time giving this vocalization, whereas with immature males sub-song increased. The difference in the proportion of time spent giving sub-song between adult and immature males was significant only in January and March (Fig. 6.9). In March, adult females spent more time in this activity than did immature females ($P < 0.05$).

The diurnal pattern of sub-song production was bimodal (Fig. 6.10). Except for adult males, the rest generally produced most sub-song during the early morning and early afternoon. The diurnal peaks of time

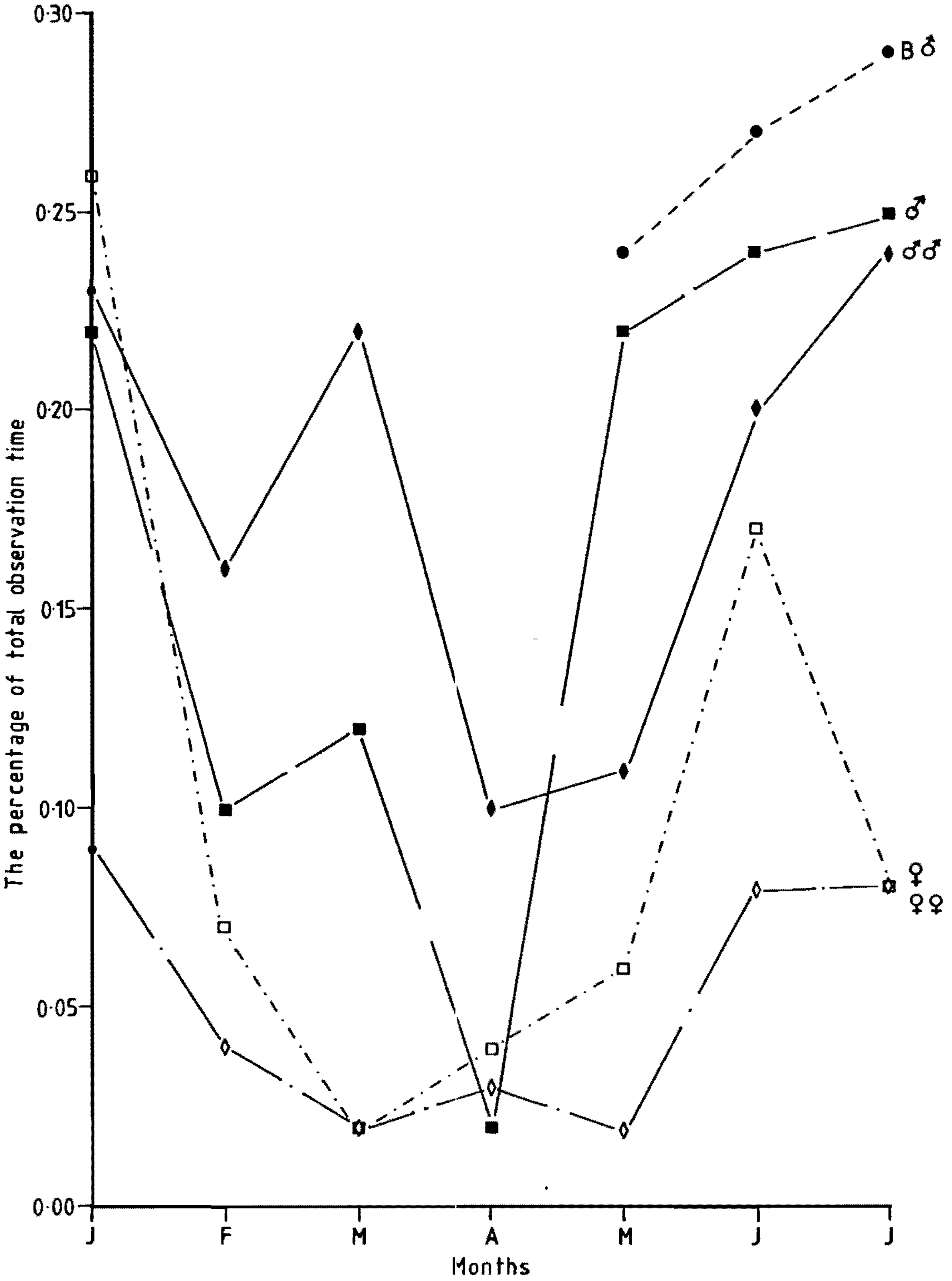


Figure 6·11 The monthly percentage of observation time Robins "chucked" during the non-breeding season.

♂♂ - adult males, ♂ - immature males, B♂ - bachelors,
♀♀ - adult females, ♀ - immature females.

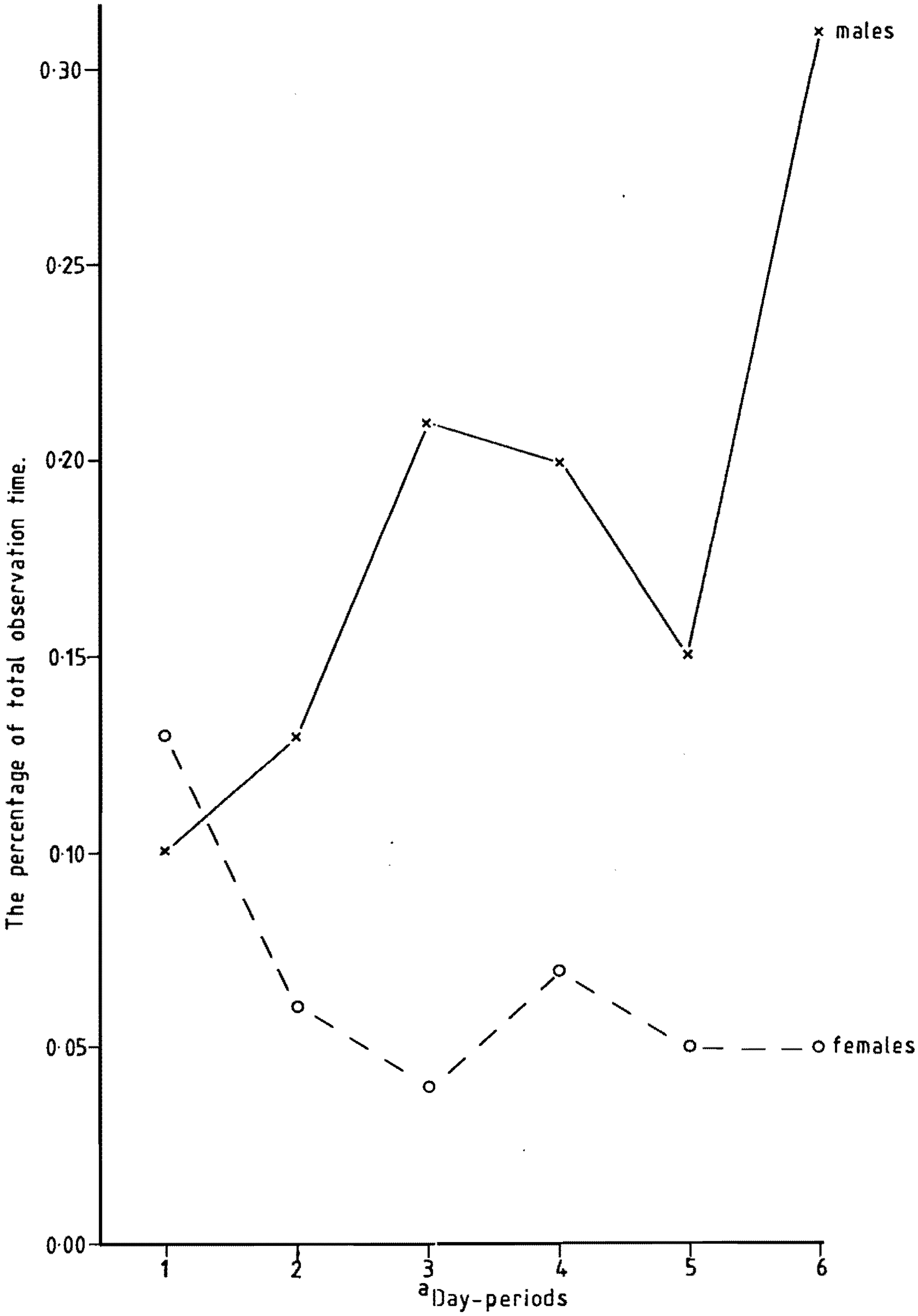


Figure 6·12 The diurnal patterns of "chucking" for male and female Robins during the non-breeding season.

a The division of the daylight hours into six equal-lengthed day-periods.

devoted to sub-song by adult males occurred during the late morning and mid-afternoon. There was no difference in the proportion of time that females of the two age classes spent giving sub-song during each day-period. However, adult males spent significantly more time in this activity from mid- to late morning than did immature males.

6.4.4. "Chuck" calls

By using sound spectrograms, Hay (1975) showed that "chucks" were syllables with a short period and a large frequency range. They were given as individual syllables or groups of syllables, and were the most commonly heard sounds, being used in many situations and in a variety of forms. The sounds timed as "chucks" during this study included only those which had no obvious context. For example, Robins gave loud staccato "chucks" in response to predators, a behaviour which was categorised as an interspecific interaction. Most timed "chucks" seemed to be "contact chucks" (Hay 1975), a quiet call usually of one syllable given by foraging birds when out of sight of other birds.

During the breeding season, males spent very little time "chucking", except in the prelaying stage and while rearing juveniles (Fig. 6.2). Females also spent an increased time "chucking" when rearing juveniles, as well as while selecting the nest-site.

During the non-breeding season, immature and adult Robins of the same sex spent a similar time "chucking", but males spent more time giving this call than did females ($P < 0.05$) (Table 6.1). On a monthly basis (Fig. 6.11), the proportion of time spent "chucking" generally decreased from January to April, after which it increased until nesting. A comparison of the monthly percentages of time devoted to this activity by immature and adult males revealed no statistical differences (Fig. 6.11). Furthermore, immature and adult females "chucked" for similar proportions of time during each month. Only in March of the non-breeding season did males spend more time "chucking" than did females ($P < 0.05$) (Fig. 6.11).

Statistical analysis showed that male Robins of both age classes devoted a similar time to "chucking" during each day-period. The same was true of the two classes of females. Therefore, data for the two age classes of each sex were combined and presented in Figure 6.12. The diurnal pattern of "chucking" by the two sexes was quite different.

Males "chucked" to the greatest extent in the afternoon, but females "chucked" most frequently in the early morning. Males spent significantly more time calling than did females during the late morning and late afternoon.

6.4.5. A comparison of the vocal behaviour of Outer Chetwode Island and Kowhai Bush adult males

Table 6.2 shows a comparison of the time adult males on Outer Chetwode Island and at Kowhai Bush devoted to the four vocalizations. No full song was heard throughout the three visits to the island. Males on the island spent less time giving each of the other three vocalizations than did their mainland counterparts, but these differences were not statistically significant.

Table 6.2. A comparison of the proportion of observation time that adult males on Outer Chetwode Island and at Kowhai Bush spent giving four types of vocalizations during April to June 1978.

	Vocalizations				
Population	Full song	Sub-song	"Down-scale"	"Chuck"	Observation time (h)
Kowhai Bush:	7.74	0.13	0.18	0.11	54.3
Outer Chetwode Island:	0.00	0.09	0.05	0.08	62.9

6.5. Discussion

6.5.1. Full song

As noted by Flack (in prep.) and Hay (1975), full song was heard each month at Kowhai Bush, but very little full song was heard during the post-breeding moult. South Island Robins around Nelson were also quieter in January when moulting (Fleming 1950). Similarly, Cunningham (1955) noted that Grey Warblers and Song Thrushes *Turdus philomelos* sang least of all while moulting, as did Bissett (1978) and Gibb (1961) in studies of Pied Tits. During the early months of the moult (January-February), adult male Robins usually gave full song only after a boundary dispute.

The high frequency of full song heard in the breeding season was accounted for largely by the regular singing of bachelors. Flack (in prep.) and Hay (1975) noted this behaviour of bachelors, as have other investigators for many species (Bissett 1978, Frankel and Baskett 1961, Howard 1920, Mountfort 1935, Thompson 1972). Once a bachelor acquired a mate he abruptly stopped singing regularly, implying that his singing was mainly to attract a female.

Paired males spent little time singing when breeding and mainly sang after a boundary dispute or in response to a neighbour's song. Therefore, for these individuals, singing probably functioned mainly to proclaim ownership and defence of their territories. During the prelaying stage, males increased the proportion of time spent singing because they had "spare" time; these males foraged less ($P < 0.01$) and made fewer food-trips per hour to their partners than during the previous stage (Section 14.3, p. 243). Copulations seen in the breeding season usually took place during the prelaying stage and so full song may function to "bring the female to the same state of sexual excitement as in the male" (Dorst 1974). "The male generally assumes a fully reproductive state before the female, and the final timing of oviposition then depends on the female receiving the appropriate stimuli, both from her mate and the environment. The appropriate habitat and inter-pair displays are often essential to stimulate final oocyte development, ovulation, and insemination" (Lofts and Murton 1973). The slight increase in singing by males feeding juveniles resulted for the same reasons as discussed above; females usually began another clutch while the male raised the juveniles of the previous brood.

Two factors probably contributed to males of both age classes singing less while moulting than during the rest of the year. First, from Poulsen's work (1951) with Chaffinches, and Herrick and Harris' (1957) with Canaries *Serinus canarius*, it is known that full song production is partly dependent on the level of male hormone, testosterone, in the blood. This hormone is produced by interstitial cells, or cells of Leydig, which lie between the tubules of each testis (Welty 1975). With the regression of the interstitial cells after breeding in Green-winged Teal *Anas crecca* their hormone secretion stopped (Lofts and Murton 1973). Therefore, this lack of hormone production may account for the cessation of regular full song singing by Robins. Second, the moult is a period when birds require more food to meet the high protein demands of feather growth (Newton 1968) and the high energy needs of an increased metabolic rate

(Lustick 1970, Thompson and Boag 1976). Thus, males may have been forced to sing less in order to find sufficient food. Immature males sang less than did adult males, probably because the former spent more time foraging ($P < 0.01$) (Section 10.3.1, p. 148).

A steady increase in the frequency of song was heard after February, because both immature and adult males spent more time singing having completed the major portion of their feather replacement by then. However, during May the proportion of time devoted to full song declined when the formation and/or reinforcement of pair-bonds took place. Similarly, Bissett (1978) found that the frequency of song given by Pied Tits declined when pair formation took place. Paired female Robins reduced the time their mates sang by flying up near them and "chucking". Males responded by stopping singing and either gave the submissive "butterfly-flight" display (Section 8.3.1, p. 115) or moved towards their mates with their crown feathers raised, an aggressive posture. This behaviour on the part of the female continued for the rest of the non-breeding season so that after May, paired adult males spent little time singing. Immature paired males, however, spent more time giving full song than did their adult counterparts after May, possibly because the pair-bonds they formed were weaker than those of adult pairs which often had been paired with the same mate during the previous breeding season. Another reason may have been that immatures had to spend more time singing to learn the song syllables and phrases of their nearest neighbours. Each immature male had a song which was modified and elaborated by introducing new syllables and dropping some from its repertoire making it similar to those of its nearest neighbours (Hay 1975). When establishing a territory, immature males modified their song patterns by counter-singing with their neighbours which may have necessitated such immatures spending more time singing than did adult males. The selective advantage of singing a song like that of neighbours would be to facilitate recognition. Several workers have shown that some species can recognise their neighbours' songs (Brooks and Falls 1975, Emlen 1971, Goldman 1973). As partial support of this ability in Robins, Hay (1975) found from playback experiments of full song that the Kowhai Bush males responded strongly to song from their own population, but only weakly to song from the Outer Chetwode Island population. By singing a song that was recognised by neighbouring males, Robins may have had to expend less time and energy defending their territories against intruders. Evidence that full song helps to prevent intrusions was shown by Krebs (1977b) who found that trespassing Great Tits *Parus major* initially retreated when challenged by the song of a resident bird, even though the latter was not in sight.

Male Robins spent most time on singing early in the morning and decreased the amount as the day progressed. Indigo Buntings *Passerina cyanea* had a similar diurnal pattern of singing (Thompson 1972). However, Bissett (1978) and Gibb (1961), who studied the Pied Tit, another member of the genus *Petroica*, found that this species sang most frequently around midday. As well as individual male Robins spending more time singing in the morning, a greater proportion of males sang early in the day than later. Although a dawn chorus was not often heard at Kowhai Bush, M. Shephard (pers. comm. *in* Hay 1975) noted the existence of such a chorus on Outer Chetwode Island. Three bachelors and a paired male with contiguous territories were heard singing simultaneously during the early morning at Kowhai Bush. Such an occurrence was almost certainly a consequence of the fact that several bachelors lived next to each other and the singing of one prompted the others to do likewise.

There are several possible reasons why Robins spent more time singing at dawn than later in the day. Kacelnik (1979) investigated the influence of light intensities at the time of the dawn chorus on the food-searching efficiency of captive Great Tits. He showed that the birds' foraging efficiency was limited by light intensity for over one and a half hours after the onset of their activity on sunny days. In addition, the time the birds spent in foraging matched the profitability under experimental conditions. Thus, the poor profitability of foraging at dawn favoured the birds doing non-foraging activities then, such as singing. Poikilothermic invertebrates, the Robin's main prey, may be least active and therefore harder to locate early in the morning so that time would be more efficiently spent engaged in activities such as singing. The activity of birds was higher in the morning than at any other time (Aschoff 1967, Kacelnik 1979), and intrusions by male Great Tits attempting to establish territories, amongst those already being actively defended, were more frequent in the morning (Krebs and Perrins 1977), perhaps making song more important at dawn so as to deter potential trespassers. Also, "the pronounced effects of temperature gradients, wind gradients and atmospheric turbulence on the propagation of sound favours acoustic communication at times of the day and under weather conditions that permit most effective transmission" (Wiley and Richards 1978). Because of reduced turbulence and temperature gradients early in the morning, sounds are likely to be less attenuated (i.e. reach greater distances) when produced at that time. Thus, there is an intrinsic advantage for acoustic communication at dawn (Kacelnik 1979, Wiley and Richards 1978). Possibly, some male Robins were able to spend much of the early morning singing because they retrieved food they had stored the previous day (Section 5.4, p. 52).

Song-burst length did not change significantly from month to month so that Robins varied the length of song-bouts by singing fewer bursts. Possibly, the increase in song-bout length from May to November was caused by the bachelor's increased hormone secretion from the interstitial cells as well as greater food abundance, warmer temperatures, and longer day-lengths allowing them to spend more time in singing. Lofts and Murton (1966) found an interrelationship between the role of weather, food and biological factors on the sexual cycle of Woodpigeons *Columba palumbus*. The abrupt decline in song-bout length in December for Robins may have been related to an autonomous postnuptial regression of the testes and interstitial cells resulting in the cessation of hormone production and the commencement of the moult. That such an autonomous rhythm can exist has been shown by Lofts (1964) with African Weaver Finch *Quelea quelea* kept under an unvarying 12 hour photoperiod and thermostatically controlled temperature for 2.5 years. Under these conditions, males showed a seasonal testicular development and postnuptial regression similar to that observed in wild populations.

The slight decrease in song-bout length that arose during September 1977 seemed to be related to the lower temperature of that month compared to that for August (Table 3.1, p. 20). Verbeek (1964) showed an inverse relationship between environmental temperature and the proportion of time Brewer's Blackbirds *Euphagus cyanocephalus* spent feeding in winter. Possibly, the reduced temperature in September necessitated bachelor Robins reducing the time spent on singing so as to spend more time feeding to meet the higher maintenance energy demands at colder temperatures. Also that: "temperature is perhaps the most important modifier of the testicular cycle" (Farner and Wilson 1957) while the testes are developing after the quiescent regeneration phase was demonstrated experimentally by Farner and Wilson (1957) using White-crowned Sparrows and by Lofts and Murton (1966) from field data on Woodpigeons. Therefore, the lower temperature in September may have reduced the time spent singing by bachelors by reducing the hormone secretion from their interstitial cells.

Mean song-perch height showed a monthly trend similar to that for song-bout length. Therefore, the hormonal control of singing may also have influenced the height from which Robins sang. The value to a bachelor of singing higher in the canopy was the greater range over which his voice would be heard and his increased conspicuousness to unpaired females (Howard 1920, Morton 1975). Although Robins rarely ventured into open areas, bachelors usually sang in the top-most branches of the highest trees in their territories. Fleming (1950) and Oliver (1955) noted this behaviour of the North Island Robin, but Wilkinson and Wilkinson (1952) described the same species on Kapiti Island as always singing from a perch fairly close to the ground and never from an exposed branch.

The three variables, song-bout and burst length, and song-perch height, showed similar diurnal trends. Presumably, when males spent the greatest time singing per day-period in the early morning, the motivation was also greatest to sing higher in the trees. The increase in all three variables during the early afternoon was probably related to the daily bimodal pattern of feeding. Bachelors in the breeding season foraged less around midday than at other times of the day (Fig. 13.2, p. 233), so that more time would have been available for singing resulting in the song-bouts and bursts being longer and song-perches higher.

6.5.2. "Downscale" call

Like Hay (1975), I found that about half of the "downscales" were followed by no obvious response from the caller or other Robins. Of the remainder, approximately half were associated with interactions between members of a pair and half with territorial defence. Hay (1975) noted a "tendency for birds to move to another area immediately following this call", but my observations showed that these movements were towards their mates or neighbours.

Both Flack (1973) and Hay (1975) noted that the "downscale" was uttered most frequently while Robins were moulting and continued to be heard regularly until breeding began (Fig. 6.1). During the moult little full song was heard, the birds tended to be less territorial, and were ineffective when they tried to oust intruders. My impression was that moulting paired Robins tended to forage apart, instead of near each other, as they had done while breeding. Therefore, "downscale" calls possibly functioned to maintain contact between paired Robins and to advertise territorial possession. The call was well suited to serve these purposes as its loudness and short duration gave clues to location. Hay (1975) found that the call was variable between individuals and proposed that this allowed for individual recognition, an important feature for communicating territorial possession between neighbouring birds. Several observations support this suggestion of the "downscales" functions. A male continually gave "downscales" about every minute or two whenever his newly-acquired mate moved out of sight. She eventually responded to his calls by moving towards him, whereupon the male immediately stopped calling. A female that began nest-building in mid-July often "downscaled" as she left the nest whenever her mate had not brought her food for a while. Another female whose mate disappeared while she was incubating always "downscaled" as she left the nest in search of food. This calling only stopped when a neighbouring bachelor began supplying her with food. The territorial function of the call was evident because males often "downscaled" when involved in boundary disputes during the non-breeding season. Furthermore, males used the call more often than did females - to be expected for a species in which males carried out most of the territorial defence.

During the breeding season "downscales" were rarely heard, possibly since the call could give clues to location of the birds and therefore the vicinity of the nest to predators. In general, most birds reduce the amount of singing and calling once breeding begins (Howard 1920). Also while breeding, male Robins probably used full song to ward off intruders and once the nest-site was chosen, "downscales" presumably were not needed to maintain contact between the pair because the female usually remained in the nest's vicinity. Most "downscales" heard during the breeding season were given by bachelors, juveniles to maintain contact with their parents (Hay 1975), and immature birds reared early in the season. All these Robins were good fliers so that there was little chance of a predator using the call to track them down, compared to a nestling if it gave such a call.

Females gradually devoted less time to calling as the non-breeding season progressed, possibly because after the pair-bond had been formed the birds spent more time near each other so that frequent calling was not needed to maintain contact. Males spent the largest percentage of time "downscale" calling in April. This was the month when they ousted any immature males that had set up sub-territories encroaching on their own territories, and when the pair-bond was formed or reinforced. Because males always spent a greater proportion of time each month giving "downscales" than did females it seemed that this call was used by males mainly to advertise territorial possession. The reduction of time spent calling during May and June presumably arose because males had by then re-established their boundaries with neighbours, and intrusions into their territories took place infrequently. Both age groups of paired males suddenly increased their frequency of calling during July, possibly to promote closer pair contact as breeding began.

The high level of calling during the early morning may have functioned to re-establish contact between members of a pair if they had roosted apart, and to proclaim occupation of the territory. In the early to mid-afternoon, Robins spent less time calling, probably because they foraged most intently during that portion of the day in readiness for the night fast. Also, females reduced their calling during those periods, possibly so as not to attract their mates because males were apt to steal their food. Adults spent more time "downscale" calling than did immatures during the late afternoon, possibly to maintain closer contact between members of a pair so as to roost near or with each other. In addition, they may have satisfied their food needs quicker than the inexperienced immatures and so had time for partner-interactions.

6.5.3. Sub-song

Flack (1973) and Hay (1975) often heard sub-song from juvenile males before the onset of full song, but neither seems to have heard adults giving this form of song regularly. During this study, time-budgets for juveniles were not determined as their behavioural development was rapid and changing during the few weeks before independence. From Table 6.1 it is apparent that in the non-breeding season all sexes and ages of Robins gave sub-song, but males more so than did females.

In the breeding season, males spent little time giving sub-song, but with a slight increase during the prelaying and laying stages. Possibly, the increased production of sub-song during these stages was a displacement activity that resulted from the motivation of two antagonistic drives. During these stages there was a need to sing to proclaim sovereignty over the territory to prevent any conspecifics entering it and interfering with the reproduction of the pair. Also, full song may have helped to stimulate and synchronise the sexual behaviour of the pair (Welty 1975). However, there was probably a need to remain silent so as not to attract predators.

Breeding females spent little time giving sub-song and this mostly while selecting the nest-site and during the prelaying stage. This vocalization may have been motivated in the female to warn intruders against encroachment near the nest, even though it was unlikely to be heard by another Robin because of its low volume. During the other stages of the breeding cycle both sexes had little time for sub-song, because most time was spent finding food for themselves and their young.

Thorpe and Pilcher (1958), with particular reference to the Chaffinch *Fringilla coelebs*, found that sub-song was usually produced early in the breeding season when sexual motivation was low, and in young birds as a form of "practice" for the production of full song. Welty (1975) noted that sub-song was given by young and adult males and some adult females outside the breeding season. He concluded that sub-song was a means by which a bird "kept its hand in" and practised singing while the external demands for loud song did not exist. A similar situation seemed to arise for the Robin since sub-song was most often given by moulting birds, a time when sex hormone production was probably low (Lofts and Murton 1973, Welty 1975) - there was only a weak motivation to sing full song. Perhaps the hormonal stimulation was sufficient to motivate the birds to give sub-song, but not full song.

Once the moult was completed (April), immature males spent more time giving sub-song than did adult males, because the immatures used it as practice for full song (Hay 1975). As discussed earlier (Section 6.4.1), these immature birds modified their song in line with that of their nearest neighbours. Sub-song seemed to provide the raw material out of which, by practice and by elimination of unwanted extremes of frequency, full song was formed (Thorpe and Pilcher 1958). Bissett (1978) suggested a similar reason for the singing of sub-song by Pied Tits from a comparison of sound spectrograms of their sub-song and full song. Sub-song was often given by foraging Robins and allowed them to continue feeding at a time when they had to spend most time feeding to meet the high energy requirements of moulting or maintenance during the cold temperatures of winter. Full song was usually given from high exposed perches, a position from which food was rarely obtained.

Although female Robins were never heard to give full song, they often gave sub-song. For a species where the motivation to secure and retain a territory was high, even among females, possibly sub-song was an outlet for this drive over the months when territories were least vigorously defended and pair-bonds were weak (January-April). Once the pair-bond had been formed, the presence of a male as a partner and a defender of the territory may have elicited a response in the female reducing her motivation to give sub-song, in a similar way that the presence of a female inhibited much of the singing by a bachelor.

The diurnal pattern of sub-song was similar to that of full song, with the greatest proportion of time being devoted to singing during the early morning. I am unable to explain why adult males had a different diurnal pattern of sub-song singing compared with the other categories of Robins.

6.5.4. "Chuck" calls

Timed "chuck" calls were mainly those made to maintain contact between a pair and as alarm calls. Males spent more time than did females giving these calls, because males tended to respond to other birds' alarm calls by "chucking" and moving towards the area where the disturbance was situated, whereas females often continued feeding. This habit would be expected for a species in which males carried out most territorial defence. The singing of males from high exposed perches in the canopy resulted in them responding to the sight of a predator (Harriers, Magpies) or an alarm call by "chucking" loudly and diving to the understorey.

As would be expected, contact "chucks" were given more frequently between a pair during the nest-site selection, prelaying and laying stages of the breeding cycle than during the other stages. The former stages usually involved them moving about independently, but needing to come together regularly for the male to feed the female. While the female was nest-building, incubating or tending nestlings the male gave fewer contact "chucks", presumably because he was usually able to locate her near the nest.

When raising juveniles, females spent more time "chucking" than did males. Females kept in contact with their juveniles by contact "chucks" and often attracted them with this call to be fed, once they were active fliers. In contrast, males usually used phrases of full song to attract their juveniles and seldom maintained contact with them while foraging.

Outside the breeding season, trespassing birds often caused residents to give intermittent "chucks" after the former had been evicted. This was probably the main reason for the high level of "chucking" during the moult by all categories of Robins. Furthermore, in summer flocks of Magpies entered Kowhai Bush to feed on cicadas and the sudden appearance of one of these birds near a Robin often caused the latter to "chuck" and seek shelter. This was an understandable reaction considering the Magpies' highly interspecific territorial nature and its habit of occasionally feeding on the eggs and young of other birds (Marshall *et al.* 1972, Oliver 1955).

No obvious reason was apparent for the lower proportion of time spent "chucking" in April, compared with the other non-breeding season months, by male Robins. Possibly, it arose because the pair-bond had been formed, so that paired birds moved about near each other with less frequent "contact-chucks" being needed. Also re-establishment of territorial dominance in April meant that intruders were vigorously driven from the territory instead of being "chucked" at. During May to July, the increased time spent calling was presumably to maintain closer contact between paired birds before breeding commenced.

Males spent more time "chucking" in the late morning and late afternoon compared with females in the non-breeding season. I am unable to explain why the significant difference arose in the late morning, but two reasons may explain the late afternoon result. After the moult, bachelors and paired males were occasionally encountered in other Robins' territories. These intrusions took place in the mid- to late afternoon so that the increased time spent "chucking" would have reflected both the intruder's high state of alertness and as a response from resident Robins on sighting such strangers in or near their territories. Males often went about "chucking" at sunset; this calling stopped once they located their mates. It was possible that males attracted their mates by "chucking" in order to roost near or with them.

6.5.5. A comparison of the vocal behaviour of Outer Chetwode Island and Kowhai Bush adult males

Two reasons may account for the slightly less time devoted to subsong, "chucking" and "downscale" calling by Outer Chetwode Island males compared with that for their counterparts at Kowhai Bush. The island birds lived at a much higher density and had a greater adult survival than did the mainland Robins (Flack 1976b). Neighbouring island Robins probably recognised and saw each other more regularly and trespassed into each other's territories less frequently than did those on the mainland. Thus, on the island, such frequent calling would not have been needed to deter intruders. In addition, the island females were always chased from the area occupied by the male and so it seemed that the pair-bond was not re-established in April, as at Kowhai Bush, but was delayed until just before breeding. Therefore, the vocalizations used to maintain contact between a pair were not needed, or if so, much less frequently.

The lack of full song from the island males, I believe, was because they had to spend most of their time foraging for food over their small territories (Table 9.1, p. 132) and so could not afford to spend time singing, even if an individual was a bachelor.

6.6. Summary

Full song

Females were never heard to give full song. Males gave full song throughout the year, but spent least time doing so while moulting. From studies of other passerines, it seems that moulting male Robins spent little time singing because of reduced or a lack of hormonal stimulation when the testes and interstitial cells regressed (Lofts and Murton 1973). Bachelors spent more time singing than did paired males ($P < 0.01$). Since they abruptly sang much less when they acquired a partner it probably functioned largely to attract a female. Breeding males spent more time singing during the prelaying stage than during the other stages, possibly to help synchronise the reproductive states of themselves and their partners for copulation, and to proclaim ownership of and to defend territories. From January to April, adult males sang significantly more than did immature males, but from May to July the reverse was true. The reduced time spent singing after April by paired adult males arose because their partners usually approached them while they were singing and "chucked", to which the males responded by stopping singing. However, this habit was not so apparent for immature females so that their mates (mainly immature males) sang unhindered.

Most time was spent singing in the early morning with a reduction as the day progressed. It seems that Robins sang mainly in the early morning both because of the low efficiency of foraging then (Kacelnik 1979) and because environmental conditions were better for the propagation of sound then compared with later in the day (Wiley and Richards 1978).

"Downscales"

About half the "downscales" were followed by no obvious response from the caller or other Robins nor were the calls preceded by a particular event. Of the remainder, about half were associated with interactions between members of a pair and the other calls with territorial defence. My impression was that these calls probably served to maintain contact between paired Robins and to advertise territorial possession. "Downscales" were rarely heard in the breeding season and most frequently in early autumn (April). Male Robins spent more time calling than did females. For the combined data from all Robin categories, there was no significant change in time spent "downscale" calling from one day-period to the next. The proportion of time spent calling was highest at the start and end of the day.

Sub-song

Robins spent little time giving sub-song in the breeding season, usually less than 0.5% of time during any stage of the breeding cycle. Outside the breeding season, males spent significantly more time giving sub-song than did females, and adult males sang more than did immature males. All categories of Robins spent more time giving sub-song while moulting than afterwards. For males particularly, moulting was probably a time when sex hormone levels were low (Lofts and Murton 1973) so that they may have been motivated to give sub-song, but not full song. The singing of sub-song by immature males was probably a method of practising to sing and of modifying their song while being able to continue feeding at the same time. Except for adult males, all other categories of Robins spent most time giving sub-song in the early morning and early afternoon. Adult males had their peak times of sub-song singing in the late morning and mid-afternoon.

"Chucks"

Breeding Robins usually spent less than 0.5% of time "chucking". Females increased time spent "chucking" while selecting a nest-site, and males during the prelaying stage. Presumably, because members of a pair often moved about out of sight of each other the "contact-chucks" were given to find each other, especially for a male to feed his partner. Similarly, both adults "chucked" more once the nestlings left the nest to call the young to be fed or to warn them of danger.

In the non-breeding season, immature and adult Robins of the same sex spent similar proportions of time "chucking", but males spent significantly more time calling than did females. This difference arose because males responded to most alarm calls and disturbances in and near their territories by "chucking" and moving towards the disturbance, whereas females often remained feeding. In general, Robins in each category spent gradually less time per month "chucking" from January to April and then increased it until nesting began. The high percentage of time spent "chucking" during the moult was caused by the presence of Magpies and the frequent intrusions of immature birds. Males spent a greater proportion of time giving "chucks" in the afternoon than in the morning; for females the opposite was true.

Vocalization behaviour of Outer Chetwode Island adult males

Adult males on Outer Chetwode Island were not heard to give full song, but spent similar proportions of time giving the other types of vocalizations as did adult males in Kowhai Bush. Since almost all time was spent feeding by the island birds it was possible they had no time to give full song.

CHAPTER SEVEN

BODY-MAINTENANCE BEHAVIOUR

7.1. Introduction

There is little information in the literature concerning the body-maintenance behaviour of the South Island Robin. Flack (1979) noted that Robins regularly bathed and to do so they often crossed the territories of other Robins. B.D. Lloyd (pers. comm.) has seen Robins sunning in summer. However, no descriptions have been made of the various body-care activities.

Body-maintenance behaviour comprised several activities. These were defined, following Potts (1976), as those which served "to remove sources of irritation and extraneous material, cared for the body surface and plumage, and counteracted the effects of muscular inactivity." The major activities involved with body-care were bathing, preening and sunning, with head-scratching, anting, toe-nibbling, beak-wiping, stretching and the body-shake as minor activities. Some of these activities have been collectively called "comfort movements" by authors describing them of other birds (Ude Shankar 1977, Welty 1975). Apart from their significance in comparative studies, body-maintenance activities provide a basis for the study of sexual and agonistic behaviour in birds since elements of the latter have frequently been shown to derive from the former (van Iersel and Bol 1958, Dunham 1966).

Each kind of body-maintenance activity is described here. Three of the activities (bathing, anting and sunning) were timed individually, and the results presented and discussed. In later chapters on monthly time-budgets, the time spent in the various body-maintenance activities is combined to become "body-maintenance" behaviour.

By making timed observations of Robins bathing, anting and sunning I set out to answer the following questions:

1. Were these activities confined to particular months or seasons?
2. What proportion of the Robin's time was devoted to each activity?
3. Did Robins have a diurnal pattern of involvement in each activity?
4. Were anting and sunning essential activities to the well-being of the birds?

7.2. Methods

Body-maintenance activities were timed to the nearest second. Preening by Robins engaged in boundary disputes was considered a displacement activity, and was recorded as territorial-defence behaviour. Bathing, sunning and their "associated-preening" activities, and anting were timed individually, but time taken in the other body-care activities was not recorded separately.

From June 1977 to September 1978, each bout of bathing was timed from the moment a Robin hopped into the water and until it left, even if no bathing movements eventuated. A bout of bathing was occasionally composed of a few sessions in the water interspersed with short periods on land. Each session was timed and then combined to give the length of the bathing bout. Head-scratching, preening, wing-beating and the shaking movements associated with drying the plumage after bathing were timed when the bird left the water and ceased when it switched to another activity. From meteorological records (G 23351, Kowhai Bush), I was able to determine the ambient temperature at the time of each bout of bathing at the weather station. Bathing Robins were sometimes encountered when I was not timing behaviour. On such occasions the time of day that bathing took place was recorded.

Anting Robins employed characteristic movements when wiping themselves with invertebrates. Timing of such behaviour started when they began using wiping movements and stopped when the specimen was eaten or discarded. Where possible the number of wipes per specimen was noted and the animal used retrieved.

Sunning birds were timed from the moment they assumed the characteristic sunning posture and until they began a new activity. Usually preening followed sunning and occasionally panting preceded it. Both were recorded as "associated-preening" activities. A bout of sun-bathing often involved several exposures to direct sunlight interspersed with associated-preening activities. The length of a bout was determined by adding up the time of each exposure until the bird began a different behaviour. Only during the 1977-78 summer were the associated-preening activities timed separately. I was able to place a maximum-minimum thermometer (°C) in direct sunlight, within a few metres of a sunning Robin, to record the temperature during each bout. The Robin's status and a description of the sunning site were noted.

7.3. Description of body-maintenance activities

7.3.1. Stretching

Three types of stretching movements were made by Robins.

(i) The "wing-leg-stretch" involved a wing and the leg on the same side being extended downwards and backwards from the body with the tail being fanned towards the same side. Often the toes poked through the primaries of the partially spread wing.

(ii) "Both-wings-stretch" resulted in the wings being raised over the back so that their tips came together, were held in this pose for a couple of seconds, then folded again. Very little spreading of the wings took place during these movements.

(iii) "Both-legs-stretch" was an uncommon activity which involved both legs being stretched so that the body was raised relative to the perch.

Stretching movements usually took place after long rest and preening bouts, especially when females unhurriedly left their nests following an extended stint of incubating or brooding. Similarly, Andrew (1956), Potts (1976) and Ude Shankar (1977) noted that stretching movements followed periods of inactivity with other passerines. Stretching movements "probably served to stimulate the flow of blood in the limbs, thus preparing the bird for action" (Potts 1976) or possibly they arose "because of proprioceptive feedback" (Andrew 1956) from cramped muscles.

7.3.2. Body-shaking

The feathers were fluffed, after which the body was quickly shaken from side to side. It usually involved the tail being slightly fanned and wagged, and the head shaken, although both of these components were sometimes carried out independently. Tail-wagging commonly took place after defecation; head-shaking after drinking or feeding. Such movements helped to clean the body of water, soil, food particles and faecal material. However, most body-shakes occurred in association with long bouts of preening, such as after bathing, and were important as drying movements and to rearrange displaced feathers (Ficken 1962).

7.3.3. Head-scratching

This movement was achieved by bringing a leg behind, then over a lowered wing for the claws to scratch the head; the indirect method (Simmons 1957). As described by Simmons (1961) for other avian species, the Robin had two levels of head-scratching. The "basic" level involved a precise area of the head or beak being scratched for a short time. It was carried out at any time probably in response to an irritation or to some foreign material. By comparison, the "extended" level of scratching resulted in the head being turned so that several areas were scratched in sequence before the leg was returned to the perch. The extended level of scratching was probably an important part of the feather-maintenance behaviour. Also, oiling of the head feathers was accomplished by scratching. During drying activities after bathing, Robins obtained oil from the preen-gland with the beak and back of the crown, transferred some from the beak to the toes by scratching and then applied it to the feathers of the head by scratching.

Robins were often seen "yawning": the neck was stretched forward and the mandibles opened widely. This stretching action, which tensed the throat, neck and head muscles and skin, was usually followed by a period of scratching directed at these areas. Two or three yawning movements sometimes occurred before scratching began, but occasionally yawning took place without any subsequent scratching.

7.3.4. Beak-wiping

Beak-wiping consisted of the beak being drawn, from the base to the tip, against a branch or the ground. It took place after a number of activities including killing and eating prey, feeding young and removing faecal sacs. Robins frequently wiped their beaks while killing and breaking up slime-covered animals, so that its main function seemed to be to remove foreign material from the beak and facial bristles.

7.3.5. Toe-nibbling

This action involved the beak being brought down to the toes or *vice versa* and the toes being nibbled or pecked. Bands were vigorously pecked or drawn up and down the tarsometatarsus, even when the bird had been banded for several years. Robins often nibbled at swellings on their toes caused by bird pox (Flack 1973). Toe-nibbling seemed to be carried out to relieve an irritation and to clean off adhering foreign material from the toes and legs.

7.3.6. Preening

Preening was usually preceded by a fluffing of the plumage, presumably to facilitate the grasping of individual feathers (Potts 1976). Preening movements involved a Robin grasping individual or several feathers at a time in the tip of its beak and drawing them through it, from the base of the feathers to their tips. Often a nibbling action was seen. When single primary and secondary feathers were preened, the wing was brought up towards the beak and the feather grasped at its base. As the beak moved down the feather, the wing was pulled back towards the body. Similarly, the rectrices were cocked and fanned upward and slightly to one side as they were preened.

Short preening bouts (< 1 min.) intervened between many behaviours to remove foreign material or to relieve an irritation. Bits of prey or nest material that had adhered to the plumage were seen to be removed. When hopping about on the ground Robins sometimes, momentarily, became stuck to hook-grass (*Uncinia* spp.) seed heads. They were always able to tug free, but then had to preen the clinging seeds from their feathers.

Extended preening bouts (> 1 min.) mainly occurred after bathing and sunning, but also without such prior activities. Extensive preening of several or all areas of the body characterised such bouts. During the moult, these preening bouts took place frequently and presumably helped to relieve the irritation of and to arrange emerging feathers, and removed sloughed skin, such as feather sheaths. During the moult while preening or head-scratching, Robins sometimes suddenly preened rapidly and flicked their wings. This often resulted in them loosing their balance and flying about erratically, and then returning to the perch to continue preening. These flights involved quick, exaggerated wing beats as though the bird was trying to rid itself of something clinging to its feathers or that irritated it intensely.

7.3.7. Bathing

Bathing by Robins involved the movements and postures of "method 1" described by Slessers (1970). They bathed in water of about three centimetres depth and sometimes drank as they hopped into it. This was followed by crouching into the water and partially immersing their heads, and then by shaking movements. Ducking of the head, forebody and wings, followed by quickly raising these areas, scooped water over the back and tail. The body plumage was ruffled and the wings were flicked in and out of the water, splashing droplets over the body. In intense bathing, the body was often rolled from side to side as the wing movements continued. Some birds left the water with just their belly feathers wet, while others seemed saturated all over. Robins remained very alert while bathing and fled to cover as soon as any possible danger threatened. They were always able to fly from the water, in contrast to the observations of Ficken (1962) of a captive American Redstart *Setophaga ruticilla* which could not reach a perch immediately after bathing. Unless frightened, Robins stayed in the water until bathing was completed whereas South Island Fantails left and re-entered the water many times during a bathing bout (pers. obs., Ude Shankar 1977). Once a Robin was seen to bathe in wet grass by hopping through it and making the typical bathing movements with its wings. Females that had been incubating or brooding were seen to bathe, but most bathers were birds that had just eaten a large item of food.

Bathing completed, Robins flew to a sheltered perch and began drying themselves. Initially, drying movements consisted of quick movements of the wings beside the body, interspersed with body-shakes, head-scratching and brief moments of preening. Usually the wing movements were so vigorous that a characteristic noise could be heard. Van Rhijn (1977) has shown that these movements enhanced rapid drying by direct removal of a considerable portion of the absorbed water and by distributing the rest as very tiny droplets over the feathers where it quickly evaporated. He also found that bathing was not sufficient to remove all dirt and that a bird had to perform "cleansing behaviour" for complete removal. Gradually, the frequency and duration of the Robin's wing movements decreased until towards the end of the drying process, only preening occurred, as found by Ficken (1962) for an American Redstart. Of 89 watched after bathing, two Robins dried by perching in direct sunlight. Having rid its plumage of most of the water one bird took up the sunning

Figure 7.1 The typical sunning posture of the South Island Robin; tail and exposed wing fanned, contour plumage ruffled and a side of the head facing the sun.

posture (Section 7.3.9), but the other, that was drying itself by preening, was chased by a Bellbird and so did not get a chance to sun-bathe.

7.3.8. Anting

Anting by Robins was an "active" process (Potter 1970) in which they picked up live invertebrates in the tips of their beaks and wiped them over their feathers. In "passive" anting a bird, with its body flattened against the ground, allows ants to crawl among its feathers and then removes them (Potter 1970). Robins picked up invertebrates one at a time and wiped them over the wings and tail. Generally, each treatment resulted in the animal being wiped several times, with quick jerky movements, before it was eaten or discarded. Between wipes the animal was mandibulated or dropped. Alternate wipes on either side of the body were usual, as was also noted by Clunie (1974), Kinsky (1957) and Poulsen (1956) for other species. On the side of the body to be anointed, the folded wing was brought slightly forward and out from the body so that the beak moved between the two surfaces to wipe over the undersides of the primaries, secondaries and rectrices. In addition, the tail was brought forward to the same side, but anting Robins were never seen to stumble over their tails as other workers have mentioned for some species (Potter and Hauser 1974, Poulsen 1956). The plumage was sleeked as Robins anted.

7.3.9. Sunning

All cases of sunning were of a "voluntary" nature with the Robins seeking areas of direct sunlight to assume the sunning posture in (Hauser 1957). "Compulsory" sunning, carried out by other species, involves them assuming the same posture as for voluntary sunning when they "suddenly and apparently unexpectedly were exposed to direct sunlight, under more or less extreme conditions of humidity and heat" (Hauser 1957). Other evidence that sunning by Robins was of a voluntary nature was that they often returned to the same site several times in succession to sun-bathe.

Typically, the Robin orientated the greatest surface area to direct sunlight (Fig. 7.1). The body was leaned to one side and the tail and exposed wing were fanned. Ruffling of the contour feathers occurred and

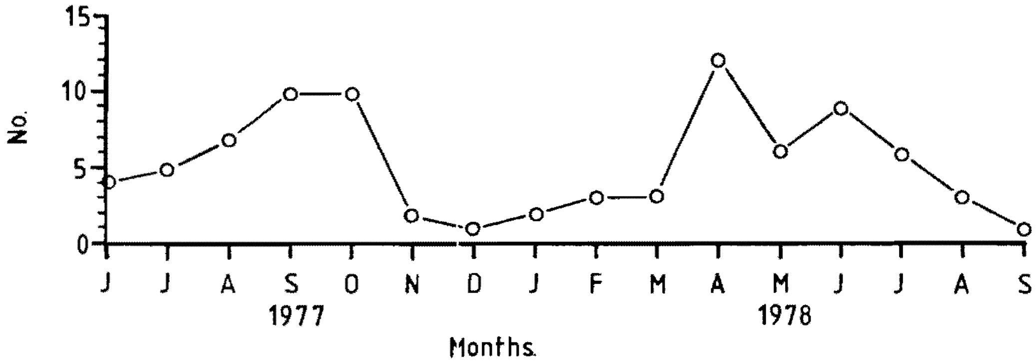


Figure 7.2 The number of occasions on which Robins were seen bathing from June 1977 to September 1978.

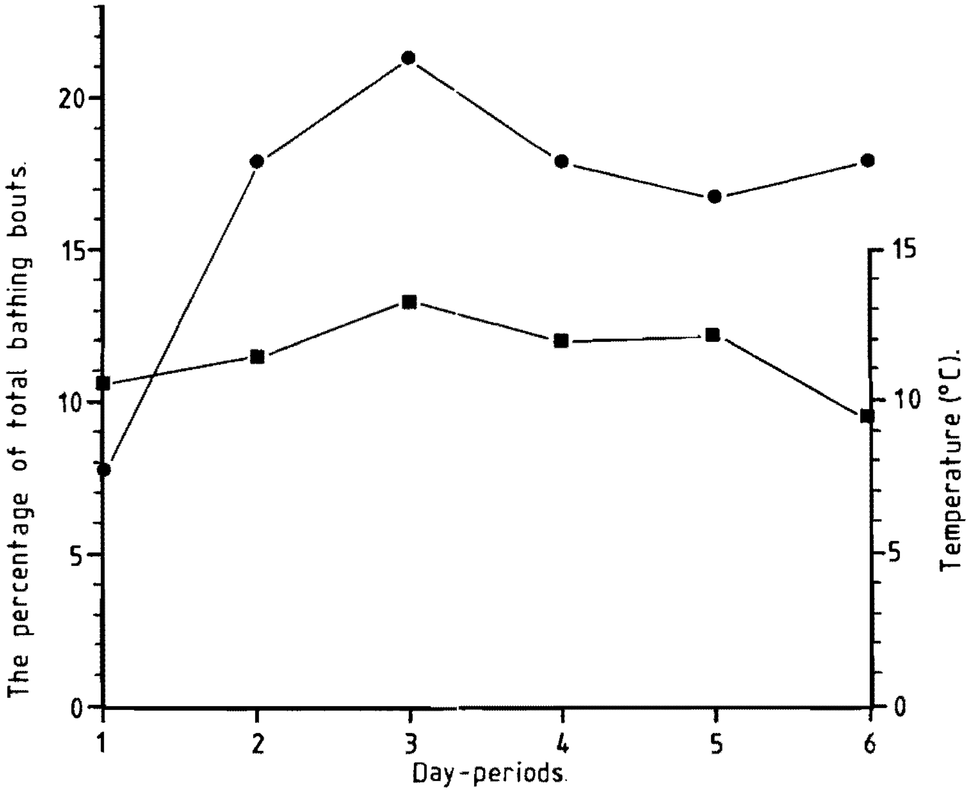


Figure 7.3 The diurnal pattern of bathing bouts (●-●, N=89), and the mean air temperature (°C)[a] during bathing bouts (■-■).

[a] The air temperature during a bathing bout was determined from the temperature records of weather station G 23351.

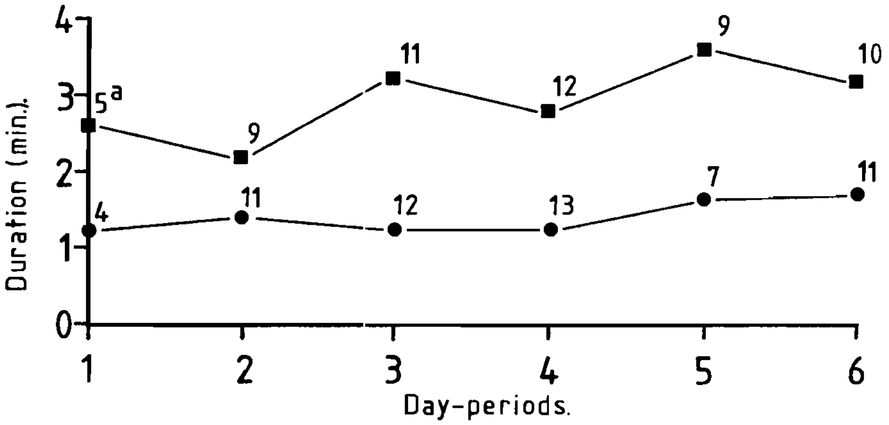


Figure 7.4 The diurnal patterns of the mean duration of bathing bouts (●-●), and associated-preening sessions (■-■).

[a] The figures above the symbols are sample sizes.

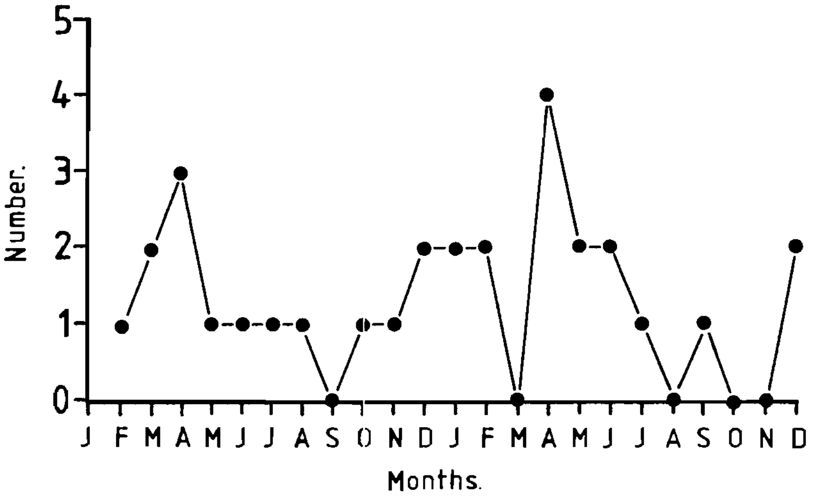


Figure 7.5 The monthly totals of anting Robins seen from January 1977 to December 1978.

the head was turned so that an eye stared into the sun. The bird kept still, except when it moved to expose the shaded side. When sunning took place in intense sunlight, Robins often began panting. All sunning birds were alert and flew off whenever threatened or alarmed.

After sun-bathing, Robins moved to a shady site and began "associated-preening" activities. Initially, these activities included much head-scratching, but gradually this gave way to mainly preening movements. Those birds that had been panting while sunning invariably spent a minute or two panting in the shade before beginning to preen. When panting, their plumage was sleeked presumably to dissipate some of the heat (Morris 1956). When the sun was not very intense, Robins sometimes remained at the sunning site to preen.

7.4. Results

7.4.1. Bathing

Robins bathed mainly in puddles on the stopbank roads adjacent to their territories, but some used water that had accumulated in holes and depressions in living and dead trees. From June 1977 to September 1978, 58 bouts of bathing were timed. On average these lasted 1.43 minutes (range: 0.23-6.20). The mean time taken for 56 drying bouts was 2.97 minutes (range: 1.07-14.65). No exact figure was determined for the proportion of the "average" Robin's time-budget that was spent on bathing and drying, but I estimate that about 0.005% of their time was devoted to these activities.

Of 84 bathing Robins, a similar proportion involved males (57.1%) or females (42.9%) ($t = 1.58$, $P > 0.1$). Robins bathed during all months (Fig. 7.2). They were seen to bathe least frequently in the early morning (Fig. 7.3). An almost constant percentage bathed through the rest of the day, but with a slight peak in the late morning. The weather station records (Fig. 7.3), shows that the ambient temperature and the frequency of bathing during the day were not always correlated. Bathing took place most often in the late morning when the temperature was highest, but in the early morning and late afternoon the two factors were not correlated. However, the diurnal pattern of bathing may be related to a combination of weather factors. Figure 7.4 summarises the mean duration of bathing and drying bouts for each day-period. In general, drying bouts gradually increased in duration through the day; bathing

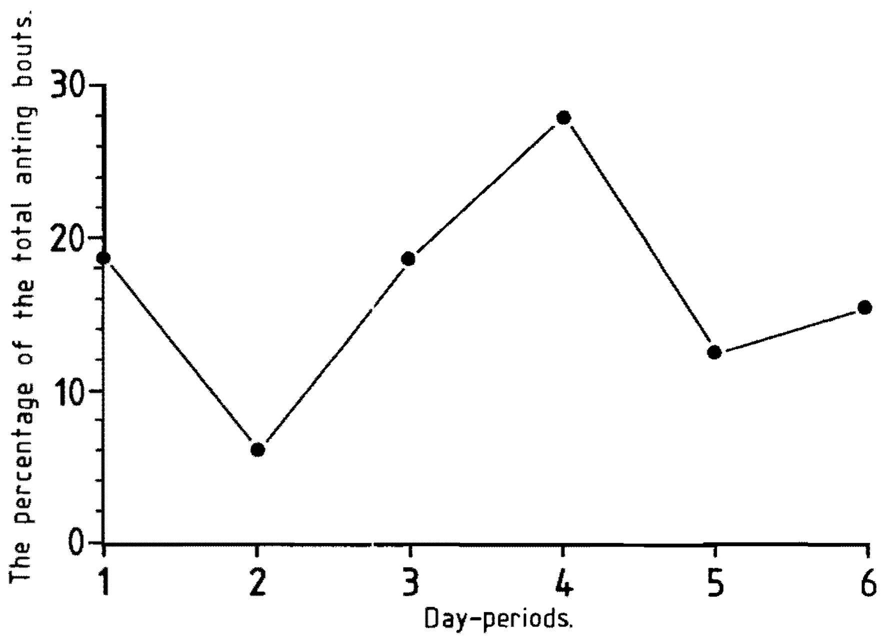


Figure 7.6 The diurnal pattern of anting (n=32).

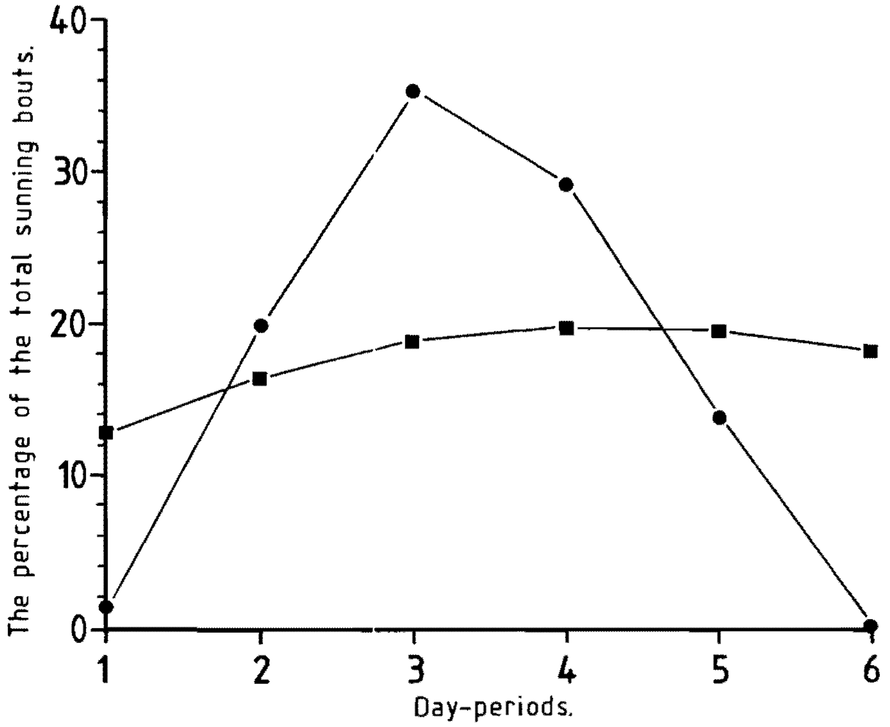


Figure 7.7 The diurnal pattern of sunning bouts (●—●, n=65) and mean ambient temperatures[a] (°C, ■-■).

[a] The temperatures were determined from the December 1977 to February 1978 records of weather station G 23351.

bouts were shortest in the early morning, late morning and early afternoon, and longest towards the end of the day.

7.4.2. Anting

Thirty-two bouts of anting were seen of which 25 consisted of Robins finding an animal, anting with it for an average of seven seconds (range: 3-21) and then eating it. Such anting bouts resulted in two to eight wipes of the animal over the wings and tail feathers. The other seven bouts involved several animals being anted with, one after another, for a mean time of 2.96 minutes (range: 0.43-13.45). In total 26.71 minutes of anting were seen, which represented less than 0.001% of the species' time-budget (n = 1370 h).

When I was able to retrieve animals that had been used for anting, they were millipedes (*Dimerogonus* sp.) (two bouts) and ants (*Huberia* sp.) (one bout). Most animals used for anting with were small and eaten immediately after the wiping actions, so that few could be identified as they were being used. All but two anting bouts took place on the ground; the exceptions occurred about three metres up tree trunks where ants were found living under decaying bark.

Anting was seen during all months of the year (Fig. 7.5). Seventy-five percent of all bouts occurred from December to May inclusive, months when at least some Robins were moulting. All bouts that resulted in more than one animal being anted with also took place in these months. Most bouts of anting happened around midday with slight increases in frequency during the early morning and late evening (Fig. 7.6).

7.4.3. Sunning

Sunning mainly occurred from December to February inclusive. Of 57 bouts, 46% took place with the bird sitting on litter, flattened grass or on the gravel of stopbank roads. Less often Robins perched on branches or sat on areas of dense foliage while sun-bathing. Table 7.1 summarises the status of sunning Robins; most had completed breeding and showed no signs of moult, or were moulting. However, nearly a quarter of sunning Robins were breeding at the time. Of 65 sunning Robins, 65% were males and 35% females ($P < 0.01$).

Table 7.1. The status of sunning Robins.

	Status						
				Rearing			
	Pre-laying	Laying	Incubating	Nestlings	Juveniles	Non-breeding	Moulting
1976-77:	1		3	2	2	9	20
1977-78:	1	3	3			17	4
%:	3.1	4.6	9.2	3.1	3.1	40.0	36.9

The mean time, range and standard deviation of sunning exposures and bouts, and associated-preening sessions are summarised in Table 7.2.

Table 7.2. Some statistics of the duration of sunning activities.

	Time (min.)			
	Mean	Range	S.D.	N
Sunning exposures:	2.05	0.07-16.32	2.19	172
Sunning bouts:	5.59	0.10-29.78	5.20	67
Associated-preening sessions[a]:	1.97	0.08- 8.35	1.84	67

[a] Recorded separately from the other body-maintenance activities only during the 1977-78 summer.

The mean duration of exposures and the associated-preening sessions were of similar length, but both had considerable ranges. Sixty-seven sunning bouts averaged 2.6 exposures (range: 1-12). The average temperature at ground level and within a few metres of the sunning Robins (n = 9) was 39.4°C (range: 29.0-44.0).

From Figure 7.7 it is apparent that most bouts of sunning took place about midday with few occurring in the early morning and late afternoon. The diurnal pattern of ambient temperature was of an increase until the early afternoon, then a slight decline until sunset. After exposure to direct sunlight, 92% of Robins preened, or panted and then preened (n = 142). Of the other occasions, three percent involved either

170	226	218	171	243	214	249	196	Sunshine hours.[a]
15	16	13	13	13	17	17	16	Mean ambient temperature (°C).[b]
0.0	3.9	10.4	11.6	0.0	26.5	29.2	29.1	Observation time(h).

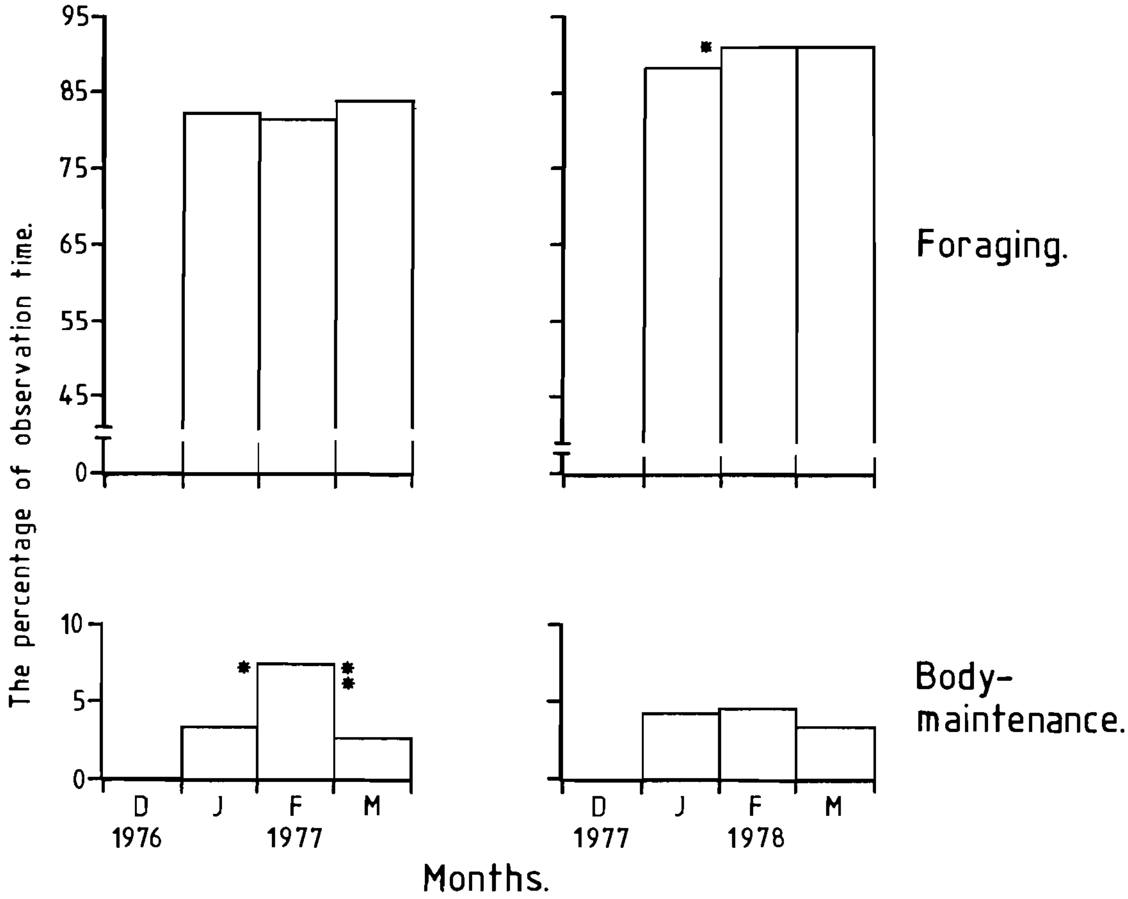


Figure 7.8 The partial time-budgets for immature Robins during the main months when adults sun-bathed.

[a] Sunshine hour records from the Kaikoura weather station G 23471.

[b] Temperature records from the Kowhai Bush weather station G 23351.

[c] The asterisks denote significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the percentage of time spent in a behaviour between two adjacent monthly samples.

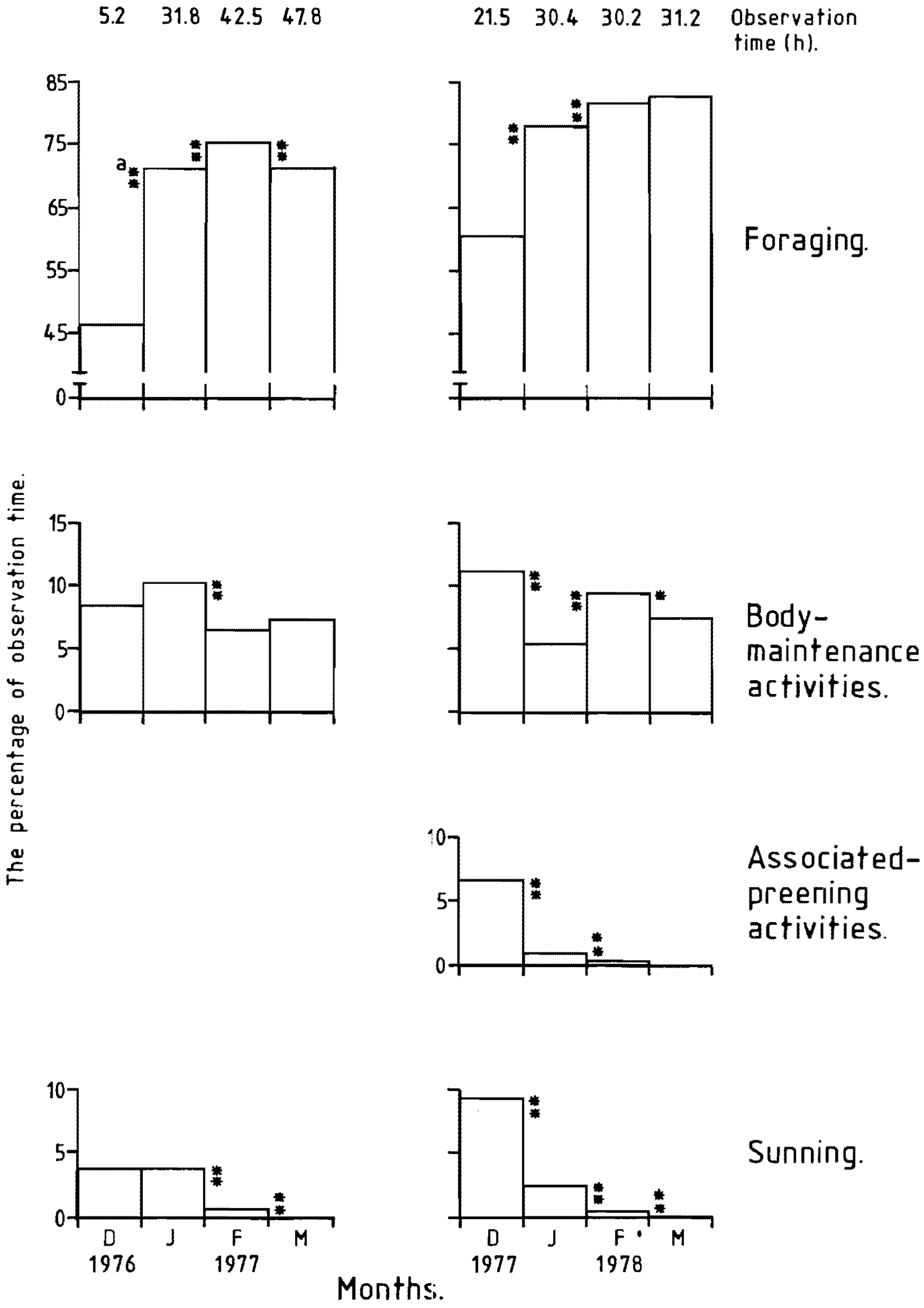


Figure 7.9 The partial time-budgets for adult Robins during the main months when they sun-bathed.

[a] The asterisks show significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the percentage of time the Robins spent in an activity between two successive monthly samples.

fleeing in response to an alarm call or an interaction with another bird, and five percent involved departures to forage. Foraging arose after sun-bathing only when the sunlight was weak and the sunning posture had been momentarily and partially assumed.

Figures 7.8 and 7.9 show the partial time-budgets for immature and adult Robins respectively during the months when most sun-bathing took place. Immature Robins were never seen to sun-bathe. Adults sun-bathed most in December, followed by a rapid decrease in the proportion of time devoted to this behaviour until little or none occurred by March (Fig. 7.9). The mean ambient temperatures and hours of sunshine tended to be greatest in January and February (Fig. 7.8).

7.5. Discussion

7.5.1. Bathing

No dust bathing was seen, although dusty places were present in territories. However, the birds often moved through the territories of other Robins to reach water (pers. obs., Flack 1979), and so evidently had a strong need to bathe because they confined most other activities to their own territories.

Was bathing confined to particular seasons? That Robins were infrequently seen to bathe during summer and autumn was most likely a consequence of a lack of available pools then, rather than them not requiring to bathe. For instance, Slessers (1970) found with eleven passerine species at several sites in Canada and the United States of America that they bathed more and longer in summer than in winter. In addition, Potter and Hauser (1974) noted a tendency for birds in temperate North America to bathe more often while moulting (in summer) than at other times of the year.

What proportion of the bird's time was devoted to bathing and drying? My observations showed that Robins spent about 0.005% of their time on this. However, during the few observations I made in rain, Robins occasionally stopped foraging and shook the rain off with the characteristic rapid wing-beats seen after bathing. It rained each month in Kowhai Bush (Table 2.1, p. 13), Robins bathed while it rained, frequently shook water from themselves when foraging in wet vegetation and were seen perched, apparently ridding their plumage of water absorbed while foraging in the rain. For these reasons and because timed observations were not made when it was raining, it seems reasonable that the birds spent more time bathing and drying than my data show.

Did Robins have a diurnal pattern of bathing? The data show that Robins bathed most often during the late morning when the temperature was highest (Fig. 7.3). Similarly, Slessers (1970) found that birds bathed more often in warm sunny weather. This may partly explain why the Robins seldom bathed early in the morning. However, in the late afternoon, when the temperature decreased, the frequency of bathing increased. On several occasions Robins were seen to bathe after sunset or in puddles with icy margins. Thus, bathing was not related wholly to ambient temperature.

Having eaten and stored a large prey item, Robins often bathed. Two explanations could account for this occurrence; either they bathed to clean their feathers of mucus and bits of prey that had adhered to them while breaking up the animal, or because, being satiated they had time to devote to body-maintenance activities. Generally, the time Robins spent in body-maintenance was inversely related to that spent foraging (Chapters 9-11).

The mean length of bathing and drying bouts per day-period, in general, increased as the day progressed (Fig. 7.4). This probably arose because bathing in the morning was mainly a quick cleansing process, with the birds resuming their foraging afterwards. However, by mid-afternoon many Robins would have satisfied their hunger and also stored some food for later use (Fig. 5.1, p. 51). Such birds would then be able to afford the time for less essential activities, to bathe and dry themselves leisurely, especially around sunset when the fading light probably reduced their foraging efficiency.

7.5.2. Anting

The only record of anting for the genus *Petroica* I located was of a North Island Robin (Kinsky 1957), ants being the animals used, as they often were by South Island Robins. However, millipedes were used on some occasions by my birds, animals which were also used by several other species when anting (Clunie 1974, 1976, Whitaker 1957).

It is not known how many species of ants and millipedes are present in Kowhai Bush and why the two species identified elicited anting from

Robins. Whitaker (1957) noted that the invertebrates birds anted with extruded or sprayed repugnant liquids. By collecting ants and millipedes at the study area, noting whether they give off defensive secretions and providing them to Robins it may be possible to determine whether Robins react to similar characteristics of these invertebrates, as did the passerines listed by Whitaker (1957).

The characteristic posture and movements associated with wiping invertebrates over the wings and tail during "active" anting (Potter 1970) by Robins seemed to be similar to the description given by Kinsky (1957) for anting by the North Island subspecies. Furthermore, photographs show that the postures used by other species when anting were similar to those of Robins: anting by a Blue Jay *Cyanocitta cristata*, figure 1, Poulsen (1956); and an anting Orchard Oriole *Icterus spurius*, figure 1, Whitaker (1957). The Orchard Oriole anted with its feathers "appressed" (Whitaker 1957), that is sleeked - as did Robins. Potter (1970) found that most anting episodes lasted 15 minutes or less. However, she also observed episodes lasting for half an hour or more, as did Dubinin (*in* Kelso and Nice 1963), Snyder (1941) and Whitaker (1957). Most anting by Robins took less than 30 seconds and involved only one animal being wiped over the plumage.

Did Robins have a diurnal pattern of anting? The diurnal pattern of anting shows that it took place most often in the early morning, midday and late afternoon; times of the day when the proportion of time spent in other body-care activities was greatest (Figs 10.7 p. 160, 10.8 p. 162, 11.3 p. 192, 11.4 p. 197). Potter (1970) noted a similar diurnal pattern of anting from work on several species, but the peak time of anting was during the early morning compared with around midday for Robins. This pattern in Robins may be related to the invertebrate's daily activity patterns and therefore their exposure to predation.

Was anting essential to the well-being of the birds? The literature about anting has been reviewed several times (Chisholm 1959, Groskin 1950, Potter 1970, Simmons 1966, Whitaker 1957), and the following reasons put forward as functions of the activity.

(i) Birds used the secretions of some species of invertebrates to soothe the skin irritated by ectoparasites (Groskin 1943, 1950).

(ii) Ant secretions were used by birds to prevent, remove or otherwise control ectoparasite infestations (Dubinin *in* Kelso and Nice 1963, Goodwin 1955, Simmons 1966).

(iii) Birds "appeared to derive sensual pleasure, possibly including sexual stimulation" from anting (Whitaker 1957).

(iv) Birds used the thermogenic properties of ant secretions to soothe their skin irritated by new feather growth (Potter 1970, Potter and Hauser 1974, Southern 1963).

(v) Ant secretions may be helpful in feather maintenance by increasing the flow of saliva for preening, removing stale preen oil and other lipids or increasing feather wear resistance by preventing the over-drying of feather oils (Simmons 1966).

(vi) Ant substances on the plumage, irradiated by sunlight, produce vitamin D, which the bird ingests during preening (*in* Whitaker 1957).

(vii) Poulsen (1956) concluded that feeding was the basic incentive and that anting was an incidental behaviour as birds tried to cleanse their heads and eyes of ant acid.

Although Robins were seen anting in each month, the activity arose infrequently. Furthermore, since less than 0.001% of the population's time was spent anting, the activity did not seem to assume an essential biological function. The fact that little time is spent in an activity is not necessarily a good measure of its importance in the biology of the species. However, for the above reasons, and because Robins ate the invertebrates with which they anted, I conclude that the anting movements were probably part of a feeding behaviour by which they removed and/or tried to avoid the irritating defensive secretions of certain prey species (Poulsen 1956). That anting took place most often while Robins were moulting and that this period included all the episodes involving more than one treatment may have been coincidental (Potter and Hauser 1974). Possibly, the invertebrates used for anting with were more active and abundant in summer and autumn, so that they were often preyed upon by Robins at that time. The instinctive and stereotyped anting movements may have been triggered by specific substances emitted by certain prey, rather than the birds carrying out the movements for a specific purpose.

7.5.3. Sunning

Several hypotheses have been proposed to explain the function of sunning by birds:

(i) Sunning increases ectoparasite mobility, facilitating their removal by preening. The evidence to support this view was that sunning was interspersed with, or followed by, preening. Robins invariably followed each exposure to high intensity sunlight by preening.

(ii) Several observers noted that birds often sunned themselves after getting wet (Bannerman 1956, Rowan 1967). Bathing by a Robin was only once followed by sunning and most cases of sunning occurred in months when water for bathing was not readily available. Therefore, I conclude that for Robins sunning was not important for drying their plumage.

(iii) Sunning is a heat absorption process. Brown and Amadon (1968) noted that the New World vultures sunned, especially in the morning, before leaving the roost. Since these authors also stated that the body temperature of the Turkey Vulture *Cathartes aura* dropped at night, sunning in this group may be connected with heat absorption. Storer *et al.* (1975) concluded that "because of the length of time spent sun-bathing, the lack of preening after each bout, and the dark pigmentation of the skin and feather bases", that it was probable that sunning in grebes functioned primarily in heat absorption. Roadrunners *Geococcyx californianus* were seen by Ohmart and Lasiewsk (1971) sun-bathing in the early morning hours and intermittently on cool, clear days. Similarly, they concluded that for this species sunning was a heat absorption process.

(iv) Sunning may be involved with feather care - exposing the preen gland to the warmth of the sun could increase the flow of oil from it (Kennedy 1969). This explanation rests on the fact that the preen gland of some species was often exposed to the sun by the raised rump feathers and that preening invariably followed sun-bathing (Hauser 1957, Kennedy 1969). I did not notice the exposure of the preen gland by sunning Robins, nor were they observed to oil themselves while preening after sunbathing; had they done so it could hardly have gone unnoticed.

(v) Sunning results in the production of vitamin D from a precursor in the preen-gland secretion spread over the surface of the feathers during preening (Simmons 1964, Weisbrod 1971, Yapp 1970). Calcium requirements are known to increase during the moult (Simkiss 1967) and sunning has been suggested as a method of increasing vitamin D production, a substance important in the assimilation of calcium.

(vi) Sunning plays a role in the moult "through its local effects in stimulating the feather papillae to develop, but also through the central nervous and endocrine systems" (Harrison 1946).

(vii) Sunning may be a comfort-motivated behaviour by which heat is applied to the skin to soothe the supposed irritation of feather emergence during moult (Potter and Hauser 1974).

To determine which of the above reasons, or combination of them, best explained why Robins voluntarily sun-bathed, I looked at the time of year and day when the activity took place, at the status of the sunning birds, and at what proportion of their time-budget was spent on sunning. More males sun-bathed than did females, presumably because when breeding much of the female's time was spent on incubating and brooding so that they had fewer opportunities in which to sun themselves compared with males. Sunning by Robins took place mainly after breeding had been completed. Those that did sun-bathe while still breeding invariably had "free" time, birds that only spent a small proportion of their time finding food for others dependent upon them. Both members of a pair had plenty of time to meet maintenance requirements late in the breeding season when involved in the prelaying, laying and incubating stages (Figs 15.1 p. 280, 15.2 p. 284, 16.1 p. 317), because temperatures were mild, daylengths long, and, apparently, ample food supplies existed. Adults with one or two nestlings or juveniles sometimes sun-bathed, especially females, because males alone satisfied their progenies' food demands. Therefore, it seems that it was those Robins that had few young or were involved in breeding stages with low maintenance requirements that sun-bathed while breeding.

No immature Robins were seen to sun-bathe, although intense sunlight needed for sunning existed. Hauser (1957) commented that young birds were seen sunning more frequently than were adults, except in the late summer moulting season when many adult birds sun-bathed. Similarly, the records compiled by Gibb (1947) suggested that juvenile birds of several species spent much time sunning. Immature Robins were not seen sunning probably because they foraged more than did adults from December to February inclusive when the latter were sunning ($P < 0.01$) (Figs 10.3 p. 152, and 11.2 p. 191). Perhaps immatures were less efficient foragers than were adults and to find enough invertebrate prey, essential to supply the amino acids required for feather development (Newton 1968), had to spend most of their time foraging and so had no time to sun-bathe. Furthermore, that immatures did not sun-bathe suggests that the activity was not biologically essential when they were moulting.

Adults sun-bathed mainly in December, with little or none during February and March. Since the monthly sunshine hours and mean ambient temperatures were higher after December, the birds could seemingly have devoted more time to sunning in January and February than they did, especially in the hot 1977-78 summer (Table 2.1, p. 13). From the partial time-budgets for adults, it is apparent that after December, when they spent less time on sunning and associated-preening activities, the birds foraged more, and spent as much or slightly less in body-maintenance. In addition, from the budgets for adult and immature Robins in the non-breeding season (Figs 10.2 p. 150, 10.3 p. 152, 11.1 p. 189, and 11.2 p. 191), it is apparent that when the birds had to forage more, body-maintenance was one of the first behaviours to decline. These results suggest therefore that sunning was a non-essential activity even for adults. In February and March drought conditions may have forced the Robins to spend longer in seeking food for maintenance and feather growth. Metabolic rates have been found to increase in moulting birds (Perek and Sulman 1945, Wallgren 1954) as a consequence of their decreased insulation and increased energy needs for feather growth (Lustick 1970, Thompson and Boag 1976).

On a diurnal basis, sunning by Robins did not occur to the extent expected for some day-periods. From Figure 7.7, it is apparent that sunning could have taken place more frequently than it did during the mid- to late afternoon because mean ambient temperatures were still adequate for it to have taken place then. Similarly, Hauser (1957) noted that "heat alone was not the motivating factor" in determining when birds sun-bathed. A possible reason why Robins did not sun-bathe as much as expected in the afternoon was probably because of their bimodal diurnal pattern of summer foraging which peaked in the mid-morning and mid-afternoon (Figs 10.7 p. 160, 10.8 p. 162, 11.3 p. 192, and 11.4 p. 197). Resting and body-maintenance activities occurred mainly about midday (Figs as above). Therefore, it seems that the birds were able to satisfy most of their food needs in the early to mid-morning and mid- to late afternoon so that around midday they had more time for less essential activities, such as sunning.

In conclusion, it seems unlikely that sunning served "any biologically essential purpose" (Potter and Hauser 1974). Because of the way that adults scheduled sun-bathing on a monthly and diurnal basis and since the weather conditions seemed adequate for sunning to have taken place when it did not, probably the activity was of secondary importance and the birds only sun-bathed after maintenance requirements had been met and "spare" time was available. The information does not allow me to determine which, if any, of the many functions ascribed to it, were fulfilled. Precise information about the timing of the Robin's moult needs to be known before this can be investigated further.

7.6. Summary

Descriptions of each of the body-maintenance activities of Robins are given in this chapter. The activities are stretching, body-shaking, head-scratching, beak-wiping, toe-nibbling, preening, bathing, anting and sunning.

Robins took a mean of 1.43 minutes (n = 58) to bathe and then followed this with drying movements for a mean of 2.97 minutes (n = 56). It was estimated that Robins spent about 0.005% of their time bathing and drying. However, Robins bathed while it rained, frequently shook water off themselves when foraging in wet vegetation and were seen perched, apparently ridding their plumage of water absorbed while foraging in the rain. For these reasons and because timed observations were not made when it was raining, it seems likely that the birds spent more time bathing and drying than my observations show. The data show that Robins bathed at a similar frequency during the course of the day, except in the early morning when they bathed least of all. The mean duration of the bathing and drying bouts tended to be longer in the afternoon.

Most Robins seen anting used ants or millipedes and did so on the ground. Of the 32 bouts observed, 25 consisted of the Robin finding an animal, anting for a few seconds and then eating it. In the other seven bouts, several animals were used one after another, for a mean time of 2.96 minutes. In total, Robins spent less than 0.001% of time anting. Since Robins spent so little time on this activity, usually anted with only a single animal and then ate it, I concluded that the anting movements were part of a feeding pattern for removing and/or avoiding the defensive secretions of a few prey species.

Only adult Robins were seen sunning. They sun-bathed mainly in December to February inclusive, when they had completed breeding and showed no signs of moult, or had started to moult. The mean duration of 172 sunning exposures was 2.1 minutes. Robins averaged 2.6 exposures during a bout of sunning. Almost all Robins preened, or panted and then preened, following an exposure. The mean duration of these associated-preening sessions was 2.0 minutes. Adult Robins spent more time sunning in December than in later months even though the monthly mean temperatures and hours of sunshine were greater in January and February. Sunning seemed to have no essential biological function for the birds because immatures were not seen to sun-bathe and adults sun-bathed less both on a monthly and diurnal basis when the weather conditions seemed most suitable for this activity.

CHAPTER EIGHT

PARTNER-INTERACTIONS, TERRITORIAL DEFENCE AND INTERSPECIFIC INTERACTION BEHAVIOURS

8.1. Introduction

Many observers have recorded the strong territorial habit of the Robin (Flack 1973, 1976a, Fleming 1950, Hay 1975, Moncrieff 1932). Both male and female Robins of a pair remained in their territory throughout the year and were aggressive towards all intruding conspecifics. Territories were defended for most of the year and only broke down to varying degrees during the post-breeding moult (Flack 1973, 1976a). Male Robins usually dominated their mates (Flack in prep.). Flack (1976a) described the use of the frontal spot and crown feathers by Robins during territorial disputes and interspecific interactions. However, I have seen no descriptions of several displays which do not involve these plumage displays. Therefore, this chapter describes Robin behaviour during partner-interactions, territorial defence and interspecific interactions.

8.2. Methods

The displays and movements associated with Robin interactions were timed and classified in one of three categories:- interactions between members of a pair, territorial defence and interspecific interactions. Sexual chases were timed and noted separately when seen. All other interactions were timed and pooled with data of the same category. These data will be presented in subsequent chapters describing Robin time-budgets.

8.3. Descriptions and results

8.3.1. Partner-interactions

Male Robins expressed dominance over their mates by erecting the crown feathers usually to a greater degree than the female, wing-lifting displays, fluffed body plumage and bill snapping. Occasionally, males pecked females to supplant them at feeding sites. This dominance over the female was a variable trait, some males always acted aggressively towards their mates while others fed amicably beside theirs. Only rarely and for short periods was a female seen to dominate her partner. This always involved an adult female who remained on her territory and paired with an immature male after her previous partner had disappeared.

Throughout the year, the most frequent type of partner-interaction involved the male approaching his mate with his crown feathers partially raised. In response the female usually erected her crown feathers, but to a lesser extent than did the male, and moved to one side. Such interactions often resulted when the male tried to use the same feeding site as the female or attempted to steal her food. When a female refused to give up prey which she could not fly off with, she "chucked", erected her crown feathers and stood over the prey. This invariably led to a brief skirmish, with the male chasing and pecking his mate. Eventually the female would display submissively by sleeking her crown feathers, crouching and making begging noises. If the male continued to peck the female, she responded with an open-beak display at him and partially exposed her frontal spot. The male then returned to eat the female's prey. Such aggressiveness by the male was usually restricted to the non-breeding season. During the breeding season, members of a pair fed amicably together with occasional crown-feather displays.

Pair formation took place throughout the year, except in January and February. A male and female Robin were considered to have formed a pair-bond after I had seen them together during several visits to the territory. Following the moult two distinctive displays were seen; the sexual chase and the "butterfly-flight" display. Sexual chases involved the male pursuing his mate. These chases began with the male following the female about on the ground with his crown feathers raised, sometimes lifting a wing and giving a soft twittering call. If the female crouched submissively the male pecked her rump. Often the female responded by moving through the ground-storey vegetation to evade this harassment. Sometimes she retreated into a site which protected her from the male's pecks. When the female did find such shelter the male perched nearby, but resumed the pursuit as soon as she ventured out. Eventually, the female was forced into flight, whereupon the male followed close behind. During the initial stages of the aerial chase, the male was often heard bill snapping and the female "chucking". Females when attempting to evade their mates, made many twisting and turning manoeuvres in flight in the upper and lower understorey while circling through the territory. The chase began at a moderate pace, but towards the end the birds seemed to be flying as quickly as possible. Chases stopped when either the

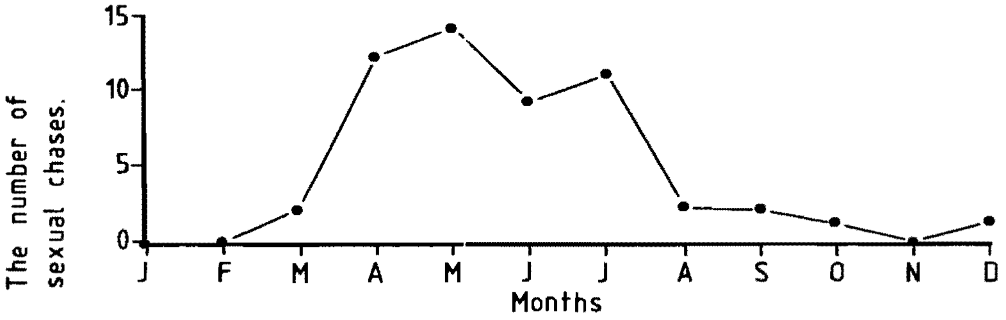


Figure 8.1 The number of sexual chases each month.

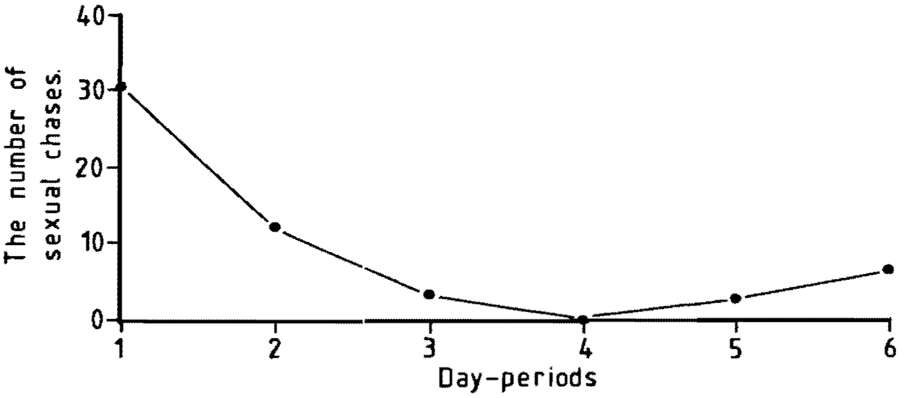


Figure 8.2 The diurnal rhythm of sexual chases.

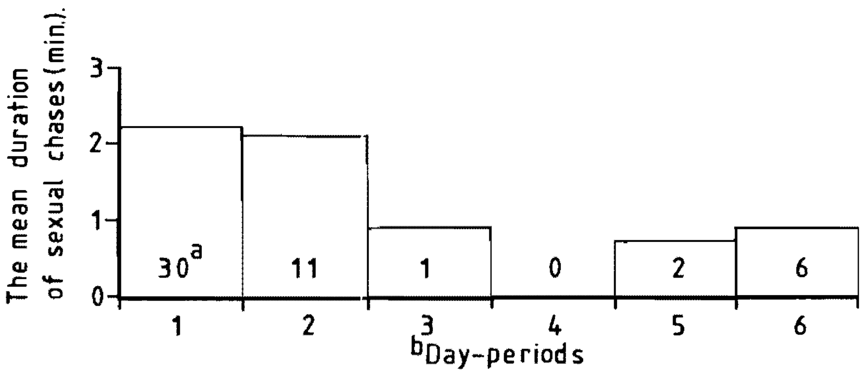


Figure 8.3 The mean duration of sexual chases during each day-period.

[a] Number of sexual chases.

[b] The division of the daylight hours into six equal-lengthed day-periods.

female eluded her mate or he gave up the pursuit. Bellbirds sometimes joined in: the Robins then dived for cover.

For a couple of minutes after the chase both birds panted, their plumage sleeked, and then began preening or foraging. After the chase the members of a pair sometimes foraged together. Some males chased their mates two or three times during a 30 to 60 minute observation. Of 54 sexual chases seen, 74% involved pairs where at least one member was an immature bird or where two adults had recently paired. One pair was seen to copulate in the interval between two sexual chases. These chases were most frequent following the moult and until breeding began (April to July) (Fig. 8.1). Most chases took place during the first two hours after dawn and occasionally later in the morning and late afternoon (Fig. 8.2). Fifty sexual chases lasted an average of 1.96 minutes (range: 0.6-4.5). The mean length of these chases per day-period was longest in the early morning (Fig. 8.3).

The "butterfly-flight" display of a male Robin involved him sleeking his plumage, fully exposing his frontal spot, drooping his wings to the perch, and lowering and fanning his tail. This posture was maintained for a few seconds with the male turning his back to the female, but with his head facing her. He then flew away with slow wing-beats of an exaggerated amplitude (butterfly-flight) while maintaining the plumage postures. The male was never seen to return to the female immediately after the display and usually repeated it if the two met within the next hour. Such a display was sometimes elicited by the female approaching and "chucking" at the male when he was singing. It was seen occasionally in autumn and winter, but mainly during the prelaying stage.

Interactions between members of a pair also involved male Robins feeding their mates. Late in the breeding season and during the moult males that had been bachelors often attracted newly independent immature females to their territories which they fed regularly and tried to attract to nest-sites. Although a few males fed their partners just before breeding began, most started courtship feeding only when nest-site selection or nest-building had begun. Courtship feeding occurred throughout the day from nest building and until the eggs hatched, after which the male rarely fed his mate. When the female began the next breeding cycle and the male was looking after the juveniles from the previous brood, she only occasionally received food from the male.

The male sang a short burst of full song to signal he was bringing food. Invariably, the female responded by flying to her mate and on landing near him gave a begging call, vibrated one or both wings, gaped and perched in a crouched stance with her beak pointed up towards the male. The male either placed the food into the female's beak, or the female grasped the food and broke it into smaller portions before eating it. Courtship feeding by Robins was not associated with copulation.

Robins were observed copulating (n = 10) more often outside the breeding season than during it, as were Black Robins (Flack MS). During the non-breeding season, copulation always took place after the moult and before noon. Most copulations involved the male mounting more than once and in each instance the pair included an immature bird. Copulation was noted during the prelaying stage of the breeding cycle, but as it was seen only twice at that time in the course of three breeding seasons it may have occurred during other stages as well.

Mounting and copulation only took place after female solicitation with a precopulatory display. This involved her approaching the male, giving a soft twittering call, and sometimes vibrating a wing. She also crouched near him with her plumage relaxed, frontal spot partially exposed and beak held horizontal or slightly upward. If the male did not approach her, the female followed him about, perching a metre or two away and continuing to solicit. When mounting did eventuate the male responded to the solicitations by flying back and forth between perches in front of her, giving a twittering call and wing-lifting displays. The male began these movements some distance from his partner, but gradually moved closer until just before mounting he was flying back and forth a few centimetres above her.

The female responded to her mate's display by increasing the frequency and volume of her call and vibrating one or both wings each time the male came close. When the male flew directly above her she assumed the copulatory posture; the legs were straightened, plumage sleeked, frontal spot fully exposed and the wings were raised level with the back to form a greater area for the male to stand on during copulation. She bowed each time the male flew near. Eventually the male landed next to the female and mounted her. He maintained his balance by vigorously flapping his wings during copulation. When the male dismounted, he immediately flew to a perch several metres from his mate, whereupon both birds began body-maintenance activities.

A display given by Robins in several situations apparently served to attract the attention of the partner or progeny. The displaying bird while perched alternately flapped its wings and gave a fast soft song, the "call-away" song (Hay 1975). If the Robin being displayed to moved towards the displaying bird, often the latter would fly off in a slow exaggerated manner while continuing to sing. Common situations in which the "attraction" display was seen were a male trying to attract his mate to nest-sites, a female bringing her mate's attention to newly hatched nestlings, a parent seemingly trying to encourage its mate to feed their nestlings and parents calling juveniles away from me or a predator. Flack (1976a, MS) noted that Black Robins and South Island Robins used this display in similar situations as each other.

8.3.2. Territorial defence

Territorial defence involved resident birds ousting intruders and displaying to neighbours at their boundaries. The behaviour of the resident males was predictable during these events as they dominated all trespassing Robins. However, females on their own territories, while dominant over female intruders, were occasionally chased by intruding males. Trespassers were vigorously chased to and sometimes over the boundary by the territory holder, except during the post-breeding moult. Moulting adults were less effective in evicting intruders and often failed to pursue them to the boundary.

A resident male on sighting an intruder sometimes approached, "chucking", with his crown feathers raised. Occasionally, a partial spot display was given by the territory holder, but once the intruder fled, as they invariably did, the resident's spot was covered. I often saw a resident male remain still as he watched a trespasser. Eventually he rushed towards it and pursued it to the boundary. Robins being evicted sometimes partially exposed their frontal spots.

Some females ousted male intruders while others remained motionless for up to ten minutes on occasion if they noticed them. Once the intruder had left the vicinity, the female either resumed whatever she had been doing or fled. When a female approached an intruding male to oust him, instead of fleeing he sometimes chased her. Whatever the intruder's response, females "chucked" loudly, which usually attracted their mates, who then ousted the Robin. On a few occasions intruding males responded to eviction by a female by giving the "butterfly-flight" display (Section 8.3.1).

During the breeding season, juveniles sometimes strayed into neighbouring territories. When attacked by the resident bird a juvenile usually did not flee immediately and so was quickly approached by the resident and pecked. Juveniles responded to these attacks by crouching, pointing their opened beaks at the aggressor and giving begging calls. Territory holders responded to these displays by stopping their attacks, but as soon as juveniles started to flee they were pursued and attacked. Similar behaviours were seen when adults chased their own juveniles from the territory once the latter were old enough to become independent. Twice when juveniles were being driven out vigorously by a parent, they assumed the precopulatory posture and gave begging calls (Section 8.3.1). In both cases the parent stopped harassing the juvenile and withdrew a short distance.

Confrontations between neighbouring Robins involved them moving along the boundary displaying vigorously. Postures used included elevation of crown feathers to create a "helmeted appearance" (Flack 1976a), wing-lifting, fluffing of the contour plumage and tail fanning. Frontal-spot displays were not seen during these disputes, but were seen by Bissett (1978) during boundary disputes between two Pied Tits. While moving along the boundary, often only 10 to 30 cm apart, one or both Robins would suddenly lunge at the other. During these skirmishes, bill snapping was heard. Often the two birds flew parallel to each other along the boundary displaying their white under-tail coverts above and to the sides of the tail. Some of these disputes lasted for up to ten minutes. Generally, disputes stopped when one of the birds began feeding. If the non-feeding opponent encroached over the boundary, the feeding individual resumed the defence of his territory, but eventually both left to feed.

The few boundary disputes watched on Outer Chetwode Island differed from those seen at Kowhai Bush. On the island little movement along the boundary occurred and no wing-lifting displays were seen. The neighbouring birds usually spent most of the time with their plumage fluffed, staring at each other.

8.3.3. Interspecific interactions

Robins chased several avian species (Flack 1976a, Moncrieff 1932), especially those near their nests, juveniles or stored food. A few species, mainly predators, caused Robins to give alarm calls or to leave the immediate area silently. A Robin's response to a predator depended on whether the Robin was breeding or not. Before Robins chased other birds they often fully displayed and flashed the white frontal-spot. The intruder sometimes withdrew apparently in response to the display. Usually the Robin gave chase with bill snapping and a continued frontal-spot display. Although Robins sometimes made repeated pursuits, I never saw a Robin catch up with and peck another bird.

Several situations resulted in Robins interacting with other birds. Both members of a pair readily drove off smaller species which ventured near their nest once building had commenced. Incubating females often left their nests to drive away other birds. Adult Robins evicted many kinds of birds from the area immediately around their juveniles while the latter were poor fliers. Robins that had stored food and were still near the cache site were often seen chasing birds away from it. The species that were seen chased by Robins several times during this study included the Rifleman, Hedgesparrow *Prunella modularis*, Brown Creeper, Grey Warbler, Fantail, Silvereye and Chaffinch. The Hedgesparrow and Fantail, in particular, were frequently pursued, often without any cause being evident. One or two Yellow-breasted Tits usually moved into Kowhai Bush during the late summer and autumn. Sometimes they were ignored by Robins, but at other times were vigorously chased. Song Thrushes, Blackbirds and Bellbirds were only evicted from the vicinity of Robin nests. In contrast, Robins on Outer Chetwode Island frequently chased the smaller female and juvenile Bellbirds. The island Robins were also occasionally seen to chase Yellow-crowned Parakeets.

Bellbirds were the only species that regularly chased Robins at Kowhai Bush. When approached by a foraging Bellbird, Robins sleeked their plumage and remained motionless or moved to cover. When chased, Robins invariably sought shelter under lower-understorey vegetation where Bellbirds seldom continued in pursuit. Three instances were seen where a female Bellbird took lining feathers from Robin nests with eggs when the Robin was absent. In one case the Bellbird was still at the nest when the owner returned. The Robin did not chase the intruder, but remained at a distance until the Bellbird left. Incubating Robins crouched low into their nests whenever a Bellbird came near.

Harriers, Magpies, Kingfishers, mustelids (*Mustela* spp.), and feral cats all elicited an alarm response from Robins. When such predators moved near Robin nests or juveniles, the adults "chucked" loudly. This vocalization invariably resulted in the other member of the pair arriving and both birds following the predator about. If the predator got close to the nest or young the "chucks" became louder and the calls were "run together in a rapid staccato manner" (Flack 1976a). Although I did not see predators close enough to a nest for them to elicit the Robin's distraction display described by Flack (1976a) and Soper (1976), it was often elicited by my presence at a nest, even before egg laying and after the nestlings had left it.

Outside the breeding season Robins varied their responses to predators. Some followed predators, such as mustelids, about for a while and "chucked". Others perched nearby and watched the predator go by without giving any calls. Roosting Moreporks at both study areas were approached by "chucking" Robins. A Kingfisher which perched in the canopy resulted in a pair of Robins "chucking" at it continually for over ten minutes, until it departed. Ground-gleaning Robins on Outer Chetwode Island flew to a perch or moved to a new foraging area whenever a Western Weka came near. When a Harrier soared just above the canopy Robins remained motionless or dived for cover.

8.4. Discussion

8.4.1. Partner-interactions

Flack (1976a) noted the dominance of male Robins over their mates. This situation was expected considering the highly territorial nature of the species and of males in particular. Furthermore, males were heavier than females (Flack in prep.), possibly giving males an advantage in disputes with their partners. Elevation of the crown feathers nearly always occurred during partner-interactions and seemed to signal varying levels of aggressiveness to other Robins. Male Robins usually raised their crown feathers higher than their subordinate mates. However, there was ambivalence in this display with the aggressive component being dominant; Morris (1958) proposed a similar cause for the display. The crown feathers were not raised on a Robin who was fearlessly chasing another, but in an aggressive situation where there was also some fear, such as approaching a mate or during a boundary dispute, this display was seen. Thus, its use was especially noticeable in situations where there was some degree of resistance by an opponent (Flack 1976a).

Sexual chases have been described for many avian species: Purple Martins *Progne subis* (Brown 1978), Chaffinches and three *Parus* species (Hinde 1952, 1953), Reed Buntings *Emberiza schoeniclus*, Yellow Hammers *E. citrinella*, Corn Buntings *E. calandra* (Howard 1929) and Snow Buntings *Plectrophenax nivalis* (Tinbergen 1939). Nice (1943) considered that the "pouncing" of male Song Sparrows *Melospiza melodia* in which they collided with their mates and then immediately flew away giving loud song was analogous to the sexual chases of *Emberiza* species. Flack (MS) describes sexual chases of Black Robins, but gives no indication of having seen similar behaviour from South Island Robins.

The sexual chases of Purple Martins were of only 15 to 40 seconds duration (Brown 1978) compared with nearly two minutes for those of Robins. The protracted length of Robin sexual chases may reflect the Robin's highly aggressive nature; Purple Martins breed in colonies and individual males defend only a small area around their nest entrances. Sexual chases mainly occurred during the early morning, with a few in the late afternoon. Similarly, the sexual chases of Reed Buntings and Yellow Hammers also took place largely in the early morning, as did the courtship behaviour of male Dickcissels (Schartz and Zimmerman 1971), European Robins (Lack 1946) and female Long-billed Marsh Wrens (Verner 1965).

Sexual chases have been considered to occur for several reasons. Howard (1929) found that they arose between Reed Buntings during the initial stages of pair formation and also after a pair had reared their first brood and were about to begin the next breeding cycle. He considered that these chases occurred because the male was physiologically ready to copulate, but that the female was not. Howard (1929) concluded that the female's flight from her mate was a definite response, a false attempt to escape. Nice (1943) noted that the "pounces" of Song Sparrows were confined typically to the early stages of the nesting cycle and took place again after the young had left the nest. She concluded that the male was not ready to copulate as pouncing had "no immediate connection with copulation", but that it may have been a "technique of the male for impressing himself upon his mate during the time of silence, of making his presence keenly felt!". Similarly, Andrew (1957, 1961) concluded that the sexual chases of Yellow Hammers were not copulation attempts by the male and that they did not arouse a sexual tendency in the female. He considered that a male had a weak sexual tendency to approach a potential mate, but that he also had a tendency to attack her, which was increased by the strong stimulus of her flight away from him. Together both tendencies were suggested to cause him to chase the female. Brown (1978) concluded that the sexual chases of Purple Martins, and Welty (1975) that such chases of birds in general, maintained or strengthened the pair-bond and/or synchronised the reproductive physiology of the pair. Flack (MS) found that Black Robin pairs engaged in sexual chases year round and that these chases frequently ended in mounting without any solicitation from the female. Two females were seen with most of their dorsum feathers worn off, which Flack thought was a result of the mountings of their partners. Because Black Robins did not use crest-feather displays, which were prominent and important for pair-bond maintenance in the South Island Robin, Flack's (MS) impression was that the sexual chases and frequent mountings by the former species served to maintain and strengthen the pair-bond.

Overall, the evidence from South Island Robin sexual chases seems to suggest that they reinforced the bond between the members of a pair. Most chases occurred during the period following the moult and until breeding began, a period when unmated Robins paired. Seventy-four percent of sexual chases involved these recently paired Robins. The initial stages of pair formation was probably a time when some form of male courtship behaviour would be expected to strengthen the pair-bond and so enhance the chances of the female remaining with him. Courtship feeding, which is assumed to serve this function (Andrew 1961, Lack 1940, Morley 1949) was not seen for Robins until just before or when breeding began, so that sexual chases may have served this function during the non-breeding season. Presumably, the sexual chases that took place after moult between birds that had previously bred together served to reinforce their established pair-bonds. The moult was a period when members of a pair moved about more on their own than previously.

Robin sexual chases did not appear to be copulation attempts by the male for two reasons. First, a female that was seen to solicit and was mounted by her mate, had not long before and a few minutes after been involved in a sexual chase. Therefore, it seemed likely that had the male wanted to mount his mate at the start of the chases, she would have been receptive. Second, the behaviour of the male at the start of the chases did not include displays seen just before copulation. Sexual chases began with a male displaying aggressively by pecking the female, bill-snapping and often he did not stop this when the female gave the submissive display. A male that was approached by his soliciting partner gave displays involving submissive components, with only a gradual approach to mount her. The feature of the sexual chases that was difficult to understand was how the aggressiveness of the male, which resulted in both birds panting from exhaustion, strengthened the pair-bond. What also was surprising was that after these chases the pair-members often fed near each other and the female showed no obvious increased fear of her mate.

Displays similar to the male Robin's "butterfly-flight" display were given by both sexes of Blue Tits and male Chaffinches (Hinde 1952, 1953), Blackbirds (Morris 1956) and Snow Buntings (Tinbergen 1939) during their courtship behaviour. Pepper (1966) described a display between a pair of Scarlet Robins in which the female "flew very slowly past the male, fluttering like a butterfly, and in doing so gently brushed her wings over his head and continued on. The male remained perfectly still until she had passed then fully extended each wing in turn, so that the wing covered his side and hid his legs". Both actions of drooping the wings and flying like a butterfly were present in the male South Island Robin's display. Mainly actions conveying submissiveness were present in the display:- the prominent frontal spot, sleeked plumage and movement away from the female. Flack (1976a) noted that the frontal-spot display given during territorial disputes was "often followed by flight away from an attacking Robin and appeared to communicate a high escape or submissive motivation". Plumage sleeking was used by birds being attacked as they crouched submissively or fled. The reasons for the exaggerated flight movements may have been to slow the male's rate of movement away from his mate and to attract her attention to the submissive components of the display.

Although the display sometimes arose outside the breeding season, it was seen mainly during the prelaying stage, the only stage when copulations were seen. For copulation to take place, the dominance of the male and the fleeing tendencies of the female must be reversed or negated (Morris 1956). This reversal of dominance roles is not uncommon between paired birds before copulation (Hinde 1953, Shoemaker 1939, Tinbergen 1939). Therefore, the "butterfly-flight" display may have been a signal to the female of the male's submissiveness and readiness to mate.

In displays by members of a pair just before copulation, submissive actions predominated. As noted by Hinde (1953) for Chaffinches and Brown (1978) for Purple Martins, it was the female who solicited copulation, moving towards their mates to seek copulation by giving submissive displays and calls. That juveniles assumed this precopulatory posture when attacked was evidence that it was a submissive display. The male's response to his soliciting mate showed his conflicting tendencies to approach and mount, and to flee. His movement towards the female was a gradual process and often the fleeing tendency seemed to predominate, as males often did not mount or dismounted before copulation was achieved. The male always fled from his mate after copulation showing that the submissive tendencies also predominated afterwards.

The postures and displays of the female Robin when accepting food from her mate were similar to the courtship-feeding displays of other passerines (Welty 1975). The amount of food supplied by the male Robin seemed to constitute an essential part of the breeding female's nutrition, as proposed by Royama (1966b) for courtship feeding in Great Tits. Since courtship feeding did not take place until breeding began, about four months after pair formation, it was unlikely that it was of great importance in reinforcing the pair-bond. In many species, courtship feeding occurs just before copulation and may act as a releaser for it (Welty 1975). However, it did not serve this function in the Robin as the female solicited for copulation, not the male. Nest-building and incubation was done solely by the female. It seemed that the frequent trips with food by the male to the female (about 3/h), allowed her to build the nest as rapidly as she did and to maintain a high degree of incubation attentiveness, than if she had had to find all her food. Evidence to support this hypothesis will be presented in later chapters dealing with the time-budgets of breeding female Robins.

8.4.2. Territorial defence

As noted by several observers, resident male Robins evicted all trespassers that entered their territories (Flack in prep., Fleming 1950, Hay 1975, Moncrieff 1932). This dominance seemed to weaken only while the birds moulted, because some adults then failed to evict intruders. As has been found for many other territorial vertebrates (Dorst 1974), a resident Robin was always dominant within his territory and trespassers usually fled when challenged. Chases continued to the boundary where the resident bird stopped his pursuit. However, Flack (pers. comm.) noted that in years of high population at Kowhai Bush the territorial behaviour of the Robins was more variable than that I saw. He often saw birds feeding in neighbouring territories and saw a greater breakdown of territorial defence during the moult, with immatures often remaining in adults' territories. In addition, occasionally an old, established bird lost part or all of its territory to a neighbouring or immature male.

When neighbouring males at Kowhai Bush meet at their boundary, vigorous displaying lasted for several minutes, presumably because they did not patrol their boundaries, which seemed indistinct. Also, they did not seem to meet each other regularly. In contrast, on Outer Chetwode Island, boundary disputes appeared to be of shorter duration and did not involve wing-lifting. These features of the disputes of the island birds may have arisen because neighbouring birds often saw each other in the small territories they inhabited (Table 9.1, p. 132), so they possibly recognised their neighbours and the exact location of the boundary (Flack 1976b).

The submissive displays of subordinate birds incorporated components of the food-begging posture of nestling and juvenile Robins, as found by Andrew (1961) for several other species. Andrew (1961) also noted that some *Emberiza* species responded when attacked by giving the female precopulatory display, as did juvenile Robins.

The exposing of the frontal spot by attacked Robins during intra-specific encounters was seen by Flack (1976a). He concluded that in such a context the spot display appeared to communicate a high escape or submissive motivation. The white spot may serve to take emphasis away from the bill rather than enhance its aggressiveness, better serving escape or submission.

8.4.3. Interspecific interactions

The frontal-spot and crown-feather displays of the Robin during interspecific interactions were described and compared with those of other *Petroica* species by Flack (1976a). I found, as had Flack, that the frontal spot was exposed when Robins displayed to and chased species which they were able to dominate. Many of these chases were related to the defence of the nest, its contents and juveniles (Flack 1976a). However, many interspecific interactions took place outside the breeding season when some species were pursued seemingly for no apparent reason. It was possible that in these cases Robins were protecting stored food of which I was unaware. But species pursued included the Grey Warbler, Yellow-crowned Parakeet and Fantail, all of which seemed to pose no threat to the Robins or their stored food, which consisted mainly of earthworms (Table 5.1, p. 50). It seems likely that these interactions outside the breeding season were the result of the highly territorial nature of the Robin extending from conspecifics to other species. Dorst (1974) noted that where the territorial habit of a species was very strong, the hostility extended to quite different species.

It is also possible that the interspecific aggression was a means of dealing with potential competitors. All the species chased at Kowhai Bush were insectivores and some fed on the ground. The two species most often chased were the Hedgesparrow and Fantail. Hedgesparrows spent much time on the ground taking small items that were also potential Robin prey. A Fantail was able to subdue quite large prey by clamping it to a perch with its foot and pecking it (Ude Shankar 1977). Although they were regularly chased, Fantails did not seem to pose a great threat to a Robin's food supply. Possibly, Fantails were chased more frequently than expected because they were attracted to me to capture prey disturbed by my movements as I followed a Robin.

The full exposure and flashing of the white frontal spot, surrounded by the contrasting dark head, may have served as a warning display during interspecific interactions as it was visible from many metres away. Flack (1976a) considered that the use of this display conserved time and energy for the Robin by threatening other species so that a chase did not eventuate and the danger of physical contact was avoided. My observations agreed with this hypothesis, but only on a few occasions did Robins not chase the individual to which they had displayed.

The Bellbird was the only species in Kowhai Bush which regularly dominated Robins and sometimes initiated aggressive pursuits of them (pers. obs., Flack 1976a). Meliphagidae, both in New Zealand and Australia, are known to exhibit interspecific territoriality (Dow 1970, 1977, Flack 1976a, Oliver 1955, St Paul 1975). Therefore, most of the chases of Robins by Bellbirds were probably a consequence of the latter's highly territorial nature. All other non-predatory species that chased Robins did so only to protect their nests and young.

As noted by Flack (1976a), Robins reacted throughout the year to predators at close quarters, by following them about and staccato "chucking". However, outside the breeding season the appearance of predators, such as mustelids, often resulted in Robins flying up to a perch and watching them move by without giving an alarm call. The list of predators given by Flack (1976a) that Robins reacted to by "chucking" agree with my observations and can be extended to include the Weasel, Ferret and Kingfisher.

8.5. Summary

Male Robins dominated their mates, expressing this dominance by erection of the crown feathers. Most partner-interactions outside the breeding season involved the male supplanting the female from a feeding area.

Sexual chases mainly took place after the moult and until breeding began. The male pursued his mate in flight about their territory. Robins that had recently paired were more often involved in sexual chases than were pairs that had bred together during the previous breeding season. Most such chases arose in the morning and had a mean length of 1.96 minutes. The sexual chases may have served to reinforce the pair-bond between the members of a pair.

The "butterfly-flight" display of male Robins was usually seen during the prelaying stage of the breeding cycle. A singing male responded when approached by his "chucking" mate by giving a characteristic plumage display and then flying away with a butterfly-like flight. Since this display showed only submissive components, it probably indicated a change to a submissive role by the male over a period when copulation occurred.

Robins were seen more often copulating outside the breeding season; perhaps it functioned to reinforce the pair-bond. Mounting occurred only after the female solicited for it by giving a precopulatory display.

Resident males chased all intruding conspecifics from the formers' territories, but the response of resident females to intruders varied. Trespassers often gave a frontal-spot display when approached and chased by territory holders, which may have served to de-emphasise the beak to better serve submission. Juveniles responded to attacks by adults by crouching and giving begging calls or by assuming the precopulatory display.

During boundary disputes, neighbouring birds moved up and down the boundary displaying vigorously. Elevation of the crown feathers, wing-lifting, fluffing of the contour feathers (especially the white breast) tail fanning, exposing of the under-tail coverts and bill snapping were seen and heard during these disputes.

Robins chased several avian species, especially when the latter approached a Robin's nest, juveniles or stored food. A frontal-spot display was usually given by Robins before chasing other birds. It is likely that some interactions were the result of the Robin's highly territorial nature extending to birds other than conspecifics, and functioned to oust potential competitors. The Bellbird was the only species that regularly chased Robins, a result of the former's highly interspecific territorial nature.

Predators elicited "chucking" and were followed about the territory. However, outside the breeding season some Robins gave no alarm calls when approached by a predator, but remained on a safe perch until the predator moved out of sight.

PART 3

TIME-BUDGETS FOR ROBINS OUTSIDE THE BREEDING SEASON

CHAPTER NINE

A COMPARISON OF THE TIME-BUDGETS FOR ADULT MALE ROBINS AT KOWHAI BUSH AND OUTER CHETWODE ISLAND

9.1. Introduction

An important aspect of this study was to determine which behaviours were most important for the survival of a Robin. Initially, an organism must spend a certain amount of time meeting maintenance demands (Verbeek 1972). This involves spending time finding enough food for the energy needs of metabolism, thermoregulation, and the procurement and processing of food. Only after these basic demands have been met can other activities requiring extra energy, such as reproduction and moulting be performed.

Flack (1975b, 1976b, in prep.) found that Robins on Outer Chetwode Island differed from those at Kowhai Bush in having a delayed breeding season and lower productivity (Table 9.1). However, when birds from the island were released onto similar nearby islands they immediately assumed an August to December laying season, clutchsize increased and pairs became triple brooded (Flack 1975a, 1978). Thus, their delayed breeding and reduced productivity seemed to be caused by an environmental factor

Table 9.1. Some population features of Robins at Kowhai Bush and Outer Chetwode Island. (Information from Flack (1976b, in prep.)).

Feature	Kowhai Bush	Outer Chetwode Island
Main egg-laying months:	August-December	September-October
Modal clutchsize:	3	2
Number of broods per season:	3[a]	<1[b]
Mean number of juveniles fledged per pair:	3.00	0.14-1.10
Territory size range per pair (ha):	1-5	0.2-0.6

[a] If no losses occurred that forced renesting.

[b] Not all birds bred.

rather than being genetically controlled. From Table 9.1 it seems that the smaller mean territory size of the island population may limit the food supply of each pair. I hypothesised therefore, that when not breeding the island birds would spend more time in behaviours associated with maintenance than would the Kowhai Bush birds and that by comparing their time-budgets I would be able to determine the priority of behaviours involved in maintenance.

As a consequence of colder temperatures, reduced invertebrate availability and shorter daylengths, winter is the time when birds spend more of the day meeting maintenance requirements (Gibb 1954, 1956, Verbeek 1972, Wright 1978). Therefore, observations of the island Robins were made just before and during the month of shortest daylength to see if Robins were spending most of their time in maintenance behaviour.

9.2. Methods

Three one-week visits were made to Outer Chetwode Island from 6-13 April, 15-22 May and 6-12 June 1978. The methods used to follow and time the behaviour of the island birds were the same as those used at Kowhai Bush (Section 3.5, p. 20). The behaviour of only colour-banded adult males was recorded on Outer Chetwode Island for two reasons. First, colour-banding of nestlings had not been carried out during the previous two breeding seasons, so unbanded birds could not be distinguished as immature or adult. Second, adult females tended to inhabit areas in which it was difficult to follow them about; viz., low scrub on steep hillsides, whereas males inhabited gullies which had bush with a high canopy and little lower understorey and ground storey - ideal habitat for observing behaviour.

During the visits, daily maximum and minimum temperatures (°C) were recorded and the mean temperature for each visit determined (Section 2.1.4, p. 12). The mean temperature during each visit was higher than that at Kowhai Bush for the same month (Table 9.2).

Table 9.2. The mean temperature (^{o}C) during visits to Outer Chetwode Island and for each month at Kowhai Bush from April to June 1978.

	—Mean temperatures for—	
Month	Outer Chetwode Island	Kowhai Bush
April:	16.9	14.1
May:	11.3	10.2
June:	12.3	6.7

9.3. Results

In Figure 9.1 the time-budgets of adult male Robins at Kowhai Bush and Outer Chetwode Island during April, May and June 1978 are presented. Plotted values are given in Appendix 3. Figure 9.2 shows the diurnal pattern of each behaviour for the two populations and Appendix 4 gives the graphed values. The results shown in Figure 9.2 were obtained by combining all the observations made over the three months which were then separated according to the day-period in which they were made. The significant results are as follows.

Compared with the Kowhai Bush population, the island birds spent more time foraging in all three months (Fig. 9.1) and in most day-periods (Fig. 9.2). The diurnal foraging pattern was quite different for the two populations. The island birds spent similar proportions of time foraging each day-period (except for a significant reduction in the late morning), while the Kowhai Bush birds foraged less in early and mid-morning than during the rest of the day ($P < 0.01$) (Fig. 9.2).

Adult males at Kowhai Bush spent more time vocalizing and in partner-interactions than did the Outer Chetwode Island birds ($P < 0.01$) (Fig. 9.1). Kowhai Bush males had a distinct diurnal pattern of involvement in these two behaviours, spending more time in them during the early and mid-morning. However, there was no diurnal rhythm for these behaviours in the Outer Chetwode Island data. Thus, the Kowhai Bush birds foraged less and spent more time in singing and partner-interactions during the early morning than afterwards (Fig. 9.2).

Furthermore, the Kowhai Bush birds spent more time in body-maintenance than did the island birds, but the data for the former males does not show an obvious diurnal pattern for this behaviour. Adult males on

Figure 9.1. The monthly time-budgets for adult male Robins at Kowhai Bush and Outer Chetwode Island in April, May and June 1978. Appendix 3 gives the plotted values.

[a]The asterisks denote significance levels: * = $P < 0.05$, ** = $P < 0.01$. Those placed next to the sides of columns indicate significant differences between adjacent monthly samples. Asterisks above the columns of the Outer Chetwode Island male time-budgets show significant differences between the proportion of observation time the island and Kowhai Bush males engaged in a behaviour for the same month.

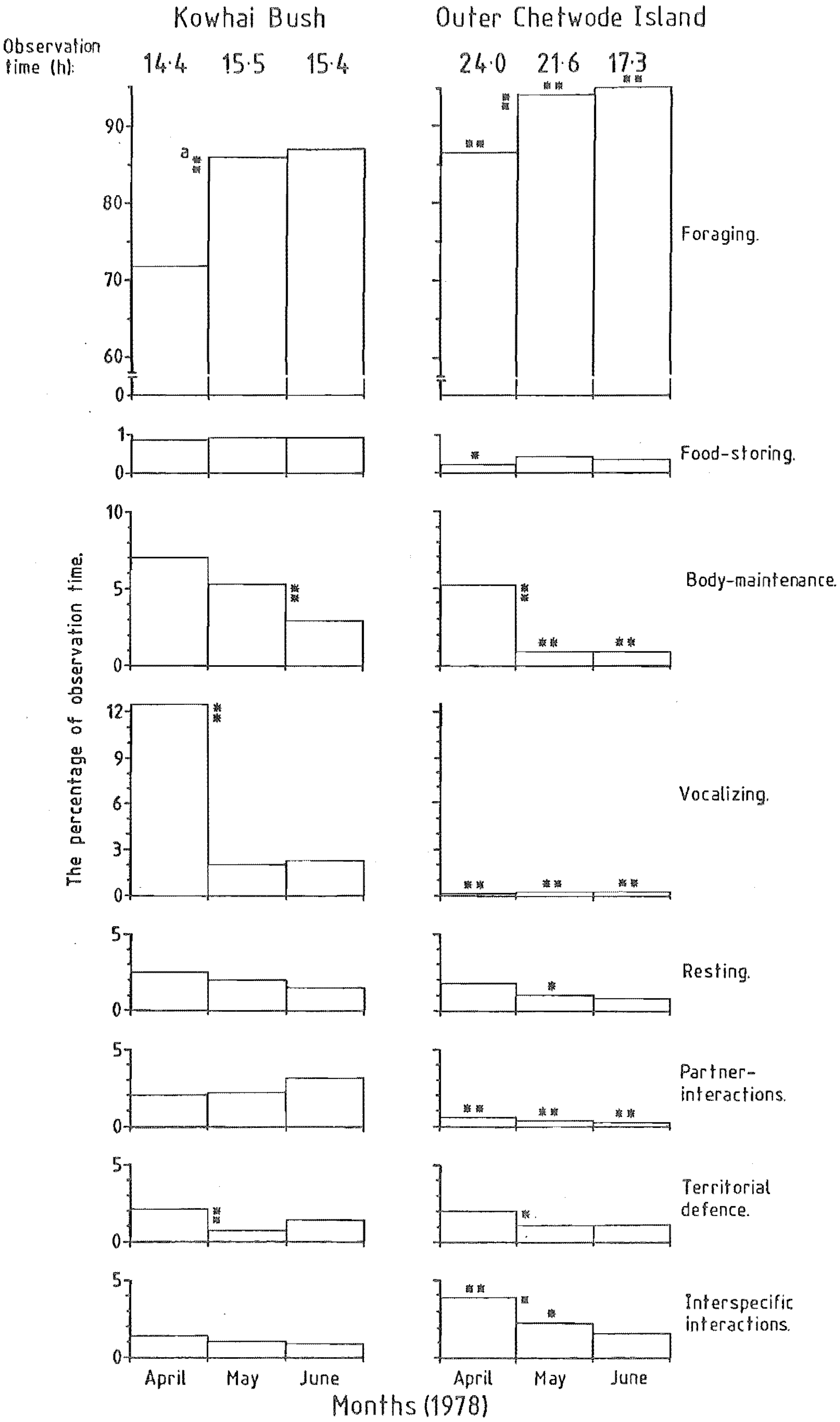
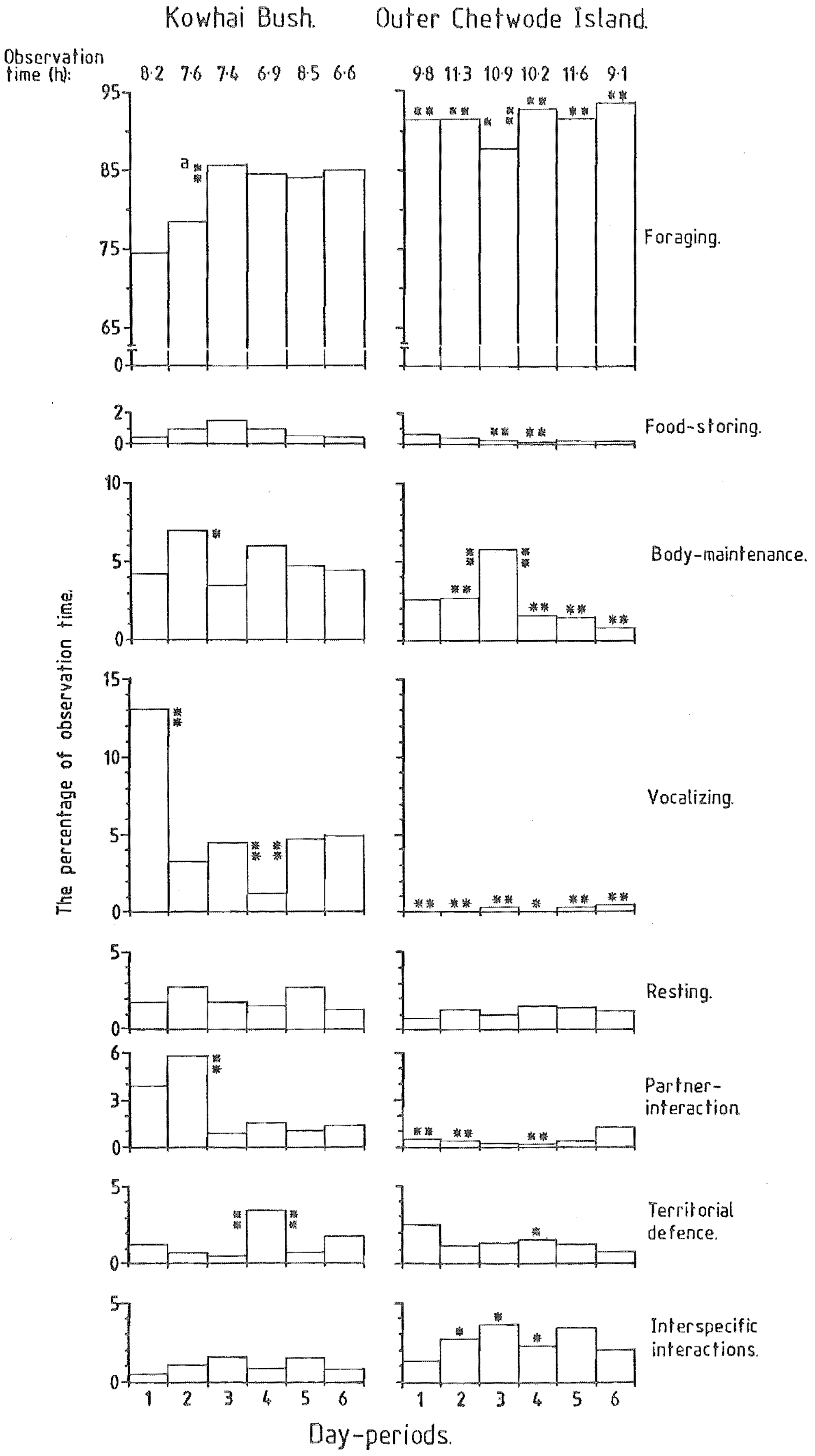

Kowhai Bush
Outer Chetwode Island
Observation time (h):
14·4
15·5
15·4
24·0
21·6
17·3
90
80
70
60
0
1
0
10
5
0
12
9
6
3
0
5
0
5
0
5
0
5
0
a
**
*
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
The percentage of observation time.
April
May
June
April
May
June
Months (1978)

Figure 9.2. The diurnal patterns of behaviours for adult male Robins at Kowhai Bush and Outer Chetwode Island during April, May and June 1978. Appendix 4 provides the plotted values.

[a]The asterisks indicate significance levels: * = $P < 0.05$, ** = $P < 0.01$. Those placed next to the sides of columns show differences between adjacent day-period samples. Asterisks above the columns for Outer Chetwode Island males denote differences between the percentage of observation time the two populations spent in a particular behaviour during the same day-period.


Kowhai Bush.
Outer Chetwode Island.
Observation time (h):
8·2 7·6 7·4 6·9 8·5 6·6
9·8 11·3 10·9 10·2 11·6 9·1
95
85
75
65
0
a
Foraging.
2
0
Food-storing.
10
5
0
Body-maintenance.
15
10
5
0
Vocalizing.
5
0
Resting.
6
3
0
Partner-interaction.
5
0
Territorial defence.
5
0
Interspecific interactions.
The percentage of observation time.
1 2 3 4 5 6
1 2 3 4 5 6
Day-periods.

Outer Chetwode Island did have a diurnal pattern of body-maintenance, with a marked increase in time spent in this behaviour during the late morning.

There was little difference between the populations in the percentage time per month spent in storing food, resting and territorial defence. Also, in neither population was a diurnal pattern for these behaviours evident, except for a significant increase in time devoted to territorial defence during the early afternoon for the mainland population.

The island birds spent more time in interspecific interactions than did the Kowhai Bush birds in April and May. Although birds of the island population devoted more time to this behaviour from mid-morning to mid-afternoon, the results show that for neither population was there an obvious diurnal pattern of interspecific-interaction behaviour.

9.4. Discussion

Although Robins on the island were at higher densities than at Kowhai Bush, I do not think that this implies a greater density of food at the former site. The mortality of adult Robins in Kowhai Bush was highest in autumn (Flack 1976b, Fig. 12.1 p. 217), when they foraged for less of the day than in winter. This suggests that the greater mortality of the mainland Robins was not related to food shortages and that their low density was a consequence of other factors.

As expected from Table 9.1, adult males on the island foraged more than did the Kowhai Bush birds ($P < 0.01$). Two possible explanations could be either that the island birds had to spend more time foraging to find enough food to meet maintenance requirements, or that they had "spare" time which they spent feeding because there was no need to spend more in other behaviours. If each species maximises its reproductive effort (Lack 1954, Lack *in* Watson 1970), one would expect that when Robins are able to meet their maintenance requirements in less than the available time they would use "spare" time for behaviours related to reproduction. Therefore, it seems more likely that the island birds spent a greater proportion of the day foraging to obtain sufficient food for maintenance.

The two study areas have similar latitudinal positions (Fig. 2.1, p. 7). Thus, both populations had similar daylengths, hence the longer time spent feeding by the Outer Chetwode Island population cannot be attributed to a difference in this factor.

Experimental work with small passerines has shown that an inverse relationship exists between food intake and ambient temperature (Davis 1955, Kendeigh 1949, Seibert 1949), with a linear increase in metabolic rates as ambient temperature decreases below the thermoneutral zone (Kendeigh 1939, Wallgren 1954, Hart 1962). Seibert (1951) suggested that several species of herons departed earlier from their roosts to feed when temperatures were lower because of increased energy demands. From observations of a flock of Brewer's Blackbirds *Euphagus cyanocephalus* in winter, Verbeek (1964) showed that an inverse relationship occurred between environmental temperature and the length of time spent feeding. Ambient temperatures were higher at Outer Chetwode Island than at Kowhai Bush so it would have been expected that the island population would have spent less, rather than more, time feeding per day than did their mainland counterparts. Thus, ambient temperature seems unlikely to be a factor affecting differences in time spent feeding.

Small birds often have morning and evening feeding maxima (Baldwin and Kendeigh 1938, Beer 1961, Gibb 1954, Lees 1948). Under mild temperatures, or when food is readily available, insectivorous species feed most intensively in the afternoon (Kuusisto *in* Morton 1967, Verner 1965). However, when an environmental factor causes birds to increase their rate of food intake or to spend longer finding the same amount, they often increase the time spent foraging in the morning. For example, White-crowned Sparrows *Zonotrichia leucophrys* feeding in mid-winter on warm, sunny days had a bimodal feeding pattern with the afternoon maximum being much greater than the morning one (Morton 1967). However, on cold, cloudy days the birds foraged intensely both in the early morning and late afternoon with a much reduced midday minimum. Lees (1948) demonstrated that the peak frequency of visits by European Robins to food-baited traps in October and November took place in the mid-afternoon. But in December and January (mid-winter), the bird's morning peak was as great as the afternoon one. Similarly, Beer (1961) investigating the feeding behaviour of the House Sparrow *Passer domesticus*, found that in winter at mild temperatures the birds activities showed a small peak in feeding in the morning and a larger one in the afternoon. However, during extremely cold temperatures the majority of feeding activity shifted to the morning. These studies suggest that during periods of environmental stress, small passerines spend more time in feeding during the morning and midday periods so that little, if any, diurnal pattern of feeding is evident. This was the situation with the Outer Chetwode

Island Robin population, although it was not clear what factors were responsible. Possibly a lower food availability and/or smaller territory size resulted in these birds having to feed longer. Flack (1974) considered "that the habitat at Kaikoura is as good or better than on Outer Chetwode Island." That food availability to the island birds was restricted by small territory size is supported by the response of these Robins when shifted to uncrowded environments (Flack 1974, 1976b). The diurnal pattern of foraging for the Kowhai Bush birds contrasted with that for the island Robins; the former spent significantly less time feeding in the early and mid-morning compared with the rest of the day. Presumably the Kowhai Bush males found sufficient food in less time to satisfy their maintenance requirements.

Vocalizations, interactions between members of a pair and body-maintenance were all behaviours which Outer Chetwode Island Robins spent less time in than did the mainland birds. Throughout the island visits full song was never heard, although the Robins there spent similar proportions of time giving the other types of vocalizations compared with the Kowhai Bush birds (Section 6.4.5, p. 76). Most full song heard at Kowhai Bush was given by bachelors, presumably to attract a mate. Bachelors were always present during this study among the population of about 30-80 birds at Kowhai Bush and probably were also present in the island population of about 120 (Flack and Lloyd 1978). It seems that the island bachelors did not sing because foraging was of a higher priority. Attracting a mate was an early stage towards reproduction, a behaviour only possible after maintenance requirements had been met (Verner 1965). Likewise, it was found by Schartz and Zimmerman (1971) that breeding male Dickcissels *Spiza americana* were forced by physiological heat stress, caused by very high ambient temperatures, to rest more. The effect on the Dickcissel's time-budget was similar to that of the island Robins, but for a different reason - to spend more time resting the Dickcissels reduced the proportion of time devoted to reproductive activity, but not that spent on maintenance. Similarly, the partner-interaction behaviour of the island adult males included no activities resulting in pair formation as did that of the Kowhai Bush Robins. The island Robins were very aggressive towards their mates, chasing them whenever they came near. As a result the members of a pair were rarely seen together, keeping to different parts of their joint territory. Although males also dominated their mates at Kowhai Bush, they were more tolerant so that members of a pair often fed near each other. In addition, the Kowhai Bush pairs participated in sexual chases (Section 8.3.1, p. 115), an activity that seemed to be involved in pair formation and the reinforcement of the pair-bond between members of established pairs. Thus, the greater proportion of time spent in partner-interactions by the mainland adult males was reproductive behaviour, whereas the interactions between members of the island pairs separated them. Likewise, Lack (1965) noted that during spells of extremely cold weather members of a pair of European Robins separated into individual territories in winter. The separation of the South Island Robin pair-members on Outer Chetwode Island may have been a response to low food availability. By achieving territorial exclusion perhaps each partner maximised his or her harvest from an area and reduced the likelihood of interference caused by the other partner taking prey from a particular area of the territory before the recovery of the prey populations (Krebs 1978). The members of a pair in Kowhai Bush did not separate, presumably because food was readily available so that there was no competition between them for it.

During May and June, the Robins on Outer Chetwode Island spent less time in body-maintenance than did their counterparts at Kowhai Bush ($P < 0.01$). The island birds used comfort movements (scratching, bill wiping and preening) to remove bits of soil or prey, but they rarely interrupted foraging to preen extensive areas of plumage as did the Kowhai Bush Robins. Possibly, the island birds preened more at night so that it did not interfere with foraging by day. The significant rise in time spent by the island males in body-maintenance during the late morning was largely a consequence of the data from two birds that took several minutes to bathe and dry themselves, compared with less than a minute for most other body-maintenance activities.

Besides foraging, interspecific interaction was the only behaviour on which the island birds devoted more time to than did the Kowhai Bush birds. Several factors contributed to this result. First, as well as the Robins, other avian species seemed to be present at higher densities on Outer Chetwode Island than they were at Kowhai Bush, resulting in the island Robins interacting more often with other species. Second, the island Robins were very aggressive towards subordinate species that ventured near their stored food. They presumably could watch their caches more closely as a result of their small territory size than could the mainland Robins. Lastly, female Bellbirds which dominated Robins at Kowhai Bush were chased by adult male Robins on Outer Chetwode Island.

Not only did the Kowhai Bush adult male Robins spend time during autumn and winter in reproductive behaviours, unlike the island Robins, but the former carried out these behaviours in the early morning. This implies that the Kowhai Bush males began the day with energy reserves either in the body or as hoarded food after the night fast. "If more food can be obtained at one time of the day than another, selection should favour those individuals that forage at the better time since an equivalent amount of food could be acquired in less time, leaving more time for other activities" (Verner 1965). For an insectivorous species, such as the Robin, food species would be less active, hence less conspicuous, at lower temperatures during the early morning. Also, it is likely that prey would be harder to see in the dull light of the early morning. Consequently, the best time for Robins to carry out non-foraging activities would be just after sunrise, as found by Kacelnik (1979) for Great Tits. From Figure 9.2 it is apparent that the Kowhai Bush birds engaged in reproductive behaviours (singing and partner-interactions) in the early morning. Similarly, Verner (1965) found that during the breeding season male Long-billed Marsh Wrens *Telmatodytes palustris* were able to store more than enough energy for their needs during the night, so that they spent a great deal of time singing and performing other non-foraging activities early in the morning.

From this comparison of the time-budgets of the two Robin populations it can be concluded that foraging to find sufficient food to meet maintenance requirements is a Robin's most important activity. Only when foraging provides an excess of food in the time available can time be spent in non-maintenance activities. In winter, Robins at Kowhai Bush that had "spare" time used it to prepare for breeding; bachelors sang to probably attract a mate and members of a pair established a closer rapport by reducing aggression. These reproductive behaviours were performed mainly in the early morning, probably because this was the least profitable time to forage for their insect prey.

In addition, this comparison of the two populations illustrates the plasticity of behaviour in passerines. Not only did the adult males of the two populations have very different time-budgets for the same months, but some activities were not exhibited by both populations. Island males were neither heard to give full song nor seen in sexual chases during my visits, but chased immature and female Bellbirds - just the reverse of male behaviour at Kowhai Bush. Similarly, the full song of island males given during the breeding season comprised syllables

(Section 6.3, p. 58) not comparable with any of those produced by the Kowhai Bush birds, and the rate of production (average time interval between syllables) differed for the two populations (Hay 1975). Flack found that the timing of breeding and reproductive potential were quite different for the two populations (Table 9.1). Thus, this comparison shows that the formulation of theories and models on bird behaviour should not be attempted on the basis of the study of just one population.

9.5. Summary

From the comparison of the time-budgets for adult male Robins at Outer Chetwode Island and Kowhai Bush it seems that in winter foraging to find enough food to meet their maintenance needs was the first priority of these birds. Once this requirement had been met, extra time was devoted to body-maintenance and possibly resting. The activities of least importance to the Robins were those related to reproduction, such as full song (vocalizing) and sexual chases (partner-interactions).

Robins on the island spent significantly more time foraging per month and per day-period than did their mainland counterparts. From the above information and the results of several studies of small passerines, it was concluded that the island Robins foraged more than did the mainland birds probably because the greater density of Robins on the island divided the food resource into smaller units so that it was less readily available to them than to those on larger territories in Kowhai Bush.

As well as spending more time in body-maintenance, the mainland birds also engaged in behaviours related to reproduction (singing and sexual chases) which the island birds did not. The diurnal patterns of the Kowhai Bush Robin's behaviours was such that most reproductive activities occurred in the early morning, a time of day when foraging efficiency was probably low, so that these behaviours took place during the day when they would have had least effect on time required for foraging.

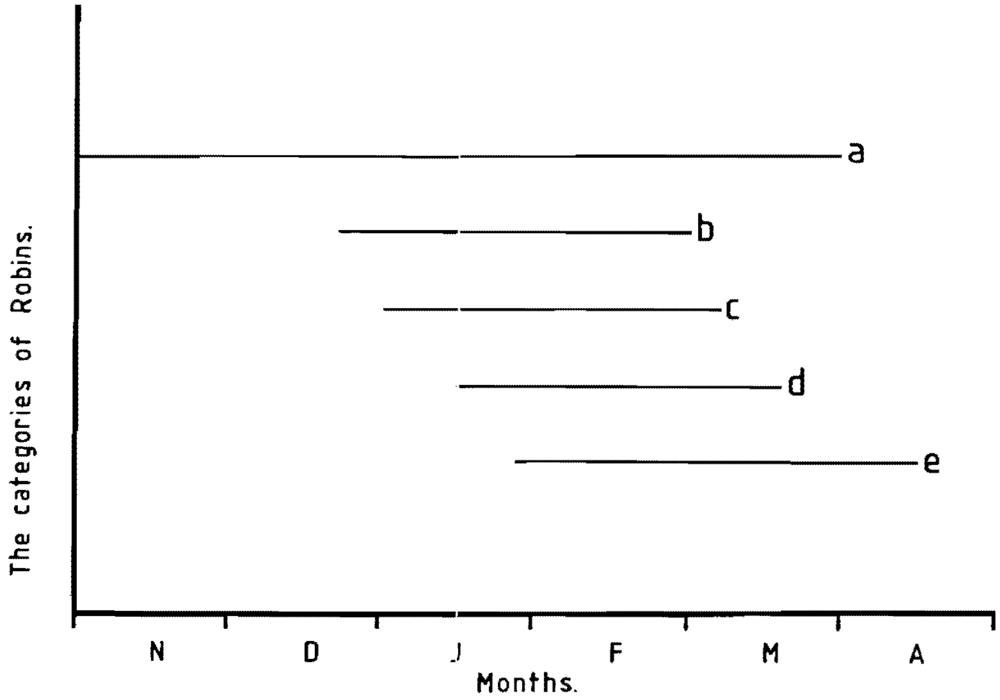


Figure 10.1 The approximate dates when five categories of Robins were seen moulting in Kowhai Bush.

[a] Immatures of both sexes.

[b] Bachelors.

[c] Adult males that had completed breeding in December.

[d] Adult females that had completed breeding in December.

[e] Adults of both sexes that completed their breeding after December.

CHAPTER TEN

THE TIME-BUDGETS FOR MALE ROBINS OUTSIDE THE BREEDING SEASON

10.1. Introduction

The monthly and diurnal time-budgets for adult, immature and bachelor male Robins outside the breeding season are described in this chapter. Two important events took place during this period, (1) the moult, followed by (2) a resurgence in territorial and sexual behaviour.

Figure 10.1 illustrates the timing of the moult for each category of Robins. Adult Robins underwent a complete post-nuptial moult, the timing of which varied with the sex of the birds and when they finished breeding. Immature birds seemed to replace all plumage, except the rectrices and remiges. Replacement of the body plumage usually began after the immatures became independent, but some birds had already replaced a small area of streaky grey breast feathers with white feathers, characteristic of adult plumage, before leaving the natal territory. Because of the long breeding season (about six months), at any one time between November and February there was considerable variation in the stage of moult of immatures. However, most immatures had completed the moult and were indistinguishable from adults by late March.

Bachelors (unpaired adult males) began moulting in December, two to four weeks before breeding birds. Both sexes of paired Robins started moulting during January, but those feeding nestlings or juveniles delayed their moult until their juveniles began finding some food for themselves. Rectrices were moulted almost simultaneously about 10 days after the moult began. For 23 adult males, the first day on which they were seen without tail feathers varied from 16 January to 9 February. The new rectrices took about a month to grow to full length. Although no Robins were caught and examined, it seemed that only one or two remiges from each wing were replaced at a time. This sequential replacement of the remiges took about ten weeks to complete, while the rest of the plumage was renewed within about eight weeks. Most adult males had completed the moult by April.

While moulting, adult Robins were secretive, quiet and ineffective in ousting intruders, but afterwards residents resumed active territorial defence. Any immature bird which had become established within part of the territory of a moulting adult male was frequently chased by the adult once the latter had completed his moult. This led either to the two birds recognising a boundary between their territories or to the immature male being ejected.

Sexual chases occurred after the moult (Section 8.3.1, p. 115). These interactions between members of a pair seemed to result from the aggressiveness of the male towards the female during pair formation. Pairs that had bred together before the moult also engaged in sexual chases. By late April and for the rest of the non-breeding season bachelors spent much of the early morning giving full song, making them distinguishable from paired males.

From the analyses and comparisons of the time-budgets I hoped to answer the following questions:

1. Were the findings from Chapter 9 also true of the behaviour for adult and immature males at Kowhai Bush throughout the non-breeding season? For example, were resting and preening low priority behaviours during summer and autumn?

2. What influence did the supposed foraging inexperience of the immature males have on their time-budgets when compared to those for adult males?

3. Why did bachelors suffer greater mortality than paired males?

4. Why did the moult take place in the summer months and what was its influence on the Robin's behaviour?

5. Did the diurnal rhythm of a behaviour for a particular category of Robin change during the course of the non-breeding season?

6. If the various categories of males had dissimilar diurnal rhythms for a particular behaviour what were the reasons for this?

10.2. Methods

Observations of non-breeding male Robins were made from January to July in 1977 and 1978. Three categories were recognised: adults, immatures and bachelors (unpaired adults). Bachelors could only be recognised from May (Section 3.3, p. 17).

The data were analysed in two ways. First, for each category of males separately, data from the two non-breeding seasons were pooled and divided into monthly samples. For each monthly sample, a time-budget was determined by calculating the percentage of the total time that the

Robins devoted to the various behaviours. These time-budgets are presented in the text as Figures 10.2, 10.3 and 10.6, the plotted values and the separate monthly time-budgets for the two non-breeding seasons are given in Appendices 5-7. Second, the data for the monthly samples were amalgamated into three seasons: summer - January, February and March; autumn - April and May; winter - June and July. For each season, the observations were divided according to the day-period in which they were made and the percentage of time per day-period that the Robins spent in the various behaviours determined. This gave time-budgets for the different day-periods which, when compared in sequence, provided the diurnal pattern of each behaviour (Figures 10.7-10.9; Appendices 8-10).

The results and discussion sections are divided into two portions: (1) the monthly time-budgets and (2) the diurnal patterns of behaviours. Within these sub-sections, the information is further divided so that the data for each behaviour are treated separately and in the same sequence as shown on the figures.

10.3. Results

10.3.1. The monthly time-budgets

(i) A comparison between the time-budgets for adult and immature males

The Chi-squared values in Appendix 5 show that the monthly time-budgets for adult males changed significantly as the non-breeding season progressed ($P < 0.005$), the same was also true of the time-budgets for immature males (Appendix 6).

(a) Foraging

Adult males spent about 74% of time foraging from January to April (Fig. 10.2), much less than the 85-90% spent by immatures ($P < 0.01$) (Fig. 10.3). From the beginning of April to the end of May, both adult and immature males significantly increased their foraging time, but adults still foraged less than did the immatures ($P < 0.01$). In June, adult males foraged more than they had in May ($P < 0.01$), spending 90% of the day foraging, which was similar to the proportion of time immatures foraged in June. From April to June inclusive, adult males foraged for a similar number of hours per day as the days shortened (Fig. 10.4), thus increasing the percentage of time spent feeding (Fig. 10.2), but immatures

Figure 10.2. The monthly time-budgets (percentage of observation time) for adult male Robins in the non-breeding season.

See Appendix 5 for the plotted values.

[a]The asterisks indicate the level of significant difference (* = $P < 0.05$, ** = $P < 0.01$) between the proportion of time they spent in a particular behaviour for two consecutive months.

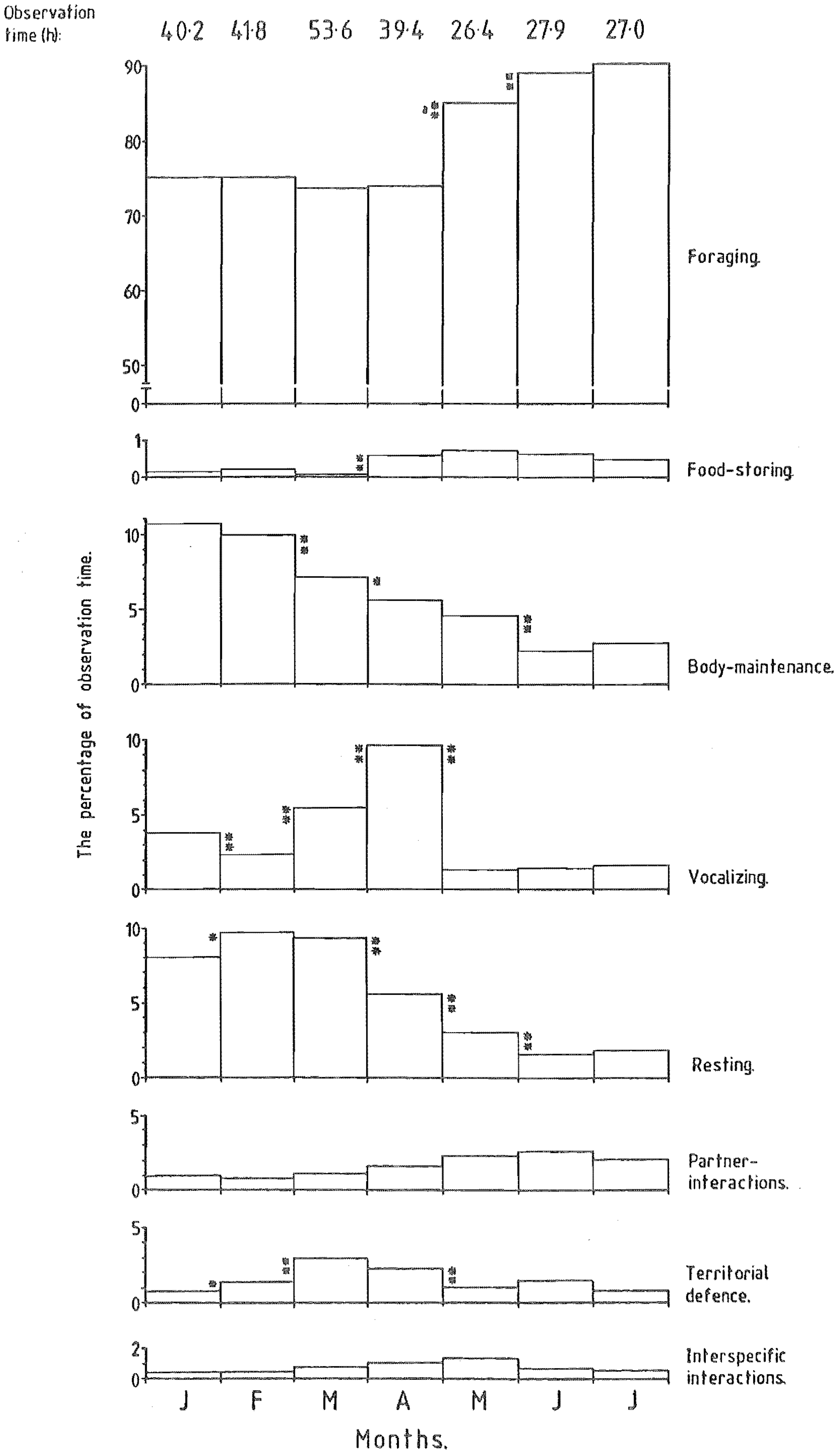
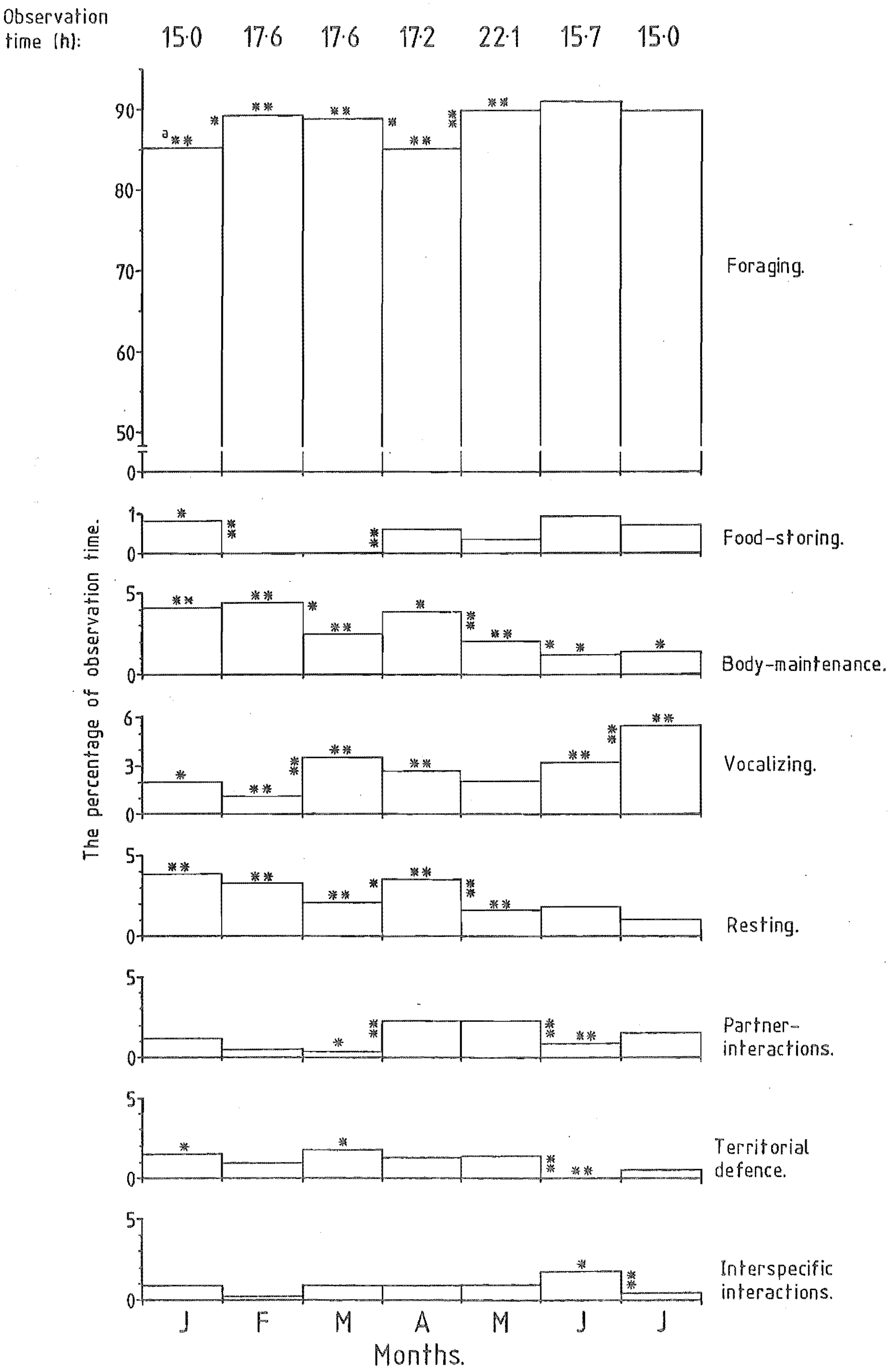

Observation time (h):
40·2
41·8
53·6
39·4
26·4
27·9
27·0
90
80
70
60
50
0
Foraging.
1
0
Food-storing.
10
5
0
Body-maintenance.
10
5
0
Vocalizing.
10
5
0
Resting.
5
0
Partner-interactions.
5
0
Territorial defence.
2
0
Interspecific interactions.
The percentage of observation time.
J
F
M
A
M
J
J
Months.

Figure 10.3. The monthly time-budgets (percentage of observation time) for immature male Robins during the non-breeding season. Appendix 6 gives the plotted values.

[a]The asterisks denote significance levels: * = $P < 0.05$, ** = $P < 0.01$. Those placed next to the sides of columns indicate significant differences between adjacent monthly samples. Asterisks above the columns show significant differences between the proportion of time immature males and adult males (Fig. 10.1) spent involved in a particular behaviour for the same month.


Observation time (h):
15·0
17·6
17·6
17·2
22·1
15·7
15·0
90
80
70
60
50
0
a
Foraging.
1
0
Food-storing.
5
0
Body-maintenance.
6
3
0
Vocalizing.
5
0
Resting.
5
0
Partner-interactions.
5
0
Territorial defence.
5
0
Interspecific interactions.
The percentage of observation time.
J
F
M
A
M
J
J
Months.

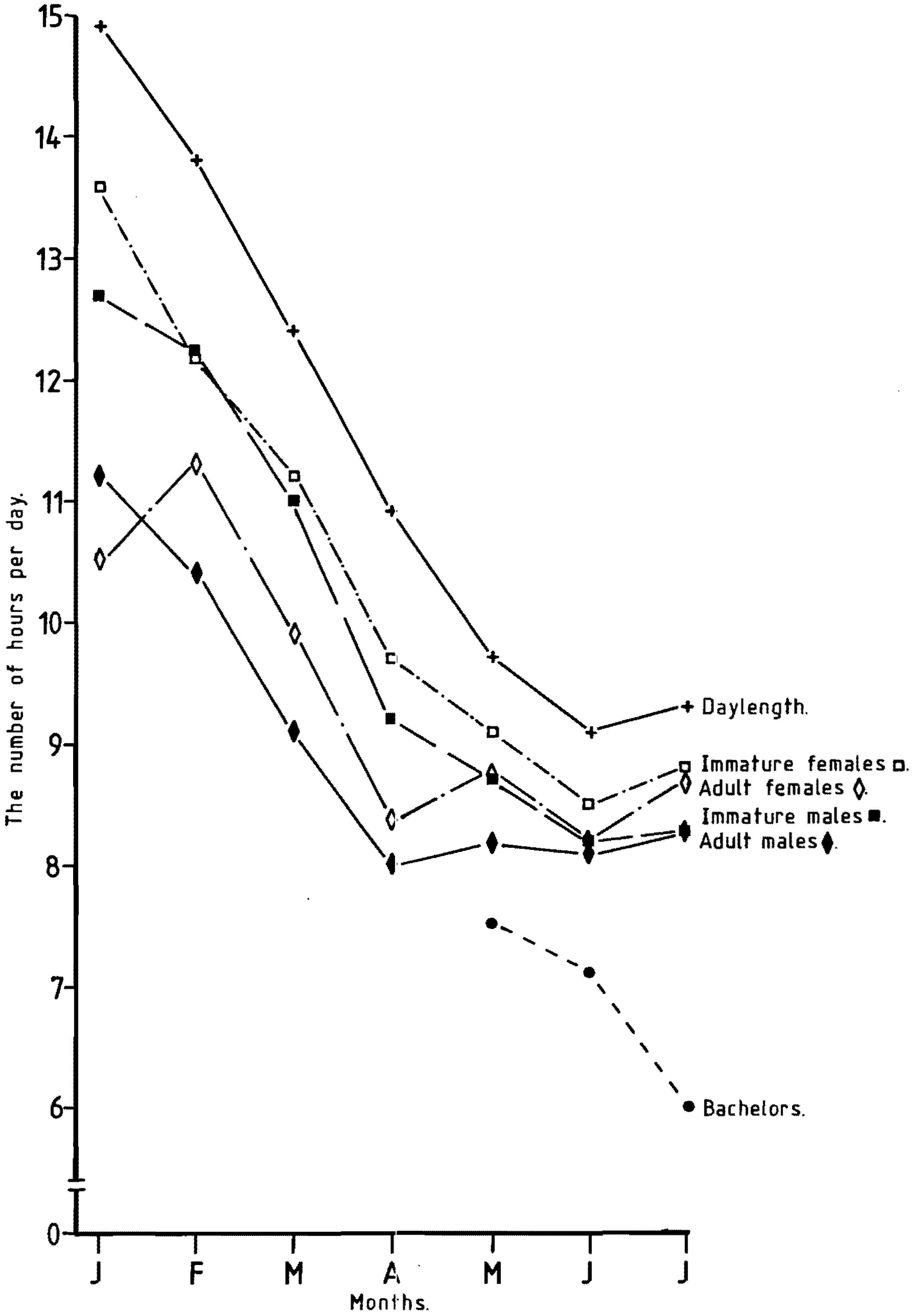


Figure 10.4 The number of hours per day spent foraging by five categories of Robins per month during the non-breeding season.

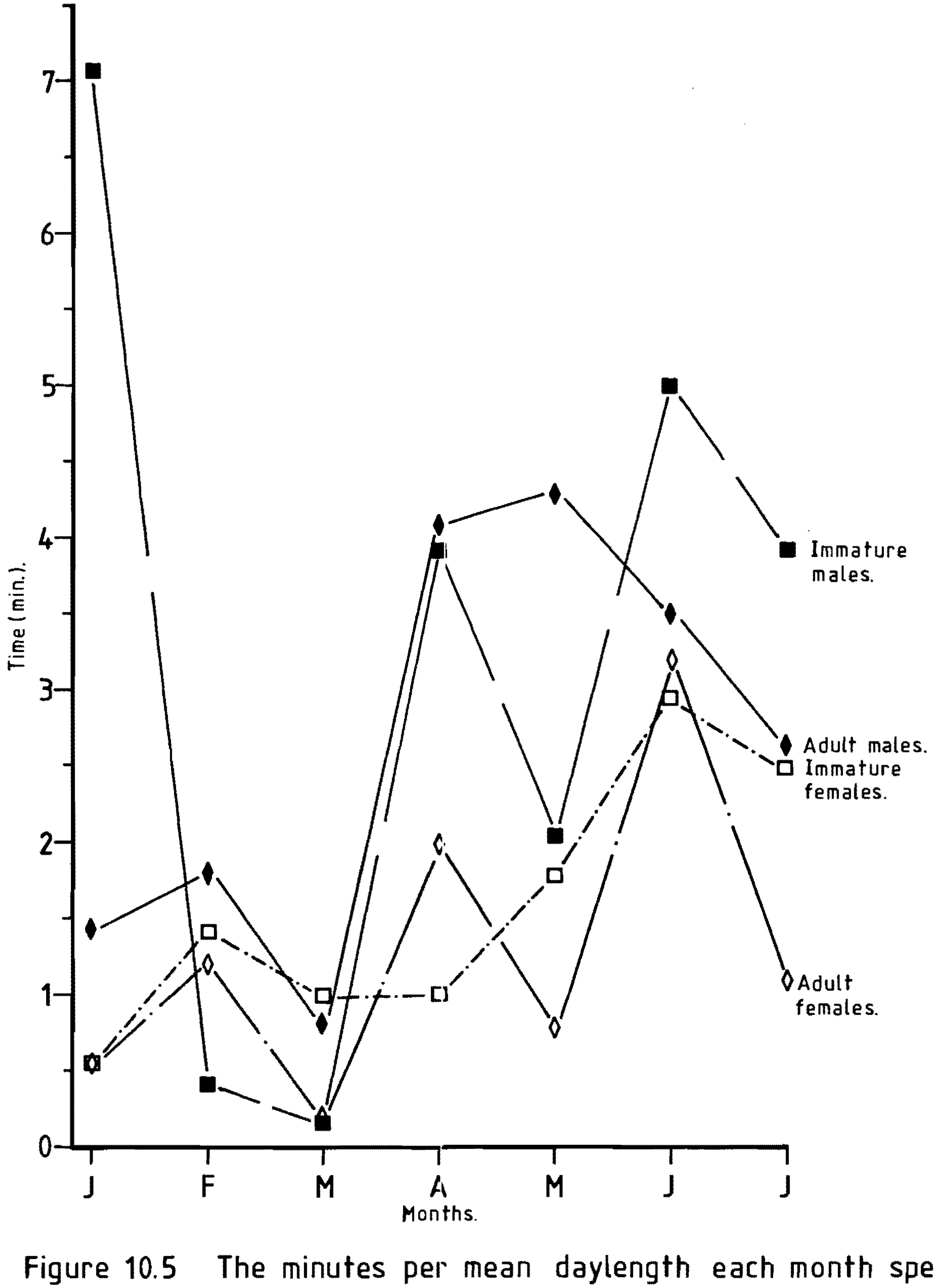


Figure 10.5 The minutes per mean daylength each month spent on storing food by four categories of Robins during the course of the non-breeding season.

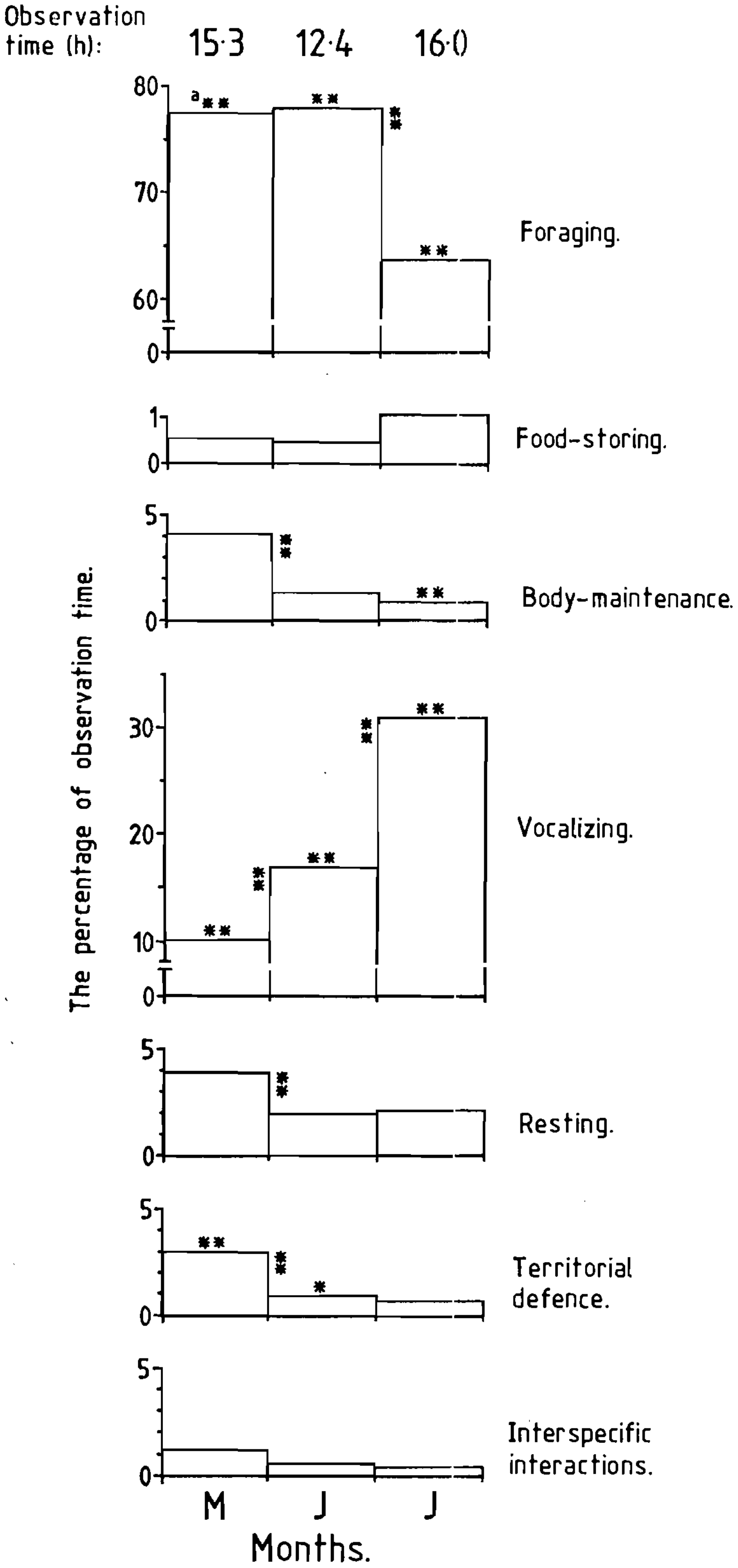


Figure 10.6 The monthly time-budgets (percentage of observation time) for bachelor Robins from May to July.
See Appendix 7 for the plotted values.

[a] The asterisks indicate significance levels: * = $P < 0.05$, ** = $P < 0.01$. Those placed next to the sides of columns denote significant differences between adjacent monthly samples. Asterisks above the columns show significant differences between the percentage of time bachelors and adult males (Fig. 10.2) spent involved in a particular behaviour for the same month.

fed for fewer hours per day from month to month.

(b) Food-storing

Adult and immature males spent a similar time storing food each month during the non-breeding season, except in January when immatures spent more time storing food than did adults ($P < 0.05$). Less than 0.2% of time was spent storing food in February and March, but for the rest of the season about 0.7% of time was devoted to this behaviour ($P < 0.01$). In general, each category of Robins spent more time storing food as the non-breeding season progressed (Fig. 10.5).

(c) Body-maintenance

Each month, adult males spent significantly more time in body-maintenance than did immatures. Both categories spent more time caring for their plumage and other external surfaces in January and February, and least during the winter months.

(d) Vocalizing

The proportion of time spent vocalizing by adult males declined from January to February ($P < 0.01$), but there was a significant resurgence in autumn (March and April) ($P < 0.01$). Over the same four-month period, the data for immature males showed a similar trend, but they sang less than did adult males ($P < 0.01$). In May, adult males markedly decreased the time spent singing and sang no more than did immatures. For the next two months, adult males spent about 1.4% of their time in this activity, whereas immature males increased the time spent vocalizing until, in June and July, they spent about 2.7% more time singing than did adult males ($P < 0.01$).

(e) Resting

As the days shortened, adult and immature males spent less time resting. From January to May, adult males rested more than did immatures ($P < 0.01$), but during the winter months both categories spent a similar time resting.

(f) Partner-interactions

Males interacted little with their mates during summer, but afterwards sexual behaviour increased. Only in March and June did the percentage of time that males were engaged in interactions with their partners differ significantly between the two male categories, adults being more active than immatures ($P < 0.01$).

(g) Territorial defence

Adult males significantly increased the proportion of time spent per month in territorial defence from January to March, followed by a decline from April through to July (Fig. 10.2). Except for January, immatures spent less time in conflict with other Robins than did adult males, with the differences being significant in March and June.

(h) Interspecific interactions

Adult and immature male Robins spent a similar time each month interacting with other species. In general, a slight increase in the proportion of time per month was spent displaying to, chasing and being chased by other species from January to May, but thereafter it declined slightly.

(ii) A comparison between the time-budgets for paired adult males and bachelors

Bachelors (Fig. 10.6) spent less time foraging each month than did paired adult males (Fig. 10.2) ($P < 0.01$). In July, paired males spent 8.3 hours foraging per day, 2.3 hours more than bachelors (Fig. 10.4). Both categories spent a similar time in body-maintenance in May and June, but in July adult males spent more time in this behaviour than did bachelors ($P < 0.01$).

From May to July, bachelors sang more than did paired adult males ($P < 0.01$). As well, during May and June, bachelors spent significantly more time than did paired adult males in territorial defence, but during July the two categories of males spent a similar time in this behaviour. There were no significant differences in the time devoted to food-storing, resting and interspecific interactions between paired and bachelor adult males. Paired males spent about 2.3% of time interacting with their partners.

10.3.2. The diurnal rhythms of behaviours

Figures 10.7, 10.8 and 10.9 show the diurnal rhythms for each behaviour (time-budgets for each day-period) for adult, immature and bachelor male Robins during summer, autumn and winter.

(a) Foraging

In general, adult and immature males had morning and afternoon peaks of foraging, with reduced activity around midday (Figs 10.7 and 10.8). The afternoon foraging peak was greater than the morning one, but this difference was least evident during winter. For both age classes, the reduced foraging about midday was more marked during summer, and almost non-existent in winter. Generally, the time spent foraging in the early morning was significantly lower than that for mid-morning. Adult males foraged less in the early morning and around midday than did immatures.

During autumn, the data show that bachelors foraged according to a diurnal pattern (Fig. 10.9) much the same as for paired males (Fig. 10.7), with morning and late afternoon peaks of foraging activity. However, the changes in foraging time from one day-period to the next were much greater for bachelors ($P < 0.01$) than for paired males ($P < 0.05$). Bachelors and paired adult males had very different foraging patterns in winter. Paired males foraged for 85-93% of each day-period, with the peak in feeding being in the early afternoon. In contrast, bachelors fed for 42-96% of each day-period, with their peak in foraging taking place just before sunset.

(b) Food-storing

The food-storing behaviour of adult and immature males differed markedly during summer. While adult males stored most food in the early morning, immatures stored almost all their food around midday. During autumn and winter, all three male categories spent a similar time storing food from one day-period to the next.

Figure 10.7. The diurnal patterns of behaviours for adult male Robins during three parts[a] of the non-breeding season. See Appendix 8 for the graphed values.

[a] Summer = January, February and March; Autumn = April and May; Winter = June and July.

[b] The asterisks denote the level of significant difference (* = $P < 0.05$, ** = $P < 0.01$) between the proportion of time adult males were involved in a behaviour during two consecutive day-periods.

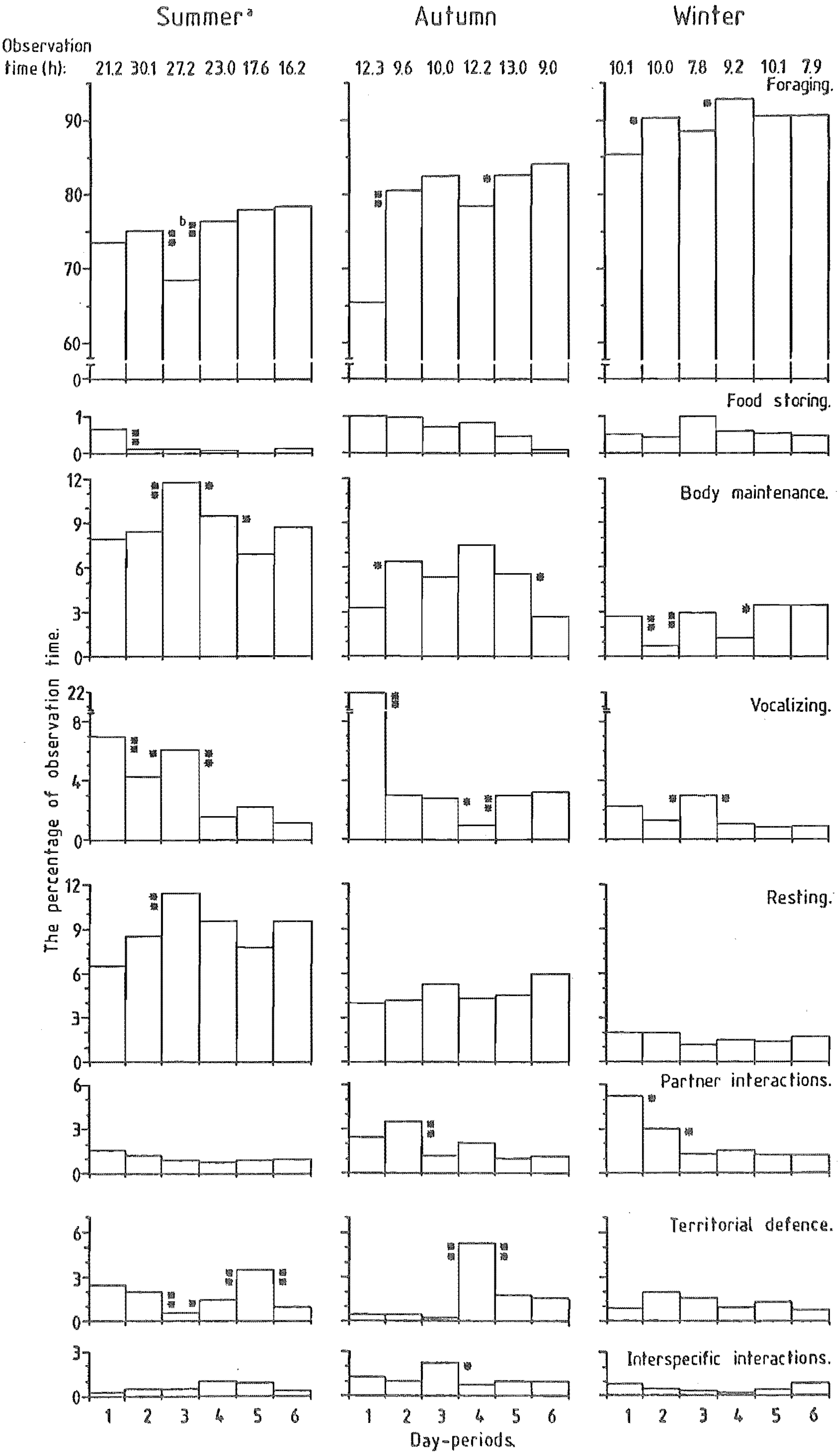

Summer^a
Autumn
Winter
Observation time (h):
21.2 30.1 27.2 23.0 17.6 16.2
12.3 9.6 10.0 12.2 13.0 9.0
10.1 10.0 7.8 9.2 10.1 7.9
Foraging.
Food storing.
Body maintenance.
Vocalizing.
Resting.
Partner interactions.
Territorial defence.
Interspecific interactions.
The percentage of observation time.
b
90
80
70
60
0
1
12
9
6
3
22
8
4
1 2 3 4 5 6
Day-periods.

Figure 10.8. The diurnal pattern of behaviours for immature male Robins during three parts[a] of the non-breeding season.

Appendix 9 gives the plotted values.

[a] Summer = January, February and March; Autumn = April and May; Winter = June and July.

[b] The asterisks indicate the level of significant difference (* = $P < 0.05$, ** = $P < 0.01$) between the proportion of time immature males were involved in a behaviour during two consecutive day-periods.

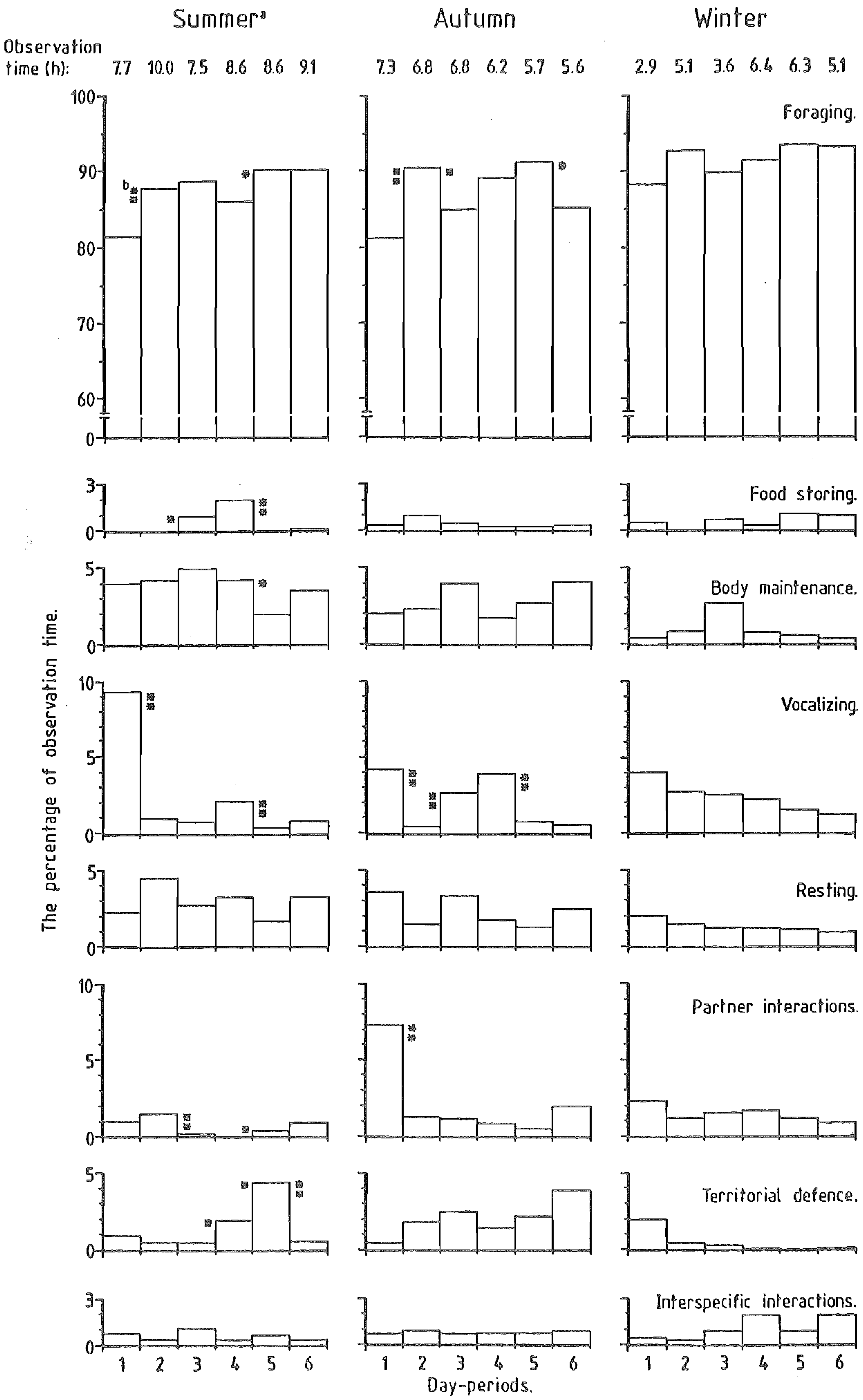
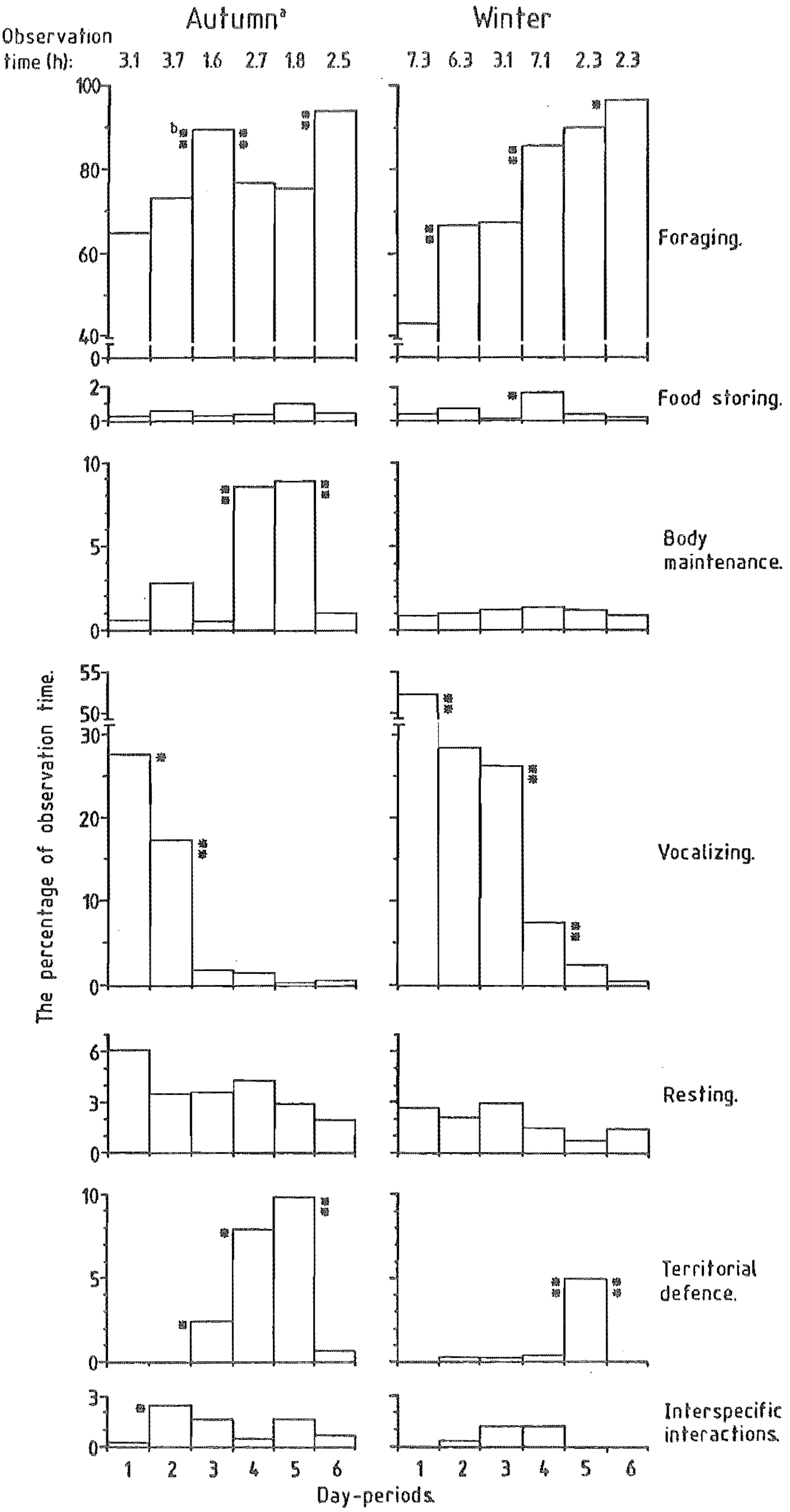

Summer^a
Autumn
Winter
Observation time (h):
7.7 10.0 7.5 8.6 8.6 9.1
7.3 6.8 6.8 6.2 5.7 5.6
2.9 5.1 3.6 6.4 6.3 5.1
100
90
80
70
60
0
b
Foraging.
Food storing.
Body maintenance.
Vocalizing.
Resting.
Partner interactions.
Territorial defence.
Interspecific interactions.
3
5
10
The percentage of observation time.
1 2 3 4 5 6
Day-periods.

Figure 10.9. The diurnal patterns of behaviours for bachelor Robins (unpaired adult males) during two parts[a] of the non-breeding season.

See Appendix 10 for the graphed values.

[a] Autumn = May <u>only</u>; Winter = June and July.

[b] The asterisks indicate the level of significant difference (* = $P < 0.05$, ** = $P < 0.01$) between the proportion of time bachelors were involved in a behaviour for two consecutive day-periods.


Autumn^a
Winter
Observation time (h):
3.1 3.7 1.6 2.7 1.8 2.5
7.3 6.3 3.1 7.1 2.3 2.3
100
80
60
40
0
b
Foraging.
2
0
Food storing.
10
5
0
Body maintenance.
55
50
30
20
10
0
Vocalizing.
6
3
0
Resting.
10
5
0
Territorial defence.
3
0
Interspecific interactions.
The percentage of observation time.
1 2 3 4 5 6
1 2 3 4 5 6
Day-periods.

(c) Body-maintenance

The time spent in body-maintenance by adult males was greatest about midday during summer and autumn. For immature males, a similar diurnal pattern of involvement in this behaviour was revealed, but with a less pronounced peak at midday and a slight increase in the late afternoon. In contrast, bachelors carried out almost all body-care activities in the early and mid-afternoon, with a significantly smaller proportion of time ($P < 0.01$) devoted to it in the morning and late afternoon. In winter, paired adult males spent most time in body-maintenance during the early morning and mid- to late afternoon, while immatures devoted most time to this behaviour at midday. In winter, bachelors spent a similar time during each day-period in body-maintenance.

(d) Vocalizing

The diurnal rhythm of vocalizing was much the same during each season for the three categories of males. Most singing was done just after sunrise, with the time spent singing decreasing during the course of the day, significantly so from early to mid-morning. Adult and immature males often had another small peak of singing around midday.

(e) Resting

In summer adult males rested mostly around midday and during the late afternoon, but the data for bachelors and paired adult males in autumn and winter, and immatures throughout the non-breeding season, revealed no obvious diurnal pattern of resting.

(f) Partner-interactions

Paired adult and immature males interacted with their mates more in the early and mid-morning than they did during the rest of the day.

(g) Territorial defence

During summer and autumn, males were involved in conflicts with other Robins mainly in the afternoon. In winter, bachelors retained this diurnal pattern of territorial defence, whereas paired males spent a similar time in this behaviour each day-period.

(h) Interspecific interactions

In all seasons, paired males interacted with other species randomly throughout the day, but bachelors spent little time interacting with other species in the early morning and late afternoon, with slightly more time devoted to it during the rest of the day.

10.4. Discussion

10.4.1. The monthly time-budgets

(a) Foraging

From January to April, adult males spent about 74% of the day foraging. This was more than the 40-60% of time spent feeding in summer reported for several other passerine species (Austin 1978, Post 1974, Verbeek 1972, Verner 1965), and much more than the 10% for hummingbirds (Pearson 1954, Stiles 1971, Wolf and Hainsworth 1971). In January and February, adult male Robins were undergoing a rapid and complete post-nuptial moult. From Figure 10.4 it is apparent that in summer the birds spent more hours feeding per day than they did in autumn and winter, even though they spent a greater proportion of their time foraging later in the non-breeding season (Fig. 10.2). By April, days were shorter and as a consequence less time was available to spend foraging than they foraged for in January and February. Therefore, from the consideration of time alone, the moult probably had to occur in summer when days were sufficiently long.

The large amount of time required for feeding at such a favourable time of year (long days, high ambient temperatures and, seemingly, abundant food supplies) can largely be attributed to the high energy demands of the moult. Payne (1972) stated that for most species of songbirds, the standard metabolic rate (SMR) when moulting increased from 5-30% above the rate for non-moulting birds. Wallgren (1954) reported a 14% increase in SMRs during the postnuptial moult of *Emberiza citrinella* and 26% in *E. hortulana*.

As the non-breeding season progressed, adult males increased the proportion of time spent foraging so that by the winter months (June and

July) they foraged for about 90% of time. Gibb (1954, 1956) reported similar findings from observations of winter feeding Rock Pipits and several species of tits (Paridae). Yellow-billed Magpies, Oystercatchers and Pukeko have also been found to spend a greater proportion of time feeding in winter than they had in summer and autumn (Verbeek 1972, Heppleston 1971, Wright 1978 respectively).

That Robins spent most of the day foraging in winter can be attributed mainly to environmental factors. There is an approximately inverse linear relationship between temperature and SMR for a bird of a given weight (King and Farner 1961, Verbeek 1964). Therefore, even if daylength and food availability remained constant, Robins in winter would have to forage for longer to satisfy the higher energy demands of maintenance at lower temperatures. However, because daylength decreased the birds probably had to find as much food as previously in less time and to store more in the intestine or as fat to sustain themselves through the longer night.

Prey abundance is also known to influence the proportion of time spent foraging. Reduced prey abundance in summer caused American Avocets *Recurvirostra americana* to spend more time feeding (Gibson 1978). Verner (1965) found that male Long-billed Marsh Wrens consumed 4.3% more energy in May than in June, but spent 30% more time feeding in May. He believed this difference was correlated with differences in insect abundance. Assuming that prey availability to Robins was lower in winter, as it seemed to be, then the increased proportion of time spent foraging then can be partly attributed to this factor.

The greater proportion of time spent feeding in winter was not related to the Robins using a more energy-demanding foraging method, they spent less time in winter flycatching and hawking (Fig. 4.1, p. 29), foraging methods which involved flight. Since flight is energetically the most expensive form of movement (Custer and Pitelka 1972, LeFebvre 1964), less energy would be required to sustain foraging in winter. Thus, it seems that the higher proportion of time spent foraging in winter by adult males, compared with earlier in the non-breeding season, can be largely attributed to shorter days, colder temperatures and, apparently, a lower availability of invertebrate prey. However, for the Robin some evidence is also present suggesting that the birds spent so much time foraging not just to meet their maintenance needs.

Generally, it is assumed that for some species of birds winter is a time when they have most difficulty in finding enough food to meet their maintenance requirements, particularly small passerines which have low energy reserves. Lack (1954) argued that food shortage is the most likely factor responsible for the control of many bird populations. The urgency with which birds feed should reflect the availability of food (Gibb 1954). In his study of the feeding ecology of five species of tits at Marley Wood, near Oxford in Britain, Gibb (1954) showed that these birds "searched for food hardest in mid-winter". At that time of year they fed most intensely, were seen feeding more frequently, and made supplanting attacks for food more often than at other times of the year, supposedly to find enough food to meet their maintenance requirements. In agreement with Gibb's (1954) findings, paired male Robins spent a greater proportion of time foraging and less time on resting and body-maintenance in winter than in summer and autumn. In addition, their foraging rate (movements and pecks per minute) was highest in winter (June and July) (Table 4.5, p. 36). Thus, my results suggest that the Robins searched for food most intensely in winter, but for three reasons it cannot be stated that they did so just to meet their maintenance needs. First, most pairs began breeding in August, by which time day-lengths and monthly mean temperatures had increased little compared with the previous two months and there was little decrease in the percentage of time they foraged over the same period. Breeding activities require extra time and energy to sustain above that required for maintenance (Verner 1965). Second, while paired males foraged for about 90% of their time in winter (Appendices 5 and 6), bachelors fed for only 60-80% of theirs (Appendix 7). Lastly, the mortality of paired Robins was lower in winter than in autumn (Section 12.2.4, p. 218). Therefore, perhaps the paired Robins devoted such a large proportion of their time to feeding and fed so intensely in winter not to meet their maintenance needs, but to build up bodily reserves in preparation for breeding. To find out which of the above possible reasons is correct it would be necessary to determine the bird's change in body weight during the course of the non-breeding season.

From January to May inclusive, immature males foraged more than did adult males ($P < 0.01$), but in June and July the two age classes foraged for similar proportions of time. For several species it has been found that immatures spent more time foraging than adults, because the immatures were less proficient at finding, catching and handling prey (Buckley and

Buckley 1974, Morrison *et al.* 1978, Recher and Recher 1969). Data were not collected to determine whether immature Robins spent longer dealing with prey than adults, but several observations showed that at least some of the immatures were less proficient at killing and breaking up large prey (Section 4.3.5, p. 37). Another indication that immature Robins were poorer foragers than adults was that the former seemed to eat more berries (Powlesland 1979). Berries have a lower calorific value and digestibility than animal matter (Taitt 1973). Possibly berries were eaten more often by immatures because they were readily available and made up for any short term deficiencies in animal-matter intake. Therefore, because of their probably lower foraging efficiency than adults and the high energy demands of a partial postjuvenal moult, immatures spent about 12.5 hours per day (an hour more than adult males) foraging during January and February. By March, daylength was slightly less than 12.5 hours and so there was probably a high selection pressure for immatures to refine their foraging techniques or die of starvation. Similarly, Morrison *et al.* (1978) considered that the development of prey-capture abilities by immature Olivaceous Cormorants *Phalacrocorax olivaceus* was probably a strong selective force that eliminated all but the rapid learners. Heppleston (1971) provided evidence that under extreme environmental conditions juvenile Oystercatchers *Haematopus ostralegus* feeding at slightly lower rates than adults were unable to compensate adequately for any food deficiency incurred. In 1965-66, he found that losses of first-winter birds accounted for 77% of the winter mortality. In the case of male Robins it seems that immatures had attained the foraging proficiency of adults by winter since both age classes spent a similar time foraging then.

Bachelors foraged less than paired adult males during May, June and July ($P < 0.01$). By July, bachelors spent 38% less time foraging than did paired males. Why? It is possible that paired adult males spent so much time feeding to increase their bodily fat reserves for use during severe weather or in preparation for the high energy demands of breeding. Mean weights of the two groups of Robins would have indicated whether bachelors weighed less than paired males, but neither I nor Flack (in prep.) weighed Robins in winter. However, if bachelors fed only to meet daily maintenance requirements one would expect them to have had lower energy reserves than did paired adult males and so to have suffered more mortality during severe weather. This hypothesis is supported by the data in Table 10.1: bachelors did suffer greater mortality than paired

Table 10.1. The percentage mortality (disappearance) for bachelors and paired adult males from May to July inclusive in 1977 and 1978 combined.

	% died	N	
Bachelors:	64	11	$P < 0.01$
Paired adult males:	18	50	

adult males from May to July inclusive. Similarly, Flack (1975a) found that the annual mortality for bachelors was greater than 80% compared with 30% for paired adult Robins. Therefore, it seems likely that at least some of the increased mortality for bachelors was related to the less time they spent foraging.

(b) Food-storing

Food-storing involved Robins hoarding prey for a day or two before eating it. Because adult and immature males spent a greater proportion of time foraging and storing food in winter than in summer it seems unlikely that the high energy demands of the moult necessitated them eating most of the prey they found in summer. Therefore, they probably could have found and stored as much food in summer as they did in winter when prey seemed to be less readily available. There is evidence that birds store fat as an overnight energy reserve (Newton 1969, Ward 1965), the amount of food eaten being determined largely by the amount of energy lost the preceding night (Kontogiannis 1968). As well as spending more time feeding when more fat reserves are used up, such as during long winter nights, it might be expected that Robins would store more food in winter. Figure 10.5 shows that most Robins spent longer per day in winter storing food than in summer. In summer, when temperatures were mild, nights short and food, apparently, readily available, presumably Robins began the day with adequate fat reserves and so did not have to find much food initially or maintain much stored food. During winter, stored food was probably of survival value to them for use when food could not be readily found, such as at dawn, when cold temperatures inhibit invertebrate activity, making them difficult to find, or if severe weather impedes foraging. Although bachelors spent much less time foraging than did adult males from May to July, the former spent as much time each month storing food as the latter. Therefore, it seems likely that all Robins were motivated to maintain a certain amount of stored food.

(c) Body-maintenance

Both adult and immature males spent more time in body-maintenance when moulting (summer) than at other times during the non-breeding season. Similarly, Austin (1978) and Gibson (1978) found that Verdin *Auriparus flaviceps* and American Avocets respectively spent more time preening during the moult than at other times. Presumably, Robins spent more time preening while moulting to remove old feathers and feather sheaths, and to arrange the developing plumage. Also, it was possible that the highly vascularized skin where feathers were growing was very sensitive and therefore a source of irritation which needed relieving. After the moult less time was spent in body-maintenance, presumably because the plumage required preening only to keep it ordered and clean.

For each month of the non-breeding season immature males spent significantly less time in body-maintenance than did adult males. During the moult, this may have arisen because adult males replaced all their plumage, whereas immatures replaced only some. For Steller Jays *Cyanocitta stelleri*, Pitelka (1958) determined that adults replaced about 1.5 times the weight of plumage compared to immatures because the latter retained their remiges and rectrices, like immature Robins. Also, part of the time adult males were involved in body-maintenance behaviour during the summer months was spent sunning, an activity missing from the immature's repertoire.

When not moulting, the proportions of time spent feeding and preening by Yellow-billed Magpies were inversely related (Verbeek 1972). This relationship between the two behaviours was also evident from the male Robin time-budgets (Figs 10.2 and 10.3). From April to June, when the proportion of time spent foraging significantly increased from one month to the next, a decrease in the proportion of time devoted to body-maintenance occurred. Furthermore, when immature males foraged significantly more per month than did adult males, the former spent significantly less time in body-maintenance than did adult males. Although adult males spent more time foraging than bachelors during May and June ($P < 0.01$), the former did not preen less than bachelors, presumably because after spending more time foraging, paired males still had as much time to spend in body-maintenance as bachelors. Thus, when Robins spent an increased proportion of time foraging to meet maintenance energy demands, one of the first behaviours to be curtailed was body-maintenance. This relationship was also apparent from the comparison of the time-budgets for Outer Chetwode Island and Kowhai Bush adult males (Fig. 9.1, p. 136). It is of interest to note that the smallest proportion of time devoted to body-maintenance was about 1.2% (6.5 minutes per day in June) by both immatures and bachelors in winter. Possibly, this is the minimum time Robins can spend preening to keep their plumage clean and ordered.

(d) Vocalizing

Moulting male Robins spent little time vocalizing in January and February. Then about half the vocalization time involved giving full song and the rest sub-song, "chucks" and "downscales" (Section 6.3, p. 58). Several studies of passerine species have also shown that the birds were less vocal while moulting (Bissett 1978, Cunningham 1955, Fleming 1950, Gibb 1954). Testosterone production by the interstitial cells and gonads stops during the moult when these cells regress and many disintegrate (Marshall 1955). By injecting birds with steroid sex hormones workers found that these male sex hormones promoted the development and functional activity of the accessory sexual structures and secondary sexual characteristics, such as singing and sexual behaviour (Herrick and Harris 1957, Lofts and Murton 1973). Similarly, Marshall (1952) and Lofts and Murton (1973) found that when the interstitial cells began to develop after the moult, a resurgence of sexual behaviour arose. Therefore, it seems likely that the low proportion of time moulting Robins spent singing and, as will be shown later, interacting with their mates and in territorial defence, and the increase in such behaviours after the moult, were related to the activity of the interstitial cells.

In March, when males had replaced most of their plumage, the proportion of time spent vocalizing increased significantly. This was as a consequence of the males spending more time giving full song, rather than an increase in the time spent giving each type of vocalization (Section 6.4, p. 62).

Middleton (1978) found that first-year *Carduelis tristis* came into breeding condition two weeks later than older males and generally had lighter testes. If this was also the case for the Robin it may explain the less time spent singing by immature males from January to May compared with adult males. If lighter testes secrete less hormone than heavier ones, immatures should receive less stimulation and so perhaps sing less frequently. In addition, it is possible that immatures sang less than adults because the former had to forage more.

During May, the proportion of time spent singing by paired adult males decreased significantly owing to the behavioural interactions with their mates (Section 6.4.1, p. 62). For the rest of the non-breeding season, paired adult males spent only about 1.3% of the day vocalizing. In contrast, paired immature males increased the proportion of time spent singing during the course of the winter months and as a result they spent more time singing than did paired adult males ($P < 0.01$). In most cases immature males were paired with immature females that presumably were either inexperienced in interactions with partners or had to spend most of the day feeding, and consequently did not intervene as readily as did adult females when their partners began singing. Also, it may have been important for immature males to sing because, having recently established territories, they had to counter-sing with neighbours to modify the syllable repertoire of their songs in line with those of their neighbours (Hay 1975).

Bachelors were not subject to restraints in singing by a mate and spent increasing proportions of time singing from May to July. That bachelors sing more than paired males has been noted for many songbird species (Bissett 1978, Frankel and Baskett 1961, Howard 1920, Mountford 1935, Nice 1943, Thompson 1972). The function of this singing seemed to be to attract a mate because as soon as a bachelor Robin became paired he abruptly ceased giving almost all full song.

(e) Resting

From the results of Chapter 9 and from the studies of other investigators it seems that the time spent resting is related to the food intake of a bird. If a Robin needed food and it was available, presumably it fed first and only rested once its hunger had been satiated. Gibb (1954, 1956) found that when food was scarce in winter, Rock Pipits and several species of Paridae fed more and rested less, as Purchas (1973) found with Rooks. Similarly, Owen (1972) established that resting by

Anser albifrons in winter was entirely dependent on the intensity with which they fed. On cold days in winter when Yellow-billed Magpies spent more time feeding, they eliminated their midday rest period to do so (Verbeek 1972). That the proportion of time spent foraging and resting were inversely related seems to be true of Robin behaviour when the time-budgets for the male Robin categories are compared. Outside the main moult period (March to July), a significant increase in foraging was correlated with a significant decrease in resting by adult and immature Robins. From January to May inclusive, immature males spent significantly more time foraging and less time resting compared with adult males. In June and July, when these two categories spent similar proportions of time foraging, they also rested for similar proportions of time. Bachelors and paired adult males spent similar percentages of time resting from May to July, presumably because the bachelors, although they foraged less than the paired males, still had sufficient time to find enough food and to rest as much as did paired males. Furthermore, as the non-breeding season progressed a decrease in the proportion of time male Robins rested arose because a greater proportion of time was spent foraging. The greater time Robins rested in summer than during autumn and winter, was related to the low proportion of time spent foraging then, and to the casting of pellets (Powlesland 1979). Since pellets were most frequently cast in summer and a period of about a minute was spent resting before each egestion, much of the time spent resting during summer can be attributed to this factor.

(f) Partner-interactions

Immature males spent significantly less time in interactions with their partners than did adult males in March and June. Presumably, the interstitial cells of immature males in March were smaller and slower to secrete sexual hormones after the moult than those of adult males, as has been found by Middleton (1978) for *Carduelis tristis*. This may have resulted in the immature males receiving less hormonal stimulation than adults did. Another possibility was that immatures spent less time in partner-interactions than did adults because immatures had less time available to devote to it after foraging. Although a very severe shortage of food was required to reduce the development and functioning of testes in birds (Lofts and Murton 1973), it is possible that when Robins had to forage more, behaviour involving interactions between partners was inhibited. Because such behaviour was partly involved with courtship it is likely that when the survival of an individual was at stake, the latter behaviour was excluded or reduced from such birds' time-budgets, as was found for adult males on Outer Chetwode Island (Section 9.4, p. 139). Unfavourable weather conditions (low temperatures) have been shown experimentally (Farner and Wilson 1957) and in the field (Lofts and Murton 1966) to inhibit testicular growth and activity. Thus, the significantly less time immature males in June spent in interactions with their partners, compared with that for adult males, may have been caused by the former having to spend more time in behaviours related to their survival.

(g) Territorial defence

Adult and immature males spent less time chasing intruders and displaying to neighbouring Robins at their territorial boundaries while moulting than later in the non-breeding season. As discussed earlier for vocalization and partner-interaction behaviours, this low level of territorial activity during the moult was probably associated with reduced or lack of sex hormone secretion from the regressed gonads and interstitial cells. While moulting, adult males tended to be secretive and when an intruder was present, the resident male usually made a brief attempt to evict it, but often not as far as the boundary or with much vigour. Boundary disputes were infrequent during the moult and any that did occur were brief.

Immature males spent significantly more time interacting with conspecifics than did adult males during January, probably because immatures were unfamiliar with the location of the boundaries of their neighbours' territories and so often trespassed. In addition, newly established immatures seemed to have to spend more time defending their territories from adult neighbours. By comparison, adult males probably recognised neighbouring adults and the position of their common boundaries so that disputes between them were less frequent and shorter.

After the moult and until May, adult males spent significantly more time in territorial defence than previously and more than immatures did. This arose because adult males began evicting any immatures that had established sub-territories impinging on their territories. Generally, this eviction took several days with the adult male chasing the immature bird whenever seen. The immature male initially skulked about the territory after being vigorously driven away. Also, during this period adult males spent more time in boundary disputes with neighbours, presumably to re-establish the location of their common boundaries. Another reason for the greater involvement by males in territorial defence in autumn was because some males, paired or not, were occasionally found outside their territories. A short chase invariably resulted when a resident sighted such a trespasser.

The time immatures spent in interactions with other Robins in March and April is not reflected in their time-budgets. I was unable to follow immature males that were being displaced from a sub-territory or that had no territory, because if I did so the resident bird was attracted as well and this inevitably resulted in the birds interacting.

Less time was involved in territorial disputes by all three categories of males in June and July compared with the previous two months. Possibly, by then each Robin recognised his neighbours' and the positions of their common boundaries. Disputes tended to be less frequent and shorter than previously. I am unable to explain why bachelors and immature males spent less time in territorial defence than did adult males in June, but the difference was significant ($P < 0.05$).

(h) Interspecific interactions

Adult, immature and bachelor males spent a similar time each month interacting with other species. Almost all interspecific interactions were of Robins chasing or being chased by other birds; interactions with mammals were seldom seen. The slight increase in time involved in such interactions after the moult was probably a consequence of the Robin's resurgence of territorial activity being directed at other species as well as conspecifics (Section 8.4.3, p. 129). However, it may also have been related to Robins' storing more food in autumn than in summer, when most interspecific interactions involved the chasing of other birds, and it seemed as though many such chases resulted from Robins protecting their stored food.

(i) The moult

The moult and nesting are events which require extra energy and time so that they never take place simultaneously, thereby avoiding excessive demands on a bird and its environment (Miller 1961). For example, passerines which started to moult and then began breeding always stopped moulting and only resumed it once the breeding cycle was completed (Miller 1961, Pitelka 1958, Verner 1965). Similarly, late-breeding Robins postponed their moult until the juveniles began feeding themselves. Thus, the timing of the Robin's moult in the annual cycle was of interest as it took place when conditions seemed to be optimal for breeding. Why did they stop breeding to moult?

During January and February (the main moult period), monthly mean temperatures were high (Table 2.1, p. 13), days long (Table 3.1, p. 20) and weather conditions relatively stable compared with earlier or later months. Droughts sometimes occurred in summer at Kowhai Bush and seemed to inhibit the activity of litter and soil-inhabiting invertebrates, but arboreal prey always seemed to be abundant. Therefore, from the point of view of environmental conditions, it seemed an ideal time for the Robins to breed.

However, from Figure 10.4 it is apparent that January, February and March were the only months with days long enough for the Robins to spend enough time feeding to meet the high energy demands of the moult. By April, not only was the daylength too short to allow foraging for the number of hours required, but the lower ambient temperatures would have increased maintenance costs. By autumn, temperatures were lower and unsettled weather was more common than in summer. A major cause of the increased energy costs of moulting results from the loss of heat from highly vascularized feather papillae and the increased surface area exposed to cool temperatures (Lustick 1970, Payne 1972). Therefore, after March moulting Robins would have incurred higher energy costs per day as a consequence of lower temperatures than during summer. Also, by autumn readily available invertebrate prey seemed to be less abundant because many of the adult stages had disappeared and some species were represented only by concealed overwintering stages. Therefore, it is less likely that a Robin undergoing the moult after summer would be able to find enough food within the daylight hours to satisfy its maintenance needs and those associated with moulting, especially during unfavourable weather. Pitelka (1958) came to a similar conclusion after studying the moult of Steller Jays and its timing in the annual cycle. He stated that "if a choice of some vital activity in the annual cycle has to be made, it is the moult which appears to be most closely adjusted to the interval of the summer when peak supplies of food for this species can be expected". Similarly, Fogden (1972) considered that the major factor in the timing of the moult for several equatorial forest passerines was a period of lean food supplies so that the moult was timed to be completed before then.

10.4.2. The diurnal rhythm of behaviours

(a) Foraging

Physiological homeostasis is maintained with energy that a bird must extract from its environment. Since foraging is synonymous with energy procurement, when food is readily available the diurnal rhythm of feeding may reflect the diurnal rhythm of an individual's energy requirements and, more likely, the most efficient times for foraging, especially for small passerines that usually have limited energy reserves (Verner 1965). When food is scarce or energetic requirements are great, birds should expand their feeding periods towards less profitable times. Adult and immature male Robins during summer, autumn and winter had morning and afternoon peaks of feeding activity, with the latter being the greater of the two. Such a diurnal pattern of foraging has been found for many species, such as the House Sparrow (Beer 1961), Rock Pipit (Gibb 1956), American Avocet (Gibson 1978), European Robin and Blackbird (Lees 1948), White-crowned Sparrow (Morton 1967) and Yellow-billed Magpie (Verbeek 1972).

Energy is consumed during the night and birds are at their minimum daily weight at dawn (Baldwin and Kendeigh 1938). Therefore, the morning foraging peak presumably occurred to make up for at least some of this energy loss and to provide for the morning's activity. The time spent feeding in the morning would be related to the amount of energy remaining after the night, the bird's foraging efficiency and the quality of prey found in the morning. The afternoon feeding peak was probably a consequence of the need to ensure that an adequate store of food was obtained to sustain the bird overnight. Robins foraged for more time per day-period in the afternoon than in the morning, possibly because in the morning, with the day ahead of them, they found only enough food to meet the energy costs of their activity. However, in the afternoon there was the need to meet maintenance demands as well as "stock-up" with food to last them throughout the night. In support of this was the finding of Baldwin and Kendeigh (1938) that birds attained their maximum weight in the late afternoon. Also, it seems logical that insectivorous birds should spend more time foraging in the afternoon when diurnal temperatures are highest since diurnally active invertebrates are most active then and hence more conspicuous to Robins. The reason for the significantly lower percentage of time spent foraging in the early morning compared with later was probably related to the profitability of foraging then. Kacelnik (1979) has shown that the foraging efficiency of captive Great Tits was limited by low light intensities for over one and a half hours after dawn even on sunny days. Furthermore, the lower proportion of time tits foraged around dawn matched their lower efficiency of foraging then. For the same reasons, it seems likely that it was less profitable for Robins to forage in the early morning because they foraged mainly on the ground under vegetation (Section 4.3.1, p. 30), a site where light intensities would have been low in the early morning.

Male Robins foraged less about midday, a situation known for a variety of animal taxa including insects, reptiles, fish, mammals and birds (Aschoff 1966). From experiments with birds kept under constant light and temperature conditions, it seemed that this midday lull in foraging activity depended in part upon persistent endogenous rhythms with an approximately daily pattern which were synchronised by entraining agents, such as environmental stimuli (Aschoff 1960, Palmgren 1949, Smith *et al*. 1969). The extent of this reduction in foraging activity for male Robins was greatest in summer when a smaller proportion of the day was spent feeding compared with later in the non-breeding season. Since the proportion of time devoted to foraging increased as the non-breeding season progressed (Fig. 10.2), the lull in foraging activity at midday became smaller (Fig. 10.7). Similarly, the time-budgets of immature males included a smaller decrease in foraging activity at midday than those of adult males, because the former spent a greater proportion of the day feeding. From the diurnal pattern of foraging and resting, it is apparent that the increased time spent feeding took place mainly at the expense of resting at midday.

(b) Food-storing

Moulting adult males spent more time storing food in the early morning than during the rest of the day. In summer most of the stored items were cicadas (Table 5.1, p. 50), which were easily caught in the early morning when cool temperatures made them slow moving. In addition, at this time cicadas that had recently emerged from their exuvia were soft and unable to fly. Why immature males did not feed on this readily available food and store some in the early morning as the adults did I am unable to explain.

During autumn and winter, there were no significant changes in the proportion of time that adult and immature males spent storing food from one day-period to the next. As was concluded from the monthly time-budgets, Robins stored part of most large prey captured, even when the proportion of time spent foraging per day-period seemed to be only sufficient to meet their maintenance demands. It seems that it was an advantage to have some food readily available when environmental conditions prevented hunting. Not having a crop, perhaps Robins could eat only a small amount of a large prey and it was advantageous to hide any excess from other animals. This suggestion seems less likely than the first because Robins often ate a part of an item, stored one or two portions and then ate some more all within a few minutes.

In winter, bachelors stored most food about midday. Since they spent relatively little time foraging in the morning, presumably they had to eat most of what they found then. Similarly, in the late afternoon, they probably foraged to make up for the low food intake in the morning and to build up bodily reserves to last them during the night.

(c) Body-maintenance

As expected from previous results (Sections 9.4, p. 139 and 10.4.1), all three categories of male Robins during summer and autumn spent more time in body-maintenance about midday when less time was spent foraging. Occasionally an increase in body-maintenance behaviour occurred in the late afternoon, even though the Robins spent as much time foraging then as they had done in the mid-afternoon. In winter, immature males and bachelors continued to carry out most body-maintenance activities at midday. However, adult paired males spent just as much time engaged in such activities in the early morning and late afternoon as they had at midday. This diurnal pattern of body-maintenance for adult males probably took place because they sang and foraged less during those times of the day than did the other two male categories, so that there was time available for preening.

(d) Vocalizing

Why Robins sang mainly in the early morning can largely be related to their diurnal pattern of foraging and the time of day when singing would best achieve its purpose. Because foraging seemed to be least efficient in the early morning, it was probably more profitable for Robins to engage in non-foraging activities at that time. Time spent vocalizing was largely the singing of full song (Section 6.4.1, p. 62), which probably functioned to ward off intruders and, for a bachelor, to attract an unmated female. Since intrusions by neighbouring Robins and movements by unmated females were likely to occur in the morning, when less time was spent foraging, it would seem best to sing then. Immature males, and to a lesser extent adult males, sometimes sang more at midday than earlier. Possibly they were unable to spend so much time singing during the mid-morning because they had not fed much during the early morning and by mid-morning conditions were favourable for foraging.

With respect to the vocal behaviour of bachelors in winter, it was possible that these birds either lost weight in the morning and made it up later in the day or they relied on stored food to sustain the large proportion of time spent singing then. Birds have been found to operate on a negative energy budget during the moult and breeding season (Wolf *et al*. 1975), so that bachelor Robins could have done the same, sustaining themselves mainly on bodily reserves which they had formed by foraging most of the previous afternoon.

(e) Resting

Although male Robins did not significantly increase the time spent resting about midday, more time was nevertheless usually spent resting then than during the other day-periods. Generally, foraging activity peaked about mid-morning and the mid- to late afternoon, and "spare" time during the early morning was spent singing and in partner-interactions, so that any increase in resting time had to occur about midday. Several other studies have shown that birds usually rested at midday, but in many cases resting took place then because conditions were suboptimal for foraging. American Avocets spent more time resting during the mid- to late morning having foraged in the early morning and with their afternoon feeding peak correlated with the time of day when prey were most abundant and available (Gibson 1978). Verdin (Austin 1976), Roadrunners *Geococcyx californianus* (Calder 1968) and Yellow-billed Magpies (Verbeek 1972) were all found to have midday rest periods correlated with very high ambient temperatures. Either the high temperatures were considered to cause physiological stress to an actively foraging bird or the heat caused invertebrates to go into hiding so that it was unprofitable to forage then anyway.

(f) Partner-interactions

Adult and immature males spent most time interacting with their partners during the early morning. This was because of the higher frequency of sexual chases in the early morning (Fig. 8.2, p. 117) and their mean duration of nearly two minutes. Interactions between members of a pair after mid-morning mainly involved skirmishes of less than 30 seconds so that less time was spent in this behaviour in the afternoon. Adult males presumably initiated more sexual chases in the early morning because it was more efficient to engage in non-foraging activities then than later in the day. In contrast, immature males had no distinct diurnal pattern of partner-interaction behaviour in winter because they engaged in fewer sexual chases then than in autumn. Possibly, this arose because immatures spent their "spare" time singing and in body-maintenance rather than in sexual chases as adults did. That sexual chases were of lower priority than the other two behaviours for immatures would be expected considering that sexual chases did not contribute to the maintenance of the individual as the other two seemed to do. Adult males did not have a diurnal rhythm of partner-interactions while moulting because they did not indulge in sexual chases then.

(g) Territorial defence

The diurnal pattern of territorial defence, which peaked in the afternoon, can be related to the Robin's diurnal patterns of foraging and singing. Neighbouring birds were most often near their territorial boundaries and therefore most likely to see each other when foraging. Little time was spent in territorial disputes in the early morning by all categories of males because they sang in the canopy then. Not only were they unlikely to notice a trespasser from the canopy, but their singing probably helped to ward off intruders. Adult males spent more time in territorial disputes during winter mornings because they sang less in winter than in autumn. Although male Robins spent most of the afternoon foraging in winter, interactions were less frequent then than during the previous seasons because either they had little time for such disputes or neighbouring Robins recognised the location of the boundaries between each other's territories and rarely went beyond them.

(h) Interspecific interactions

Adult and immature males spent a similar time per day-period in interspecific interactions during each season and such interactions seemed to arise randomly during the course of the day. In the case of bachelors, little time was taken up in interspecific interactions during the early morning because these birds spent much time singing in the canopy, a site where few interactions took place. Even when a singing bachelor was threatened by a bird of another species, the Robin dived for cover into the understorey and almost immediately began foraging, so that little time was involved in such an interaction. In the late afternoon, bachelors spent most time foraging on or near the ground where there was little chance of them interacting with other species, since these occurred mainly above the lower understorey.

10.5. Summary

From January to May, immature males foraged more than adult males, but both categories foraged for a similar proportion of time in June and July. Males foraged for a lower proportion of time, but more hours per day, in summer than in autumn or winter. That adults spent more hours foraging in summer than later, even though daylengths were longest and monthly mean temperatures highest during the summer, can be partly attributed to the high energy demands of the moult (Payne 1972).

The storing of food took about 0.7% of time for males in autumn and winter, and slightly less in summer. It is hypothesised that they spent more time storing food in winter, when they spent fewer hours per day foraging, to have some food readily available if severe weather impeded foraging.

Each month adult males spent more time in body-maintenance than immatures. Both categories spent more time in this behaviour in January and February while moulting, and least time during winter. In autumn and winter, the proportion of time they spent in body-maintenance was generally inversely related to that spent foraging.

Adults vocalized more than did immatures from January to April, but this trend was reversed in June and July. This was because, after May, the intervention by "chucking" adult females tended to curtail singing by their mates (usually adult males), but immature females did not exhibit this behaviour to so great an extent, hence singing immature males were less often interrupted.

Adults rested more than did immatures from January to May. As for body-maintenance, the proportion of time adult and immature males rested after March was inversely related to that spent foraging.

Males interacted little with their mates during summer, but afterwards their involvement in such partner-interactions increased in the form of sexual chases. The percentage of time adult males spent in territorial defence increased from January to March, followed by a gradual decline to July. As for vocalization and partner-interaction behaviours, the low proportion of time adult males were involved in territorial defence while moulting and the resurgence of such behaviours afterwards was probably related to the level of sex hormone secretion. Immatures generally spent less time in conflict with other Robins compared with adult males. However, this was biased by not being able to time the behaviour of immatures being evicted from sub-territories impinging on those of adult males from March to May. Both categories of males spent a similar time each month interacting with other species.

Compared with paired adult males, bachelors foraged less from May to July, and spent less time in body-maintenance in July. The less time that bachelors foraged in winter, compared with paired males, seems partly to explain why the former incurred a greater mortality. This risk seems to have been taken so that bachelors could sing more than paired males and hence attract a partner.

Generally, for adult and immature males there were mid-morning and mid- to late afternoon peaks in foraging, the afternoon peak being the greater. Since foraging results in energy procurement, this diurnal rhythm probably reflects the diurnal pattern of an individual's energy requirements and the most efficient time for foraging. In both age classes, the lull in foraging about midday was most evident during summer and almost non-existent in winter. In contrast, during winter, bachelors foraged for an increasing proportion of time per day-period as the day progressed.

In the course of summer, adult males stored most food in the early morning, but immatures carried out their storing about midday. However, in autumn and winter all three categories of males spent a similar time storing food each day-period.

Adult and immature males were involved in body-maintenance mainly about midday in summer and autumn. In winter, the diurnal rhythm for this behaviour was different for each category of male. Overall, the peak time of body-maintenance took place when males foraged and sang least.

Males sang most of all in the early morning, and then decreased the time spent singing through the day, probably because weather conditions in the early morning were less likely to impair acoustic transmission than conditions later in the day (Wiley and Richards 1978). In addition, low ambient temperatures and light intensities probably made early morning foraging less efficient.

Except for adult males during summer, each category of male had no distinctive diurnal rhythm of resting. Paired males (adults and immatures) spent more time interacting with their mates in the early and mid-morning in the form of sexual chases.

Generally, males spent more time in conflicts with Robins, other than their partners, in the afternoon. Paired males showed no diurnal pattern of interspecific interactions. However, bachelors spent less time in this behaviour during the morning, because while singing in the canopy they were more isolated from other species than when they were in the understorey.

CHAPTER ELEVEN

THE TIME-BUDGETS FOR FEMALE ROBINS OUTSIDE THE BREEDING SEASON

11.1. Introduction

The monthly and diurnal time-budgets for adult and immature female Robins outside the breeding season are described and compared in this chapter. From the analyses and comparisons of the time-budgets I hoped to answer questions like the following concerning events outside the breeding season:-

1. Were the trends from the comparisons of time-budgets for adult and immature males also true from the comparisons of the time-budgets for the two categories of females - did immature females forage more, and preen and rest less than adult females?

2. Were there any differences in the time spent by members of the two age classes of females in interactions with their mates and with other Robins that may have been the result of previous experience?

As described in Section 10.1, p. 146, two important processes took place during the non-breeding season, (1) the moult followed by (2) a resurgence in territorial and sexual behaviour. The timing of the moult for adult males and females differed (Fig. 10.1, p. 145). Females without rectrices were seen from 28 January to 1 March, about a fortnight later than were their mates.

11.2. Methods

The data from the timed observations of adult and immature females' behaviour were analysed as for the male categories (Section 10.2, p. 147), providing monthly (Figs 11.1 and 11.2, Appendices 10 and 11) and diurnal time-budgets (Figs 11.3 and 11.4, Appendices 12 and 13) for the two categories of female Robins.

The results and discussion sections are divided into two portions: (1) the monthly time-budgets and (2) the diurnal patterns of behaviours. Within these sub-sections, the information is further divided so that the data for each behaviour are treated separately and in the same sequence as shown on the figures.

11.3. Results

11.3.1. The monthly time-budgets

The Chi-squared values in Appendix 10 show that the monthly time-budgets for adult females changed significantly from month to month as the non-breeding season progressed ($P < 0.005$), as they also did for immature females (Appendix 11).

(a) Foraging

Figure 11.1 shows that adult females spent the least proportion of time per month foraging in January (70.2%). The proportion of time they spent foraging per month increased during the course of the season, significantly so in February, May and July ($P < 0.01$), so that by July adult females foraged for 93.5% of time. In contrast, immature females spent 91.2% of time foraging in January (Fig. 11.2). The only significant increase in foraging throughout the season for them arose in May ($P < 0.01$), and from May to July they foraged for about 93.8% of time. During each month, except July, immature females foraged significantly more than did adult females ($P < 0.01$).

(b) Food-storing

In general, for immature females the proportion of time and the minutes per day spent storing food each month increased through the non-breeding season (Figs 11.2 and 11.3 respectively). For adult females, the data show that the time they spent storing food changed markedly from month to month (Figs 11.1 and 11.3). For each month the members of the two age classes devoted a similar time as each other to this behaviour. Adults significantly increased the proportion of time spent in food-storing in April and June ($P < 0.05$) (Fig. 11.1), but no significant increases were apparent from the monthly results for immature birds. Outside the breeding season, Robins stored an average of six prey items a day, immature females slightly more than did adult females.

Figure 11.1. The monthly time-budgets for adult female Robins during the non-breeding season.

Appendix 11 gives the plotted values.

[a]The asterisks indicate significance levels: * = $P < 0.05$, ** = $P < 0.01$. The asterisks at the sides of the columns show significant differences between adjacent monthly samples.

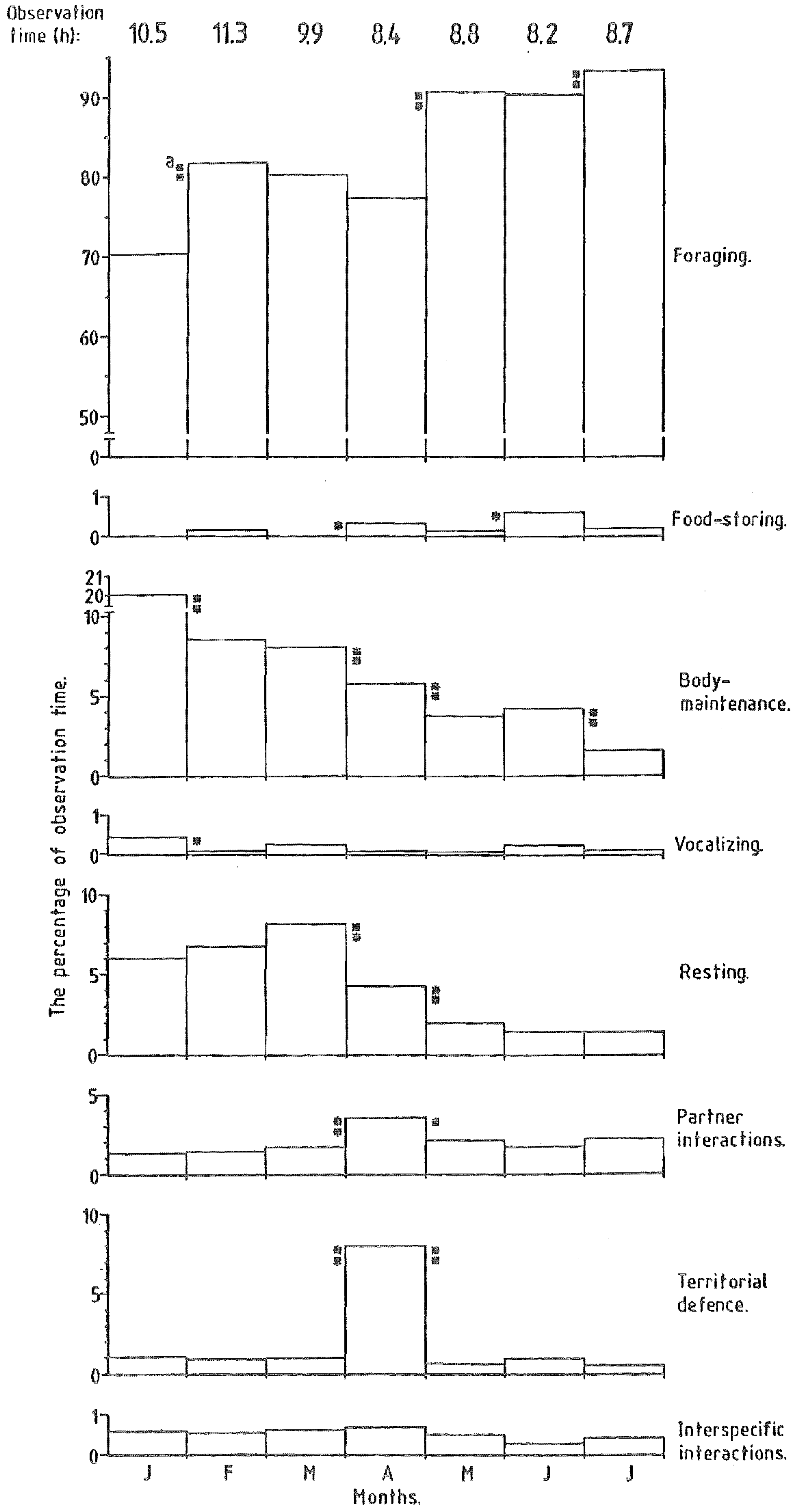
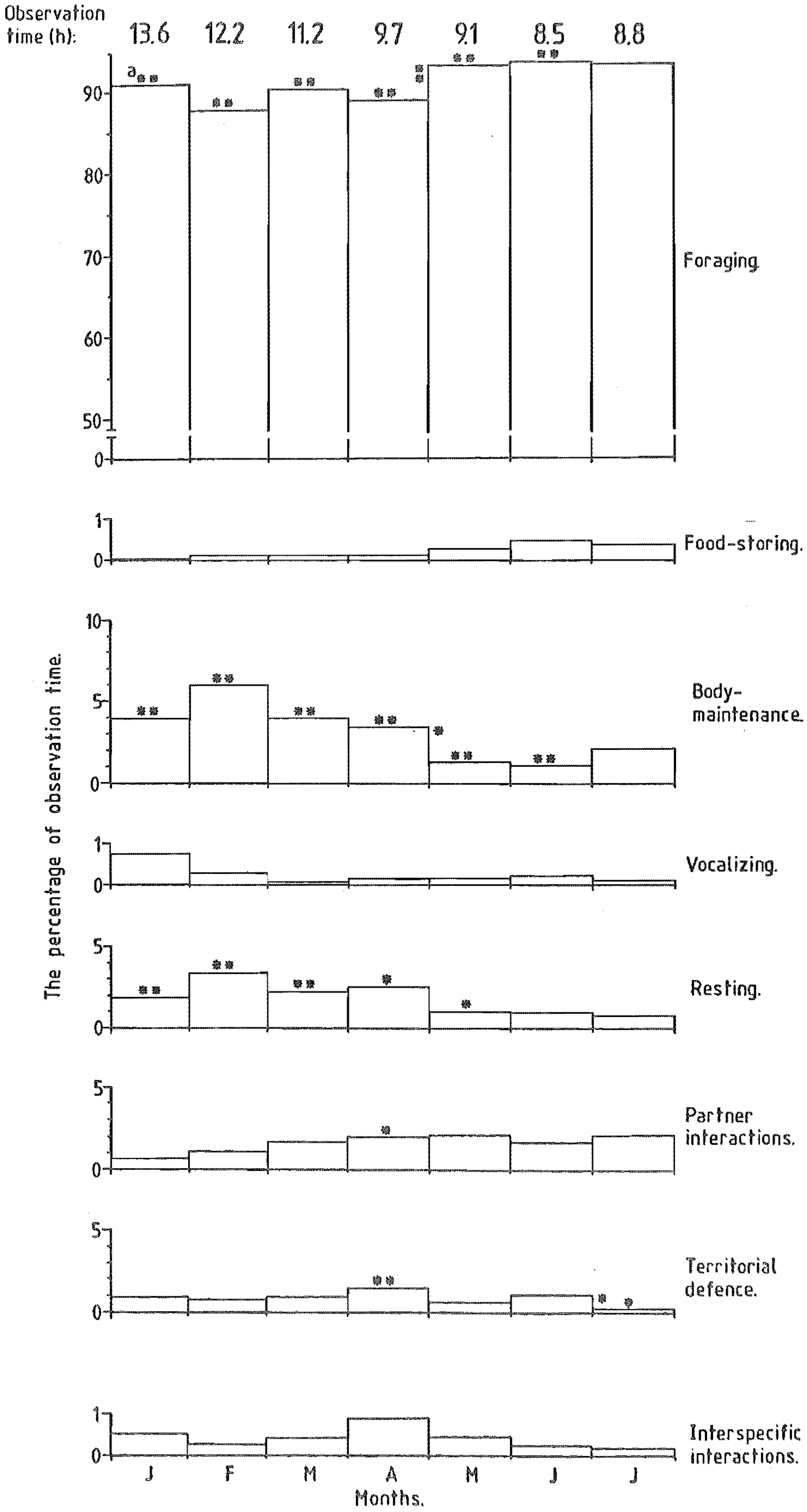

Observation time (h):
10.5
11.3
9.9
8.4
8.8
8.2
8.7
90
80
70
60
50
0
a**
**
**
Foraging.
1
0
Food-storing.
21
20
10
5
Body-maintenance.
Vocalizing.
Resting.
Partner interactions.
Territorial defence.
Interspecific interactions.
The percentage of observation time.
J
F
M
A
M
J
J
Months.

Figure 11.2. The monthly time-budgets for immature female Robins during the non-breeding season.

See Appendix 12 for the plotted values.

[a]The asterisks indicate significance levels: * = $P < 0.05$, ** = $P < 0.01$. The asterisks at the sides of the columns show significant differences between adjacent monthly samples. Those above the columns show the months when immature females and adult females (Fig. 11.1) spent significantly different percentages of observation time in a particular behaviour.


Observation time (h):
13.6
12.2
11.2
9.7
9.1
8.5
8.8
a**
**
**
**
*
*
**
**
90
80
70
60
50
0
Foraging.
1
0
Food-storing.
10
5
0
**
**
**
**
*
**
**
Body-maintenance.
The percentage of observation time.
1
0
Vocalizing.
5
0
**
**
**
*
*
Resting.
5
0
*
Partner interactions.
5
0
**
*
*
Territorial defence.
1
0
Interspecific interactions.
J
F
M
A
M
J
J
Months.

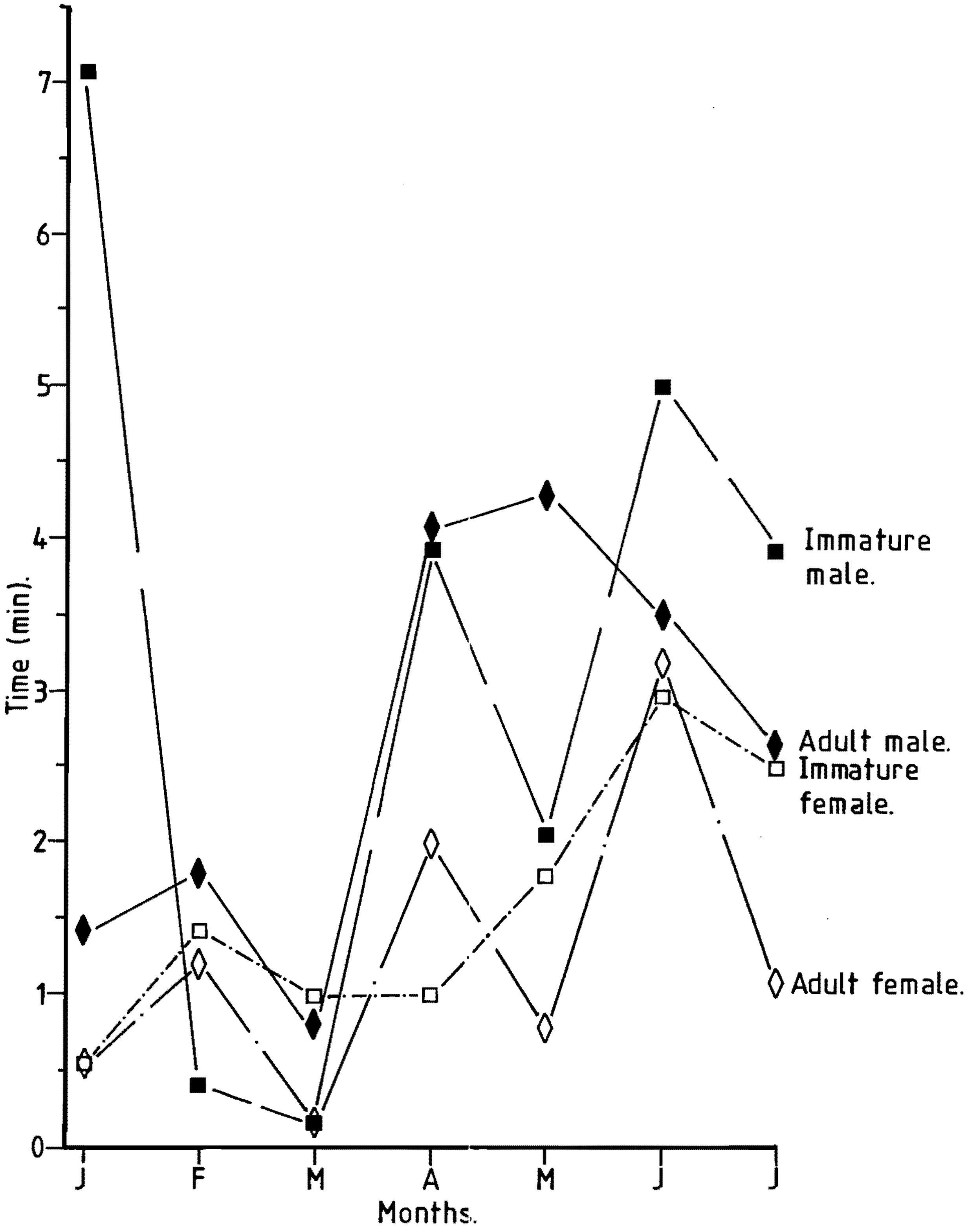


Figure 11.3 The minutes per mean daylength each month spent on storing food by four categories of Robins in the non-breeding season.

(c) Body-maintenance

Adult females spent a similar proportion of time or less from month to month during the course of the non-breeding season in body-maintenance (Fig. 11.1), as did immature females (Fig. 11.2). From the high involvement of 20.3% of time spent in this behaviour by adults in January, the proportion of time declined significantly in February, April, May and July so that by the latter month only 1.7% of time was spent in body-maintenance. By comparison, immature birds spent from 6.0% of time during February to 1.2% in June in body-maintenance. Except for July, this was significantly less time per month than was spent by adults (Fig. 11.2). For females of both age classes, a significant increase in the proportion of time spent foraging was correlated with a significant decline in body-maintenance for the same month.

(d) Vocalizing and interspecific interactions

Adult females spent a similar proportion of their time from month to month vocalizing and in interspecific interactions as the non-breeding season progressed, as did immatures. For each month, the two categories of females spent as much time as each other in these two behaviours.

(e) Resting

Female Robins rested most while moulting (January to March), and devoted gradually less time to this behaviour from April to July. Adults spent significantly more time resting than did immatures from January to May inclusive (Fig. 11.2).

(f) Partner-interactions

Both age classes of females spent the lowest proportion of time per month in partner-interactions in January, with, generally, a gradual increased involvement in this behaviour as the season progressed. An exception to this trend arose in April when adult females devoted a significantly greater proportion of time to this behaviour than in May. April was the only month that adult females spent more time in partner-interactions than immatures did ($P < 0.05$).

(g) Territorial defence

During each month, adult females spent from 0.5 to 1.2% of their time in territorial defence, except in April when it was 8.1% of time (Fig. 11.1). In comparison, immature females always spent less than 1.4% of time per month in territorial disputes (Fig. 11.2). In April and July, immatures devoted significantly less time to this behaviour than did adult females.

11.3.2. The diurnal patterns of behaviours

(a) Foraging

The data show that foraging by females followed a bimodal pattern during summer and autumn, but in winter there was only one peak daily (Figs 11.4 and 11.5). The peak times of foraging in summer for adult females occurred in the early morning and late evening, with the former being the greater of the two (Fig. 11.4). They spent significantly less time foraging in the late morning than during the previous and subsequent day-periods ($P < 0.01$). The peak times of foraging in summer for immature females differed from those for the adults. Immatures foraged most in the late morning, with their lull in foraging taking place in the early afternoon (Fig. 11.5). They spent a similar time foraging in the mid- and late morning, and as occurred for adult females, this afternoon peak in foraging was lower than the morning one.

Both age classes had a similar diurnal pattern of foraging during autumn. An increasing proportion of time per day-period was spent foraging as the morning progressed. A significant decrease in foraging occurred in the early afternoon, followed by a significant increase over the remainder of the afternoon. As arose in summer, in autumn the female's morning foraging peak was slightly greater than the afternoon one.

In winter, adult and immature females gradually increased the time spent foraging until the mid-afternoon, after which it declined. During this season there was no lull in foraging by members of either age class.

(b) Food-storing

The results show that neither age class of females had a distinct diurnal pattern of storing food during the three seasons, no significant change took place in the proportion of time they devoted to storing food from one day-period to the next (Figs 11.4 and 11.5). However, in summer and autumn, females generally spent least time storing food during their lulls in foraging.

(c) Body-maintenance

For each season, the results show that adult and immature females had a different diurnal pattern of body-maintenance behaviour. In summer, adult females spent significantly more time in body-maintenance each day-period through the morning ($P < 0.01$), followed by significant declines in the early and late afternoon. In contrast, immatures spent a similar time in body-maintenance during each day-period, except for a marked increase in the early afternoon ($P < 0.01$).

In autumn, adult females spent significantly more time in body-maintenance during the mid- and late morning, and early afternoon than during the other day-periods. By comparison, immatures spent a similar time in this behaviour from one day-period to the next.

In winter, adult females spent a similar time in body-maintenance each day-period, except for a decline in the early afternoon ($P < 0.05$). During the same season, immatures spent significantly less time in body-maintenance during the early morning and mid-afternoon compared with that for the subsequent day-periods. It is of note that when females significantly increased the time spent foraging they generally significantly decreased their involvement in body-maintenance during the same day-period.

(d) Vocalizing

The diurnal pattern of vocalizing for adult and immature females was similar for each season. In summer while moulting, they spent most time per day-period vocalizing in the early morning. Significantly less vocalizing was carried out in the mid-morning than previously, with the time spent vocalizing remaining fairly constant for the rest of the day. During autumn and winter, both age classes vocalized for a similar time

Figure 11.4. The diurnal patterns of behaviours for adult female Robins during summer, autumn and winter.

Appendix 13 gives the plotted values.

[a]The asterisks at the sides of the columns show the levels of significant difference (* = $P < 0.05$, ** = $P < 0.01$) between adjacent day-period samples for a particular behaviour.

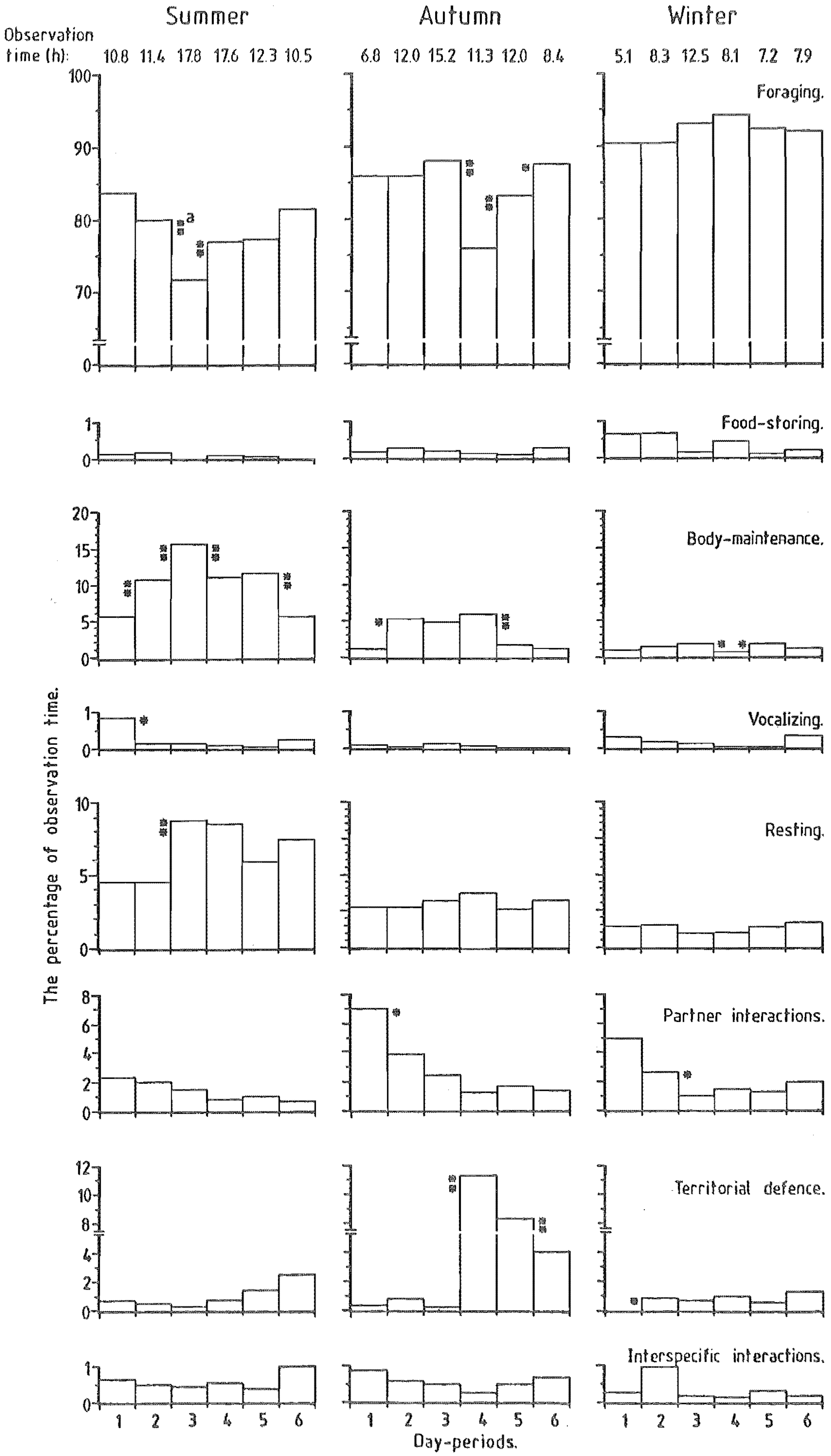
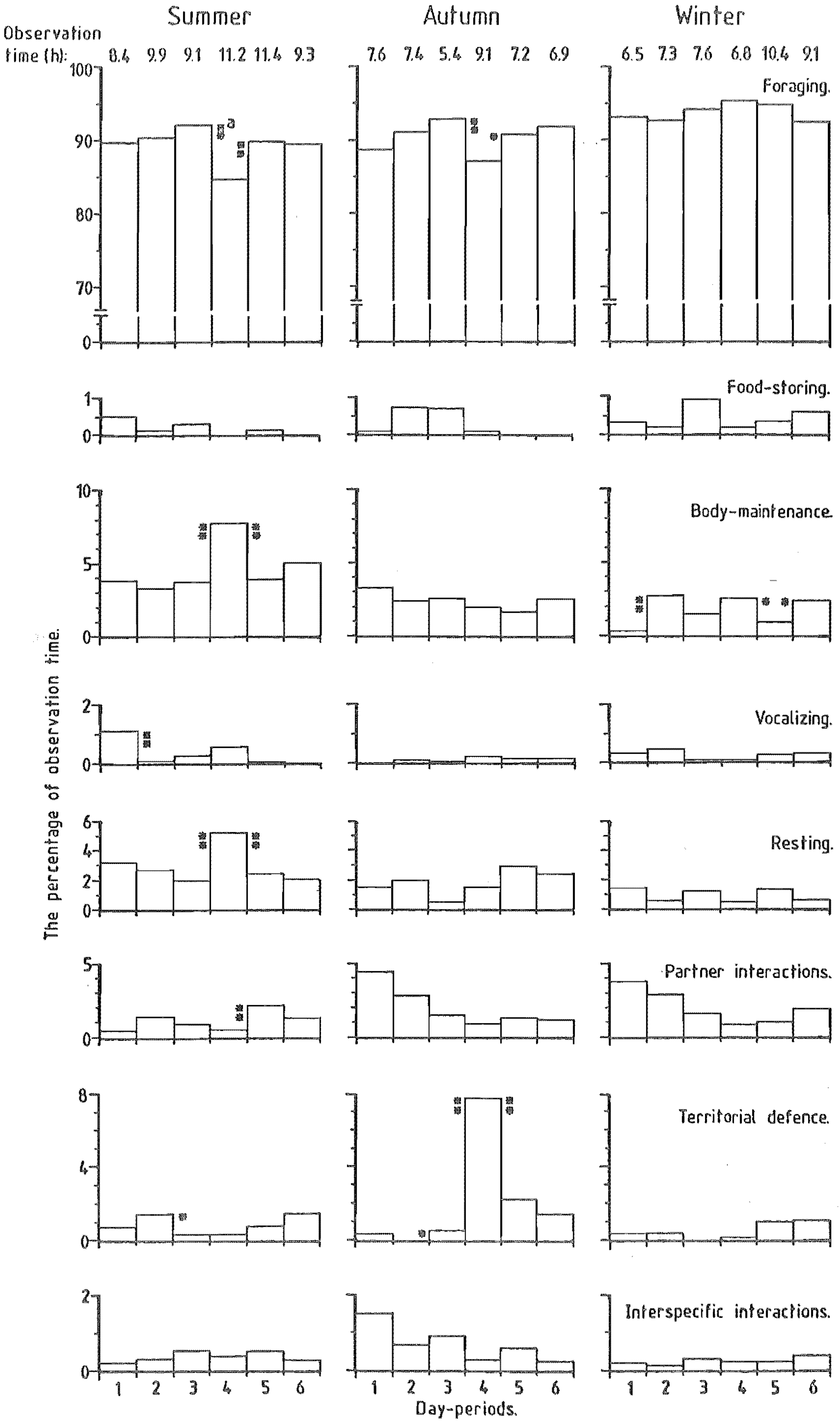

Summer
Autumn
Winter
Observation time (h):
10.8 11.4 17.8 17.6 12.3 10.5
6.8 12.0 15.2 11.3 12.0 8.4
5.1 8.3 12.5 8.1 7.2 7.9
Foraging.
100
90
80
70
0
**a
**
**
**
*
Food-storing.
1
0
Body-maintenance.
20
15
10
5
0
**
**
**
**
*
**
* *
Vocalizing.
1
0
*
Resting.
10
5
0
**
Partner interactions.
8
6
4
2
0
*
*
Territorial defence.
12
10
8
4
2
0
**
**
*
Interspecific interactions.
1
0
The percentage of observation time.
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
Day-periods.

Figure 11.5. The diurnal patterns of behaviours for immature female Robins during summer, autumn and winter.

See Appendix 14 for the plotted values.

[a] The asterisks at the sides of the columns show the levels of significant difference (* = $P < 0.05$, ** = $P < 0.01$) between adjacent day-period samples for a particular behaviour.


Summer
Autumn
Winter
Observation time (h):
8.4 9.9 9.1 11.2 11.4 9.3
7.6 7.4 5.4 9.1 7.2 6.9
6.5 7.3 7.6 6.8 10.4 9.1
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner interactions.
Territorial defence.
Interspecific interactions.
The percentage of observation time.
100
90
80
70
0
1
10
5
2
6
4
8
a
1 2 3 4 5 6
Day-periods.

from one day-period to the next.

(e) Resting

In summer, adult females rested least of all in the early and mid-morning. During the late morning their involvement in this behaviour nearly doubled ($P < 0.01$) compared with previously, and did not significantly decline during the afternoon. In contrast, the results show that immature females had a pronounced peak in resting during the early afternoon ($P < 0.01$), but otherwise devoted a similar time to this behaviour each day-period. During autumn and winter, adult females devoted a similar time to resting from one day-period to the next, as did immature females.

(f) Partner-interactions

During the course of summer days, a gradually decreasing time was spent in partner-interactions by moulting adult females (Fig. 11.4). For the same season, immature females behaved quite differently. They spent a similar time engaged in partner-interactions through the morning and early afternoon, but then significantly ($P < 0.01$) became more involved in this behaviour during the mid-afternoon (Fig. 11.5).

In autumn and winter, birds in both age classes showed similar diurnal patterns of partner-interaction behaviour. They spent the greatest time per day-period in this behaviour during the early morning followed by a decline during the course of the morning until it increased slightly in the mid- to late afternoon.

(g) Territorial defence

Generally, female Robins spent more time in territorial defence in the afternoon than in the morning. During summer and winter, the afternoon increase in such disputes was not significant, but in autumn it was ($P < 0.01$).

(h) Interspecific interactions

Adult females spent a similar time in interspecific interactions from one day-period to the next during each of the three seasons, as did immatures.

11.4. Discussion

11.4.1. The monthly time-budgets

Many features of the female's time-budgets and the reasons for their occurrences are the same as those already discussed for males' time-budgets (Section 10.4, p. 166). Therefore, where such features are common to both sexes they will be discussed only briefly here.

(a) Foraging

The increased proportion of time spent foraging by adult females in February over that carried out during January ($P < 0.01$) can largely be attributed to their starting to moult, an energy-demanding process involving the rapid replacement of all feathers. For several species of birds it has been found that the standard metabolic rate for moulting birds increased by about 30% above that for non-moulting birds (Payne 1972, Perek and Sulman 1945, Wallgren 1954). Half of this increased metabolic rate, which would increase the food requirements of the birds, seemed to be caused by the loss of heat from highly vascularized feather papillae and the other half by the increased surface area exposed to cool temperatures (Lustick 1970).

The significant increase in the proportion of time spent foraging by adult females in May compared with in April, and the high involvement in foraging (about 90% of time) being maintained in June and July can be attributed largely to lower air temperatures, shorter days and possibly reduced food availability. For birds of a given weight there is an approximately linear relationship between air temperature and standard metabolic rate (King and Farner 1961, Verbeek 1964). In agreement with this statement, Schildmacher (*in* Dorst 1974) found that as the temperature dropped the Village Weaver *Ploceus cucullatus* ate an increasing proportion of its body weight in food. Therefore, because the monthly mean temperatures declined during the course of the non-breeding season (Table 2.1, p. 13), the Robins probably spent a greater proportion of time each month foraging to meet their increased maintenance requirements. However, the decreasing daylengths (Table 3.1, p. 20) and, apparently, reduced prey availability, probably also necessitated that the birds foraged for a greater proportion of time in the later months of the non-breeding season compared with earlier. The longer nights would have required the birds spending more time finding prey to sustain themselves during the night. A reduced prey abundance has been shown to cause some species to spend longer foraging (Gibson 1978, Verner 1965). Robin prey, especially large species, seemed to be less abundant during winter than previously. Therefore, these three factors probably combined to cause the adult females to forage for a greater proportion of time in winter to meet their maintenance requirements.

The significant increase in foraging time in July over the June figure for adult females (Fig. 11.1), when the monthly mean temperatures (Table 2.1, p. 13) and daylengths (Table 3.1, p. 20) increased slightly, was perhaps caused by them searching for extra food to increase their fat reserves in preparation for breeding. Most females had laid their first clutches by late August.

The greater proportion of time spent foraging from January to June by immature females, compared with that for adults ($P < 0.01$), was probably caused by the former's poorer proficiency at finding, catching and handling prey. Several observations showed that some immatures were less proficient at killing and breaking up large prey than were adults (Section 4.3.5, p. 37). These reasons have been found to cause immatures of several other species to spend more time feeding than adults: for example, Royal Terns *Sterna maxima* (Buckley and Buckley 1974), Olivaceous Cormorants (Morrison *et al.* 1978) and Little Blue Herons *Florida caerulea* (Recher and Recher 1969).

(b) Food-storing

The small proportion of time devoted to the hoarding of food from January to March may have been caused by drought conditions in 1977 and 1978 reducing the availability of prey so that the birds ate most of their prey immediately to meet the high food requirements of the moult. In contrast, in early April 1978, 468 mm of rain fell after which prey were abundant. Earthworms were so readily available that it seemed the Robins selected mainly small ones to eat. On withdrawing a large worm from its burrow the Robin often left it, but ate a smaller worm found a few seconds later. Small earthworms were eaten whole whereas large ones had to be broken up first. These readily available earthworms and other soil inhabiting prey, presumably brought about the significant increase in food-storing in April 1978 (Appendix 11). Likewise, the significant increase in such behaviour in June 1978 may have been related to very high rainfall during the previous month (Table 2.1, p. 13) and a resultant increase in prey abundance.

Gwinner (*in* Purchas 1973) suggested that Ravens *Corvus corax* stored more food following periods of food shortage. A similar reasoning may explain why members of both age classes of females spent more time each day during the course of the non-breeding season storing food (Fig. 11.3), even though they spent less hours per day foraging then (Fig. 10.4, p. 153). It seems possible that they stored more food in winter because of the survival value of having a readily available cache when prey could not be easily found. Then, during the summer months when, apparently, prey were readily available, the Robins spent less time storing food, perhaps because they rarely experienced food shortages and so less often continued foraging and storing surplus prey once their hunger was satiated.

(c) Body-maintenance

The very high proportion of time spent by adult females in body-maintenance during January was because they sun-bathed then (Fig. 7.8, p. 104). The reduction in body-maintenance during February, when these birds started to moult, was a consequence of a reduction in sunning and in associated-preening activities. This was true both for 1977 and 1978 ($P < 0.01$) (Fig. 7.8).

The reduction in the percentage of time spent in body-maintenance by both age classes of females as the non-breeding season progressed may have been a result of their new plumage requiring less maintenance. During the moult, much time was spent removing worn feathers and feather sheaths and arranging the growing feathers. Another possible reason for this reduction in body-maintenance was that the time spent in the behaviour was inversely related to that spent foraging, as was found for male Robins (Sections 9.4, p. 139 and 10.4.1, p. 166) and Yellow-billed Magpies (Verbeek 1972). For both adult and immature females, a significant increase in time spent foraging was correlated with a significant decrease in body-maintenance. In support of this suggestion was the fact that for those months when immature females spent more time foraging than did adult females ($P < 0.01$), those of the former category spent less time in body-maintenance ($P < 0.01$) than did adult females. In July, when both age classes spent a similar time foraging, they also devoted a similar time to body-maintenance. Thus, the evidence strongly suggests that during the non-breeding season the time Robins devoted to body-maintenance was inversely related to that which they required for foraging in order to find sufficient food for their maintenance.

(d) Vocalizing

Females called little (< 0.5% of their time per month) and did not markedly change the proportion of time they devoted to this behaviour as the season progressed, because of the short duration of their calls (< 5 s) and that they gave them at a similar frequency each month.

(e) Resting

The general decrease in resting through the non-breeding season by females and the fact that adult females rested more than did immatures from January to May ($P < 0.05$) can largely be related to the proportion of time they foraged. Several observers have found that when birds spent more time feeding, they rested less (Gibb 1954, 1956, Owen 1972, Purchas 1973, Verbeek 1972). For male Robins after summer, a significant increase in foraging was correlated with a significant decrease in resting (Figs 10.2, p. 149 and 10.3, p. 151). Such an obvious correlation was not evident from the female monthly time-budgets; although they rested less each month when they spent significantly more time foraging, the decline in resting was not always significant. Thus, it seems that for female Robins during the non-breeding season, as for males, resting and body-maintenance were lower priority behaviours - when more time was spent foraging to meet their maintenance requirements it was at the expense of body-maintenance and resting.

(f) Partner-interactions

The time a female spent in interactions with her mate tended to be determined by the actions of the male, the dominant bird. The low proportion of time spent by females in such interactions during summer, compared with that spent in this behaviour later in the non-breeding season, seemed to be a consequence of the secretive and solitary behaviour of adult males while moulting. The increasing proportion of time devoted by both age classes of females to interactions with their partners as the non-breeding season progressed was the result of the resurgence of territorial and sexual behaviour in the males, particularly evidenced by sexual chases (Fig. 8.1, p. 117).

Adult females spent significantly more time interacting with their mates in April than during March and May, because males began singing full song to which their mates responded by approaching and "chucking". This often led to mate to mate interactions for a minute or so. Although adult females continued to react to their mates' songs after April, they did so less often, presumably because adult males sang less then ($P < 0.01$) (Fig. 10.2, 149). Immature females did not "chuck" at their singing partners as readily as did adult females, which may explain why immature females spent less time in partner-interactions during April than did adult females ($P < 0.05$).

Immatures spent less time interacting with their mates than did adult females - was this a consequence of the immature's inexperience in such interactions? This may have been part of the reason. However, since immatures foraged more than did adults from January to June ($P < 0.01$), it was also likely that immatures had less time than adults to devote to non-maintenance behaviours, such as partner-interactions.

(g) Territorial defence

I am unable to explain why immature females spent less time in territorial defence in July than did adult females ($P < 0.05$), but the difference in April ($P < 0.01$) was the result of the way that birds of the two age classes responded differently to intruding males (Section 8.3.2, p. 120). Adult females tended to remain motionless for as long as an intruder remained in sight, but immatures either approached the intruder or fled from him. Females that were unable to alert their mates by giving alarm calls when an intruder was present, were often vigorously chased by the latter. Perhaps this difference in response was a result of experience; adult females seemed to prefer to remain unnoticed rather than suffer the consequences if their mates did not respond to their calls. The reason why such interactions arose mainly in April was because it was then that adult males were mostly seen trespassing.

(h) Interspecific interactions

Both groups of females spent a similar time in interspecific interactions each month, probably because such interactions took place at random throughout the non-breeding season.

Were the trends from the comparisons of time-budgets for adult and immature males also true from the comparisons of the time-budgets for the two categories of females? For most behaviours this was the case. As the data showed for males, immature females foraged significantly more and spent less time in resting and body-maintenance than did adult females. Members of the two age classes of females spent a similar time storing food and in interspecific interactions, as did the two age classes of males. Also, for both sexes, adults interacted with their partners either slightly or significantly more per month than did immatures. Considering the two age classes involvement in territorial defence, there was no clear cut difference between them for either sex. For some months immatures defended their territories more than did adults, and *vice versa*.

However, vocalizing was the one behaviour that differed between adult and immature Robins of the two sexes. Immature and adult females vocalized for a similar time each month, whereas the two categories of males spent significantly different proportions of time vocalizing each month, except in May. This result was a consequence of the difference in the duration of the calls and songs of the two sexes and whether vocalizing and foraging were compatible behaviours. Females gave mainly short duration calls and sub-song while on or near the ground. Thus, they were able to switch between the two behaviours without reducing their time spent foraging much. However, because males gave mainly full song when vocalizing, which they sang for several minutes at a time in the canopy, they could not vocalize without interrupting their foraging.

11.4.2. The diurnal patterns of behaviours

(a) Foraging

Female Robins during summer and autumn had a bimodal diurnal pattern of foraging, as did male Robins (Figs 10.7, p. 159 and 10.8, p. 161) and many other passerines: for example, the Rock Pipit (Gibb 1956), European Robin and Blackbird (Lees 1948), White-crowned Sparrow (Morton 1967) and Yellow-billed Magpie (Verbeek 1972). Outside the breeding season, because foraging is mainly synonymous with energy procurement for self-maintenance, the bimodal feeding pattern may reflect a diurnal pattern in the bird's food requirements and the most efficient times for foraging.

There is some evidence that diurnal birds store fat as an overnight energy reserve (Newton 1969, Ward 1965) and that the amount of food eaten is determined largely by the amount of energy lost the previous night (Kontogiannis 1968). Thus, the morning feeding peak may have occurred to replace at least some of the energy used at night and to provide energy to support the morning's activities. The exact position of the morning peak of foraging was probably related to several factors, such as the amount of bodily energy left after the night and therefore the urgency with which feeding was necessary, and the most efficient time for foraging.

Moulting adult females foraged more in the early morning than later possibly to catch cicadas, the latter being sluggish in the cool, early-morning temperatures. Also, it is possible that the high energy demands of the moult, especially from heat loss during cool nights as a consequence of their reduced plumage insulation, may have necessitated them spending much time feeding in the early morning.

Even though immature females spent more time foraging each day-period than adult females did, the former's peak time of foraging took place in the late morning. Perhaps immatures had this later peak time of foraging because they were less successful than were adults at finding and catching prey earlier in the morning.

The afternoon peak time of foraging that occurred during the late afternoon for female Robins during summer and autumn was probably related to a "stocking up" with food to sustain them throughout the night. In agreement with this suggestion was the finding of Owen (1972) that White-fronted Geese accumulated about 6.3 g of grass in their oesophagi towards evening, but only 0.5 g earlier in the day. Likewise, the crops of

Budgerigars *Melopsittacus undulatus* were only partially full from mid-morning and until mid-afternoon, containing an average of 0.6 g of seed. However, in the late afternoon the birds fed avidly and went to roost with crop contents averaging 2.35 g, significantly heavier crops than at all other times of the day (Wyndham 1980). Baldwin and Kendeigh (1938) showed that several passerine species attained their maximum daily weight in the late afternoon.

The midday decline in foraging by females in summer and autumn has been found for a variety of animal taxa (Aschoff 1966) and seemed to depend upon endogenous rhythms which were synchronised by environmental stimuli (Aschoff 1960, Palmgren 1949, Smith *et al.* 1969). However, a midday lull in foraging for females did not always occur as their patterns of foraging in winter show. When Robins foraged less about midday, they often spent more time resting and preening then. Knowing the low priority of resting and preening in their time-budgets, it seems likely that they had no midday lull in foraging during winter because the birds had to continue foraging to find enough food to meet their maintenance requirements.

Female Robins changed their peak time of foraging to about midday in winter, probably because low temperatures and light intensities in the early morning and late afternoon reduced their foraging efficiency then. Presumably, it was more profitable to spend more time foraging at midday when temperatures would have been highest and invertebrates possibly more conspicuous.

(b) Food-storing

Females spent a similar time storing food from one day-period to the next during summer, autumn and winter, and spent more minutes per day storing food as the days shortened (Fig. 11.3) and as they foraged for a greater proportion of time per month. This suggests that they found a similar amount of surplus food during each day-period or that the stored food was not surplus, but that as they experienced more frequent food shortages they were motivated to store some food during the course of the day to prevent such shortages. Which, if either, of these suggestions is correct I am not sure. Obviously, to determine the reasons for and factors influencing this behaviour in Robins much more work needs to be done.

(c) Body-maintenance

The proportion of time females devoted to body-maintenance was inversely related to that they spent foraging (Section 11.3.1). Therefore, one would expect their diurnal pattern of body-maintenance to be the converse of foraging, which occurred in summer for both categories of females. The abrupt increase in preening by immatures during the early afternoon mainly involved them preening all or most of their plumage or bathing and then preening. During the other day-periods, preening bouts tended to last only a few seconds to remove foreign matter or relieve a source of irritation. Because adult females foraged less each day-period than immatures, the former had more time to spend in body-maintenance. For much of the increased time adults spent in body-maintenance they were engaged in sunning and in its associated-preening activities (Fig. 7.8, p. 104). That their peak time of body-maintenance in the late morning did not coincide with the time of highest temperatures (early afternoon) supports the hypothesis that Robins preened most when they required least time for foraging.

During autumn, adult and immature females did not spend significantly more time in body-maintenance when they foraged significantly less around midday. Instead, both categories were more involved in territorial defence, a behaviour of greater priority than body-maintenance and for which they had to stop foraging.

The diurnal pattern of body-maintenance for immatures in winter is as expected considering their pattern of foraging. However, the significant changes in body-maintenance for adult females in the mid-morning and mid-afternoon were not related just to the changes in time spent foraging then, but also to changes in time spent storing food, resting and in interactions with their partners.

(d) Vocalizing

Females spent slightly more time giving "downscales" (Fig. 6.8, p. 68), sub-song (Fig. 6.10, p. 71) and "chucks" (Fig. 6.12, p. 74) in the early morning and late evening in the non-breeding season. This same diurnal pattern for the combined vocalizations is only marginally apparent (Figs 11.4 and 11.5), because "downscales" and "chucks" were of only a few seconds duration and formed such a small proportion of the female's time-budgets. The significantly increased time spent vocalizing in the early morning compared with in the mid-morning during summer for both categories of females arose because they gave more sub-song in January (Fig. 6.9, p. 70) than later in the non-breeding season.

(e) Resting

In summer, adult and immature females rested most during the late morning when they spent least time foraging. Aschoff (1960, 1966) found that caged passerines were less active in the middle of the day under constant light and temperature conditions and he considered that this reduction was caused by endogenous rhythms. However, field studies have shown that birds rested mainly about midday because it was a sub-optimal time to forage as a consequence of very high ambient temperatures (Austin 1976, Calder 1968, Gibson 1978, Verbeek 1972). It was unlikely that midday temperatures in summer within Kowhai Bush were high enough to inhibit invertebrate or Robin activity. I conclude that female Robins rested more at midday because they had found sufficient food to meet their energy requirements for the morning and early afternoon and had enough time ahead to find sufficient food to sustain them during the night.

During autumn, adult females rested for a similar time from one day-period to the next even though they foraged less ($P < 0.01$) in the early afternoon than at other times. Probably, the large proportion of time they were engaged in territorial disputes in the early afternoon meant that little remained for increased resting then.

(f) Partner-interactions

The time females spent in partner-interactions each day-period was largely determined by their mates. In summer, adult females spent gradually less time in such interactions as the day progressed because their mates (mainly adult males) had a similar diurnal pattern of initiating these interactions (Fig. 10.7, p. 159). Similarly, the diurnal pattern of partner-interaction behaviour for immature females, while different to that for adult females, does reflect the pattern of such interactions for immature males (Fig. 10.8, p. 161), their partners.

The diurnal patterns of partner-interaction behaviour for adult and immature females during autumn and winter were the same as for each other and for adult and immature males. These diurnal patterns of partner-interactions largely reflect the frequency and duration of sexual chases during the course of the day (Figs 8.2, p. 117 and 8.3, p. 117 respectively).

(g) Territorial defence

When paired, females were rarely seen outside their territories. Therefore, territorial-defence behaviour for females invariably involved interacting with intruders or with neighbours in boundary disputes. During all seasons, both categories of females generally spent more time in territorial disputes in the afternoon, possibly because males sang much more in the morning, and this may have helped to ward off intruders then. The increased time adult and immature females spent in territorial defence in the afternoon, than they did in the morning ($P < 0.01$) during autumn, was caused by trespassing adult males interacting with resident females. At other times of the non-breeding season such males seldom trespassed.

(h) Interspecific interactions

Females spent a similar time each day-period in interspecific interactions during each season, presumably because neither female Robins nor other species had behaviours that caused them to interact more frequently with each other during one day-period or another. The protection of stored food seemed to be the main reason for much of the time Robins spent in this behaviour. Therefore, because stored food and other avian species were usually present in Robin territories, interspecific interactions involving food-protection occurred randomly throughout the day.

11.5. Summary

Generally, female Robins foraged for an increasing proportion of time as the non-breeding season progressed. They rested and preened most in summer and least in winter. From January to June, immature females foraged significantly more, and spent significantly less time in resting and body-maintenance per month than did adult females. For both age classes, a significant increase in foraging from one month to the next was usually correlated with a significant decline in resting and body-maintenance. Since foraging is synonymous with energy procurement and self-maintenance, and because of the above correlation, body-maintenance and resting were considered low-priority behaviours for these birds.

Both adult and immature females had a bimodal diurnal pattern of foraging in summer and autumn. The morning peak in foraging activity was greater than the afternoon one, with a lull in foraging at midday when they spent more time in resting and body-maintenance. These peaks of foraging activity can probably be related to the bird's hunger in the morning after the night fast and the need to "stock-up" with food in the afternoon to sustain them during the coming night. In winter, members of both age classes had one diurnal peak of foraging, which occurred at midday. Because in winter temperatures were low, days short, and food, apparently, more scarce than previously, they had to forage for a similar proportion of time throughout the day to meet their maintenance requirements. As was apparent from the monthly results, when females foraged significantly more during a day-period, they generally spent significantly less time in body-maintenance then. A similar correlation was occasionally apparent between time spent foraging and resting per day-period for immature and adult females.

Table 12.1. Statistical comparisons of the proportion of time per month adult male and adult female Robins spent in each behaviour during the course of the non-breeding season. Appendices 5 and 11 contain the values tested to obtain the results shown below.

		Behaviours[a]							
Month	Sex	F.	Fst.	Bm.	V.	R.	P.	Td.	Ie.
J	M	0.01[b]	NS		0.01	0.05	NS	NS	NS
	F			0.01					
F	M		NS	NS	0.01	0.01	NS	NS	NS
	F	0.01							
M	M		NS	NS	0.01	NS	NS	0.01	NS
	F	0.01							
A	M		NS	NS	0.01	0.05			NS
	F	0.01					0.01	0.01	
M	M		0.01	NS	0.01	0.05	NS	NS	0.01
	F	0.01							
J	M	NS	NS		0.01	NS	NS	NS	NS
	F			0.01					
J	M		NS	0.01	0.01	NS	NS	NS	NS
	F	0.01							

[a] F. = foraging, Fst. = food-storing, Bm. = body-maintenance, V. = vocalizing, R. = resting, P. = partner-interactions, Td. = territorial defence, Ie. = interspecific interactions.

[b] 0.01 = $P < 0.01$, 0.05 = $P < 0.05$, NS = not significant. The placement of the probability values at the level of M (male) or F (female) denotes which sex spent the significantly greater proportion of time in the behaviour.

CHAPTER TWELVE

A COMPARISON OF THE TIME-BUDGETS FOR MALE AND FEMALE ROBINS OUTSIDE THE BREEDING SEASON

12.1. Introduction

Comparisons are made between the time-budgets for adult males and adult females, and between those for immature males and immature females. The seasonal mortality of adult and immature Robins is described and the time-budget results discussed to determine whether they help explain the seasonal pattern of mortality.

From the comparisons of the time-budgets I hoped to answer questions like the following concerning events outside the breeding season:-

1. Were the trends in the time spent in each behaviour from month to month through the non-breeding season similar for male and female Robins?
2. When their partners were singing, what did females do?
3. Considering that males generally dominated females (Chapter 8), did paired females spend less time defending territories than did males?
4. Did females have different diurnal patterns of involvement in a behaviour from that for males?
5. Was Robin mortality highest in winter when the birds foraged for the greatest proportion of time?

12.2. Results

12.2.1. Comparisons between the monthly time-budgets for adult males and adult females

Adult females spent more time per month foraging than did adult males each month of the non-breeding season ($P < 0.01$), except in January when the reverse was the case, and in June when no significant difference arose (Table 12.1). Both sexes foraged for a greater proportion of time after April than during the previous months ($P < 0.01$) (Figs 10.2, p. 150 and 11.1, p. 188). Except during May, adult males and females spent similar proportions of time per month storing food and in interspecific interactions. Males devoted more time to these behaviours in May than did females ($P < 0.01$).

Table 12.2. Statistical comparisons of the proportion of time per month immature male and immature female Robins spent in each behaviour during the course of the non-breeding season. Appendices 6 and 12 contain the values tested to obtain the results shown below.

		Behaviours[a]							
Month	Sex	F.	Fst.	Bm.	V.	R.	P.	Td.	Ie.
J	M		0.01[b]	NS	0.01	0.01	NS	NS	NS
	F	0.01							
F	M	NS	NS	NS	0.01	NS	NS	NS	NS
	F								
M	M	NS	NS	NS	0.01	NS		NS	NS
	F						0.01		
A	M		NS	NS	0.01	NS	NS	NS	NS
	F	0.01							
M	M		NS	NS	0.01	NS	NS	0.05	NS
	F	0.01							
J	M		NS	NS	0.01	NS	NS		0.01
	F	0.01						0.01	
J	M		NS	NS	0.01	NS	NS	0.05	NS
	F	0.01							

[a] F. = foraging, Fst. = food-storing, Bm. = body-maintenance, V. = vocalizing, R. = resting, P. = partner-interactions, Td. = territorial defence, Ie. = interspecific interactions.

[b] 0.01 = $P < 0.01$, 0.05 = $P < 0.05$, NS = not significant. The placement of the probability values at the level of M (male) or F (female) denotes which sex spent the significantly greater proportion of time in the behaviour.

Both sexes of adult Robins generally spent less time in body-maintenance from month to month as the season progressed. In January and June, females devoted more time to this behaviour than did males ($P < 0.01$), but in July this trend was reversed ($P < 0.05$). Males vocalized more each month than did females ($P < 0.01$). Furthermore, males rested for a similar or significantly greater time per month than did females. Both sexes rested most in summer when moulting and least during winter.

The time adults of both sexes spent in partner-interactions each month of the non-breeding season was similar, except in April when females spent more time in this behaviour than did males ($P < 0.01$). Males spent more time in territorial defence in March than did females ($P < 0.01$), but the reversed was true for April. During the other months, the two categories of Robins spent similar proportions of time in territorial disputes.

12.2.2. Comparisons between the monthly time-budgets for immature males and immature females

In February and March, the two categories foraged for a similar time, but immature females foraged more than did immature males during the other months of the non-breeding season ($P < 0.01$) (Table 12.2). Similar to the results for adults, immature males spent more time each month vocalizing than did immature females ($P < 0.01$). From January to April inclusive, the two categories of immature Robins spent a similar time each month in territorial defence. However, in May and July males spent more time in territorial disputes than did females ($P < 0.05$), but the reverse was true for June ($P < 0.01$). For the other five behaviours (food-storing, body-maintenance, resting, partner-interactions and inter-specific interactions), generally immature males and immature females spent a similar time per month in each behaviour.

12.2.3. Comparisons of the diurnal patterns of behaviours for male and female Robins

Generally, the diurnal patterns of each behaviour for male and female Robins of the same age class were similar, except for foraging and vocalizing (Figs 10.7, p. 160, 10.8, p. 162, 11.4, p. 196 and 11.5, p. 198). For males, the peak time of foraging usually took place in the afternoon, but for females it was in the morning. Females vocalized

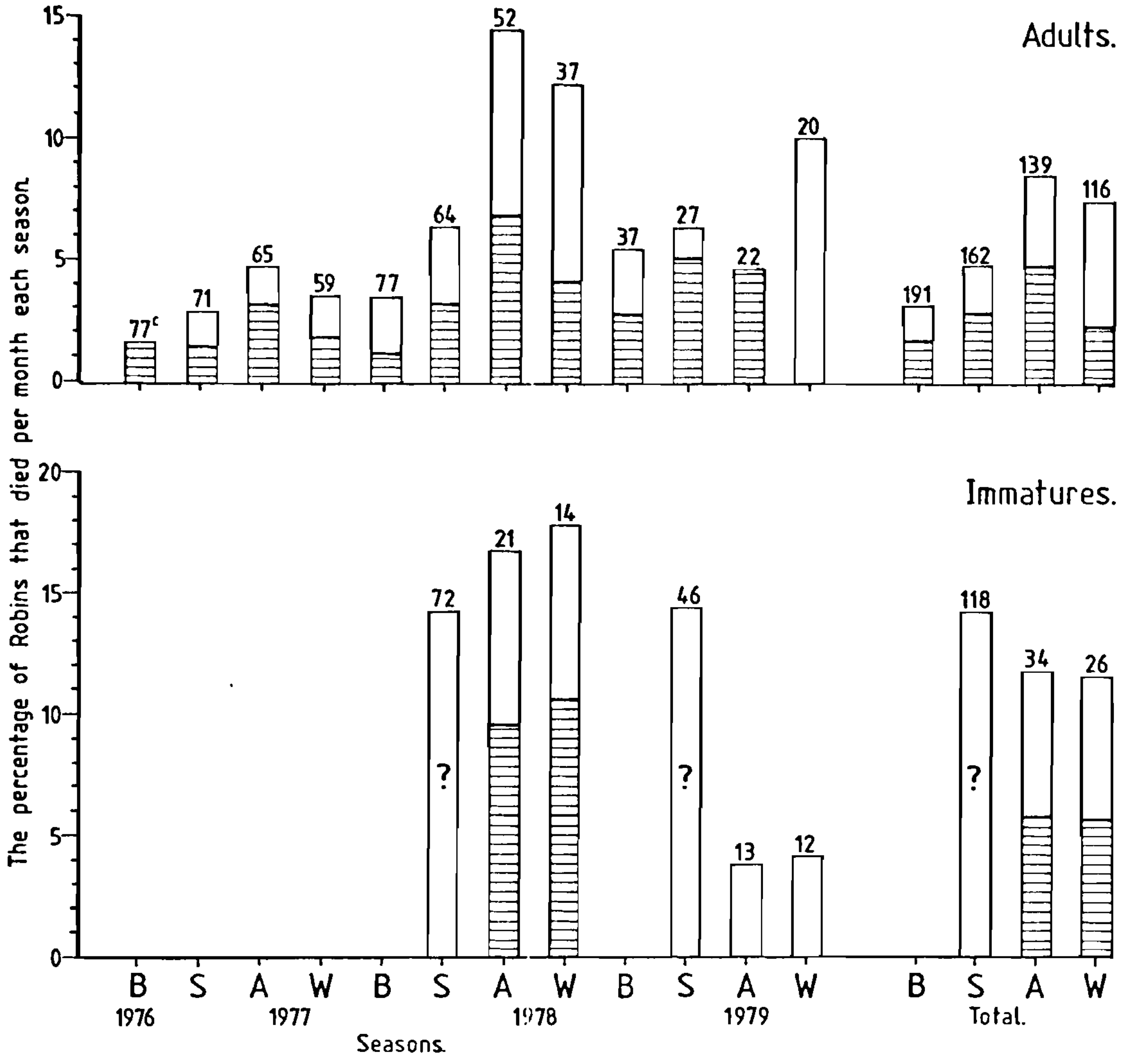


Figure 12.1 The percentage of adult and immature Robins that died (disappeared) per month each season[a,b] at Kowhai Bush from the 1976 breeding season to the 1979 winter, and in total.

[a]B=breeding season (August - December).
S=summer (January - March), [b]for immatures this season was from November to March.
A=autumn (April - May).
W=winter (June - July).

[c]The figure above each column is the number of Robins present at the start of each season. The blank and cross-hatched areas of the columns indicate the proportion of Robins that died that were males and females respectively. A question mark in a column indicates that the proportion of Robins that died and were males or females was unknown.

for a similar time throughout the day, whereas males vocalized much more in the early morning and around midday than during the other day-periods.

12.2.4. Robin mortality

From August 1976 to July 1979, the mortality of adults was highest in autumn (Fig. 12.1). For the combined years data (total), of the 116 adults present at the start of winter 70 were males. From Figure 12.1 it seems that more males than females died in winter ($t = 0.96$, $P > 0.2$), because of the disparity in the number of males to females. However, a greater percentage of bachelors (unpaired adult males) died in winter than did paired adult males ($t = 1.82$, $P < 0.1$) (Table 12.3).

Table 12.3. The percentage of adult females, paired adult males and bachelors (unpaired adult males) that died (disappeared) during the 1977, 1978 and 1979 winters.

Category	Number alive at the start of winter	Percentage that died during winter
Adult females	46	10.9
Adult males	60	13.3
Bachelors	10	40.0

For the other seasons, a similar percentage of adult males and adult females died (Fig. 12.1).

For the combined 1978 and 1979 years data, a greater percentage of immatures died per month than did adults in summer ($t = 1.93$, $P < 0.1$), autumn ($t = 0.04$, $P > 0.9$) and winter ($t = 0.02$, $P > 0.9$). The immature's highest mortality occurred in summer.

12.3. Discussion

12.3.1. Comparisons of the monthly time-budgets for Robins of the same age, but of differing sex

Were the trends in the time spent in each behaviour from month to month as the non-breeding season progressed similar for male and female Robins? Yes, in general, paired Robins in the four categories showed similar trends in the time they spent in each behaviour from month to month during the course of the non-breeding season. However, for particular months, males and females sometimes devoted significantly different proportions of time to a behaviour.

(a) Foraging

Adult females foraged less than did adult males in January ($P < 0.01$), because females did not start to moult until late January, about a fortnight later than did males. Moulting birds have a standard metabolic rate about 30% higher (Payne 1972) and an increased protein requirement (Newton 1968) compared with non-moulting birds. Therefore, the greater time spent foraging by males compared with that for females in January was a consequence of the male's increased energy needs associated with their moult.

During February and March, adult females foraged more than did adult males ($P < 0.01$), because the former were at an earlier stage of the moult. Thompson and Boag (1976) and Dolnik and Gavrilov (1979) have shown for moulting Japanese Quail and Chaffinches respectively that metabolised energy usage (energy intake as food minus the energy lost in excreta) increased abruptly during the initial days of the moult and then gradually decreased. If the same trend in energy requirements occurred during the moult for Robins, then the higher proportion of time spent foraging by females in February and March can probably be ascribed to this factor.

The greater time adult and immature females foraged during April and May compared with that for adult and immature males respectively ($P < 0.01$) seemed to be related mainly to females spending less time vocalizing ($P < 0.01$) than did males. When their partners were singing, what did females do? The time spent singing by males was presumably used by females to forage. During the winter months, immature males continued to sing more ($P < 0.01$) and forage less ($P < 0.01$) than did immature females. I am not sure why this disparity in foraging time arose. However, because in June adult males increased their foraging to the level of their mates (adult females) and sang less than did immature males, presumably males restricted the time they spent foraging in order to sing.

In July, adult females foraged more than they had in June ($P < 0.01$) and than did adult males in July ($P < 0.01$), perhaps to build up fat reserves required to start the first breeding cycle. The energy cost of building a nest, development of the oviduct and egg formation would almost certainly be greater than the costs of sperm production and territorial defence for males (King 1973).

(b) Food-storing

I am unable to explain why immature females spent less time storing food than did immature males in January ($P < 0.01$) and why adult females spent less time storing food than did adult males in May. In general, the various categories of Robins spent similar proportions of time storing food in a particular month, even though they often foraged for significantly different proportions of time then.

(c) Body-maintenance

Adult females spent more time in body-maintenance than did adult males in January ($P < 0.01$). Most females were not moulting then and so they had more "spare" time from foraging to spend sunning and in associated-preening activities than did adult males that were moulting. Similarly, in June adult females preened more than did adult males ($P < 0.01$), presumably because males spent this time singing. During June, these two categories of Robins spent a similar time in each of the other behaviours, except for body-maintenance and vocalizing. In July, the trend reversed with adult females preening less than did adult males ($P < 0.05$). Because the time Robins spent in body-maintenance was usually inversely related to that spent in foraging, the above result probably arose as a consequence of females foraging more in July than in June ($P < 0.01$).

Unexpectedly, male immatures and female immatures spent a similar time in body-maintenance each month, even though they foraged for significantly different time during most months. It seems that females foraged more than did males because the former vocalized less than did males. Perhaps immature males did not spend less time in body-maintenance than did immature females because both categories were spending the minimum time possible in plumage care. Generally, immature birds spent less time during autumn and winter caring for their plumage than did adults ($P < 0.05$).

(d) Resting

During February, April and May, adult females rested less than did adult males, probably because the former category foraged more. However, in January when females foraged less than did males, females did not rest more than did males. Presumably, during this month adult females preferred to spend most of their "spare" time sunning and preening rather than resting. Also, it seems that females had little control over the time they spent foraging and in partner-interactions, territorial disputes and to some extent interspecific interactions, and so the behaviours they could most readily control were body-maintenance and resting. Since some time would have to be spent maintaining their plumage, presumably females were compelled to rest less when they had to spend more time foraging and in interactions.

Immature males rested more in January than did immature females ($P < 0.01$), probably because females foraged for longer ($P < 0.01$). For the subsequent months of the non-breeding season, the two categories rested for similar proportions of time even though females foraged more than did males during some months. As previously suggested, perhaps rather than reduce their involvement in resting, males foraged less to spend more time singing. This may indicate that Robins require at least some time to rest by day.

(e) Partner-interactions

Each April all adult females were paired and therefore were involved in partner-interactions. However, not all adult males were paired, but because I could not distinguish these bachelors until May, the behaviour of adult males timed in April included that of some unpaired males. This seems to be the reason why adult females were more involved in this behaviour in April than were adult males ($P < 0.01$).

The significantly greater time during March that immature females interacted with their mates compared with that for immature males ($P < 0.01$), was probably a consequence of some immature females being paired with adult males, whereas almost all immature males were paired with immature females. In March, adult males spent more time displaying to and chasing their mates than did immature males ($P < 0.01$). However, other than the above two cases, males and females of the same age class spent as much time as each other interacting with their partners.

(f) Territorial defence

Did paired females spend less time defending territories than did males? For a species where males seemed to require a territory before they could establish a pair-bond with a female, and where males invariably dominated females so that a lone female was unable to defend a territory against neighbouring males, one would expect a male to spend more time defending the pair's territory than his partner. Except for the April result, this was true for adult birds, especially if the time paired males sang was included as territorial behaviour - it seemed to have such a function. The reverse of the expected trend in April may be explained by the fact that during this month some adult males wandered outside their territories. An adult female noticing such an intruder often remained motionless for several minutes while the latter was in sight rather than confront him. By comparison, an adult male invariably ousted a trespasser on seeing him, which took only a few seconds to carry out unless the intruder was a neighbour and the chase ended in a boundary dispute.

Immature males spent as much time or significantly more per month in territorial defence than did immature females, except in June. This difference in June arose because immature males spent so little time in territorial disputes then even though they held territories. There were no obvious reasons for this reduced time spent in territorial defence by immature males.

(g) Interspecific interactions

Most of the time Robins were engaged in interspecific interactions involved them chasing other avian species. As one might expect from the male Robin's greater aggressiveness and territorial nature, they spent as much or significantly more time per month in interspecific interactions than did females.

12.3.2. Comparisons of the diurnal patterns of behaviours for male and female Robins

Did females have different diurnal patterns of involvement in a behaviour from that for males? Except for foraging and vocalizing, the diurnal patterns of each behaviour for male and female Robins of the same age class were similar. A possible reason why males had their peak time of foraging in the late afternoon, rather than in the morning as females did, seems to be mainly related to the male's diurnal pattern of singing. Females seemed to forage while their partners sang. As discussed in Sections 6.5.1 (p. 76) and 10.4.2 (p. 178), males sang mainly in the early morning probably because foraging was least efficiently carried out then (Kacelnik 1979) and it was the best time of the day for sound propagation (Wiley and Richards 1978). Presumably, the daily energy requirement of a male in the non-breeding season was the same as or slightly more than for a female taking into account the male's greater involvement in territorial defence. Thus, having foraged less than did females in the morning, males probably foraged more than did females in the afternoon to make up for their lower food intake in the morning.

12.3.3. Robin mortality

Since adult and immature Robins spent a greater proportion of time foraging in winter than during summer and autumn, I expected more of them to die in winter. However, from the combined years data, the mortality of adults and immatures was highest in autumn and summer respectively.

During each season, immatures suffered slightly higher mortality than did adults. At Kowhai Bush, the survival of juveniles after fledging and before independence was usually high, sometimes reaching 85% (Flack 1979). Therefore, most of their mortality during summer occurred once they became independent of their parents and had to find all their own food. Their dispersal out of the study area did not seem to be responsible for the disappearance of many immatures. Searches outside the study area each year revealed that a similar number of banded immatures left the area as unbanded ones came in. Possibly, the high mortality of immatures in summer was caused by them starving. Several studies have shown that immature birds were less efficient foragers than were adults (Groves 1978, Dunn 1972, Buckley and Buckley 1974, Recher and

Recher 1969). Since in summer immature Robins foraged significantly more than did adults (Figs 10.3, p. 152 and 11.2, p. 190), it seems highly probable that immatures were less efficient foragers than were adults. Perhaps this factor was also responsible for the higher mortality of immatures compared with that for adults in autumn, but by winter both age classes spent a similar time feeding.

The data for 1977, 1978 and the three years combined show that adult mortality was highest in autumn and least while they were breeding, as was found by Flack (1973, 1976b) for previous years. Many of those that died in winter were bachelors (Table 12.3, Flack 1975a). Therefore, by comparison the mortality of adults in autumn would have been much greater than that for winter if the number of bachelors that died each winter was deleted from the results. The deaths of bachelors seems to be related to the significantly less time they spent foraging compared with that of paired adult males (Section 10.4.1, p. 166).

Why did paired adult Robins have a greater rate of mortality in autumn than they did in winter when they spent a greater proportion of time foraging in the latter season? I considered it possible that, because of the high energy requirements of the moult, Robins which raised progeny in January and February, and therefore postponed their moult, may not have been able to find sufficient food in autumn to sustain their moult as ambient temperatures, daylengths, and apparently, invertebrate availability declined. Table 12.4 shows the proportion of birds which died that had finished breeding before and after 31 December. Summer and autumn were the seasons for which the mortality was determined.

Table 12.4. The proportion of adult Robins that died (disappeared) during the combined summers and autumns of 1978 and 1979 in relation to the date of completion of breeding.

	Robins that finished breeding	
	before 31 December	After 31 December
Number alive on 31 December:	50	29
The proportion that died in summer and autumn:	44%	38%
	$P > 0.05$	

There is no significant difference between the proportion of Robins that died from the two groups, therefore a late start to the moult had no obvious influence on their longevity.

Flack (1976b, 1979) considered that the regularly increased mortality of adults in autumn was related to competition between adults and immatures for territories. The population at Kowhai Bush has reached 88 breeding birds (Flack 1979), but over the three years of this study it was never that high and declined to its lowest levels since censuses were taken in 1971 (Fig. 12.1). From January 1977 much of the forest that formerly had been occupied by Robins was unoccupied and so there was ample habitat for immature birds. Because the male was responsible for establishing and defending the pair's territory, from Flack's suggestion that Robin deaths in autumn were related to immatures competing for space with adults finishing their moult, males would be expected to suffer more mortality than did females. However, it is apparent that slightly more adult females died in autumn than did adult males ($t = 1.00$, $P > 0.2$) (Fig. 12.1).

Several other observations suggested that territorial disputes were not an important cause of the increased mortality of adult Robins in autumn during this study. At no time was an adult, male or female, ousted from its territory or dominated by a non-territorial immature bird, just the opposite took place. Any immature bird that trespassed into an adult male's territory after the latter had completed his moult was chased without hesitation to the boundary. Moulting adult males chased intruders, even if rather ineffectively, but not *vice versa*. Generally, there were no immatures that did not have a territory by April. Any non-territorial birds were quite mobile, being seen at places often a kilometre or more apart within a few days. They did not seem to be involved in territorial disputes with any one adult bird for more than a day or two.

The time-budget results (Figs 10.2, p. 150 and 10.3, p. 152) show that immature males had less time to spend in territorial disputes than did adult males, because in autumn (April and May) immatures foraged more than did adults ($P < 0.01$). Also, when adult males died during summer and autumn immatures did not shift into the vacant territories, so that competition for "prime" habitat did not seem to be a cause for competition. Therefore, because space was not limiting, immature males were dominated by resident adult males, and slightly more adult females died in autumn than did males, the increased adult mortality in autumn seems not to have been related to competition for territories. More work needs to be carried out into possible reasons for the deaths of immature and adult Robins outside the breeding season before any particular cause can be ascribed.

12.4. Summary

In January, adult females foraged less than did adult males ($P < 0.01$), probably because few, if any, of the former had by then started to moult. Since most males were moulting in January and moulting birds require more food than non-moulting individuals (Thompson and Boag 1976), males had to forage more than did non-moulting females. From March to May, adult females foraged more than did adult males ($P < 0.01$), probably because the energy requirements of moulting birds are highest initially and then gradually decrease (Dolnik and Gavrilov 1979, Thompson and Boag 1976), and females were at an earlier stage of the moult than were males. In June, both sexes spent a similar time foraging, but in July adult females foraged more than did adult males ($P < 0.01$).

Both sexes of adults spent less time in body-maintenance in winter than they did in summer. In January, because females sun-bathed much more than did moulting males, the former, which had not begun to moult, devoted more time to body-maintenance than did males ($P < 0.01$). In July, adult females preened less than did adult males ($P < 0.01$), probably because foraging had priority over preening and females foraged much more than did males then ($P < 0.01$).

Males vocalized more each month than did females ($P < 0.01$).

In February and March, immature males and immature females foraged for a similar time, but during the other months, immature females foraged more than did immature males. Since males vocalized more each month than did females ($P < 0.01$), and females foraged while their partners sang, it seems that the males reduced their foraging in order to sing.

Except for foraging and vocalizing, generally the diurnal patterns of each behaviour for male and female Robins of the same age class were similar. For males, the peak time of foraging occurred in the afternoon, whereas for females the peak was in the morning. Presumably, this was because males vocalized more in the morning than afterwards, and, in order to make up for their low food intake in the morning, they had to forage more in the afternoon. Females did not sing and so foraged for most of the morning.

The immature's highest mortality occurred in summer. Each season, immatures suffered higher mortality, although not significantly, than did adults. Immatures foraged more than did adults in summer and autumn, suggesting that the former were less efficient foragers than were adults. Thus, perhaps more immatures died of starvation than did adults.

The highest mortality of adults took place in autumn, even though they spent a greater proportion of time foraging and presumably meeting maintenance requirements in winter. The reasons for this regularly increased adult mortality in autumn were not apparent from the time-budget data.

PART 4

TIME-BUDGETS FOR BACHELORS AND BREEDING ROBINS ENGAGED AT EACH STAGE OF THE BREEDING CYCLE

CHAPTER THIRTEEN

THE TIME-BUDGETS FOR BACHELOR ROBINS IN THE BREEDING SEASON

13.1. Introduction

The time-budgets for bachelors (unpaired adult males) in the breeding season are described in two sections: (1) monthly and total time-budgets, and (2) the diurnal patterns of behaviours during three portions of the breeding season. Total time-budgets were determined from the combined monthly data recorded over the entire breeding season.

It was concluded that the high mortality of bachelors in winter was related to the significantly lower time they spent in foraging then compared with that by paired adult males (Section 10.4.1, p. 166). Thus, it is hoped that the results from the breeding season will allow the priority of singing in relation to foraging for bachelors to be determined.

13.2. Results

13.2.1. The monthly and total time-budgets

Bachelors foraged for about 55% of the day each month (Fig. 13.1 and Appendix 15). The proportion of time decreased from July to August ($P < 0.01$), increased in September ($P < 0.05$), and then decreased each following month, significantly so in December ($P < 0.05$). The trend from month to month in time spent on body-maintenance was the reverse of that for foraging. Of note is the small proportion of time bachelors spent on body-maintenance in September compared with in August and October ($P < 0.05$), and the nearly five-times increase in December over the November value ($P < 0.01$) (Fig. 13.1).

From August to October, bachelors sang for about 30% of their time, with a gradual decline from month to month. A significant increase in singing arose in November ($P < 0.05$), followed by a decline in December ($P < 0.01$). Bachelors foraged less and sang much more than did males involved in any of the breeding-cycle stages ($P < 0.01$) (Table 13.1).

The time bachelors spent in territorial defence varied significantly from month to month from 0.0 to 1.3% of their time. They spent a similar proportion of time each month in storing food (0.3%), resting (6.0%) and interspecific interactions (0.5%).

Figure 13.1. The monthly and total time-budgets for bachelor Robins during the breeding season. The plotted values, given in Appendix 15, are from the combined data recorded in the 1976 and 1977 breeding seasons.

[a]The asterisks indicate significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the percentage of observation time bachelors spent in a behaviour between adjacent months. The asterisks along the ordinate axis show which behaviours changed significantly in the percentage of time bachelors devoted to them from July (Fig. 10.6, p. 155) to August.

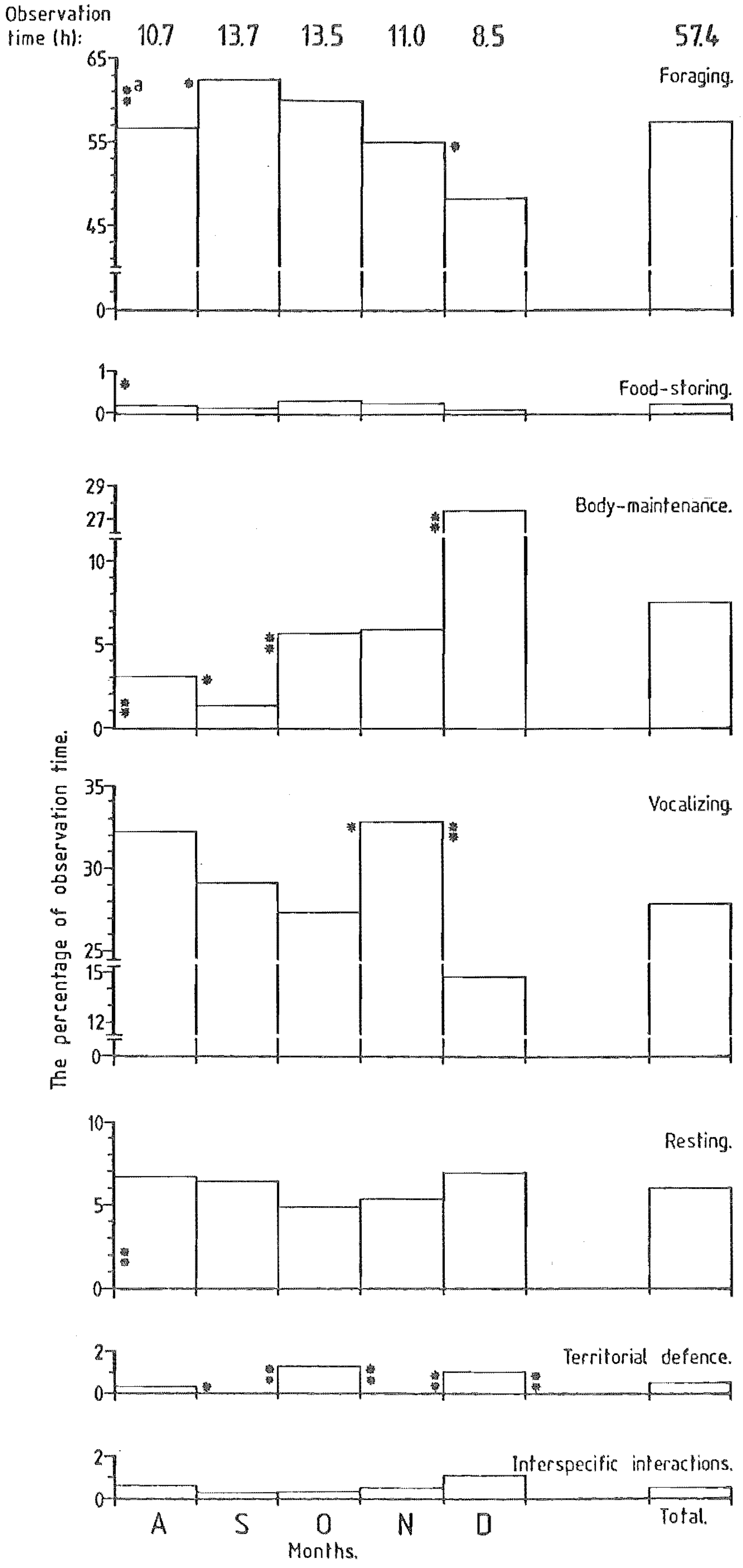

Observation time (h):
10.7
13.7
13.5
11.0
8.5
57.4
Foraging.
65
55
45
0
a
Food-storing.
1
0
Body-maintenance.
29
27
10
5
0
Vocalizing.
35
30
25
15
12
0
Resting.
10
5
0
Territorial defence.
2
0
Interspecific interactions.
2
0
A
S
O
N
D
Months.
Total.
The percentage of observation time.

Table 13.1. A comparison of the percentage of total observation time spent by bachelors and breeding males in foraging and vocalizing.

Status	Percentage of time spent in: Foraging	Vocalizing
Bachelors	57.4	27.9
Paired males involved in the:		
Nest-site selection stage	60.8	7.1
Nest-building stage	75.2	6.3
Prelaying stage	67.6	15.7
Laying stage	74.0	4.5
Incubation stage	78.4	2.2
Rearing of nestlings	83.3	1.4
Rearing of juveniles	79.4	4.3

13.2.2. The diurnal patterns

During each portion of the breeding season, bachelors foraged least in the early morning (Fig. 13.2 and Appendix 16). During the early and middle portions, the time spent foraging increased as the day progressed, significantly so until noon. Such a trend is not apparent from the data for the late segment, foraging declined significantly in the late morning and mid-afternoon. The birds spent a similar time storing food from one day-period to the next during each portion of the breeding season.

Throughout the breeding season, bachelors devoted least time to body-maintenance in the early morning and most about midday and late afternoon. The diurnal pattern of bachelor vocalizing tended to be the reverse of foraging. Most singing was carried out in the early morning, with less during the rest of the morning ($P < 0.01$), decreasing gradually during the course of the afternoon. Bachelors tended to rest most in the early or mid-afternoon.

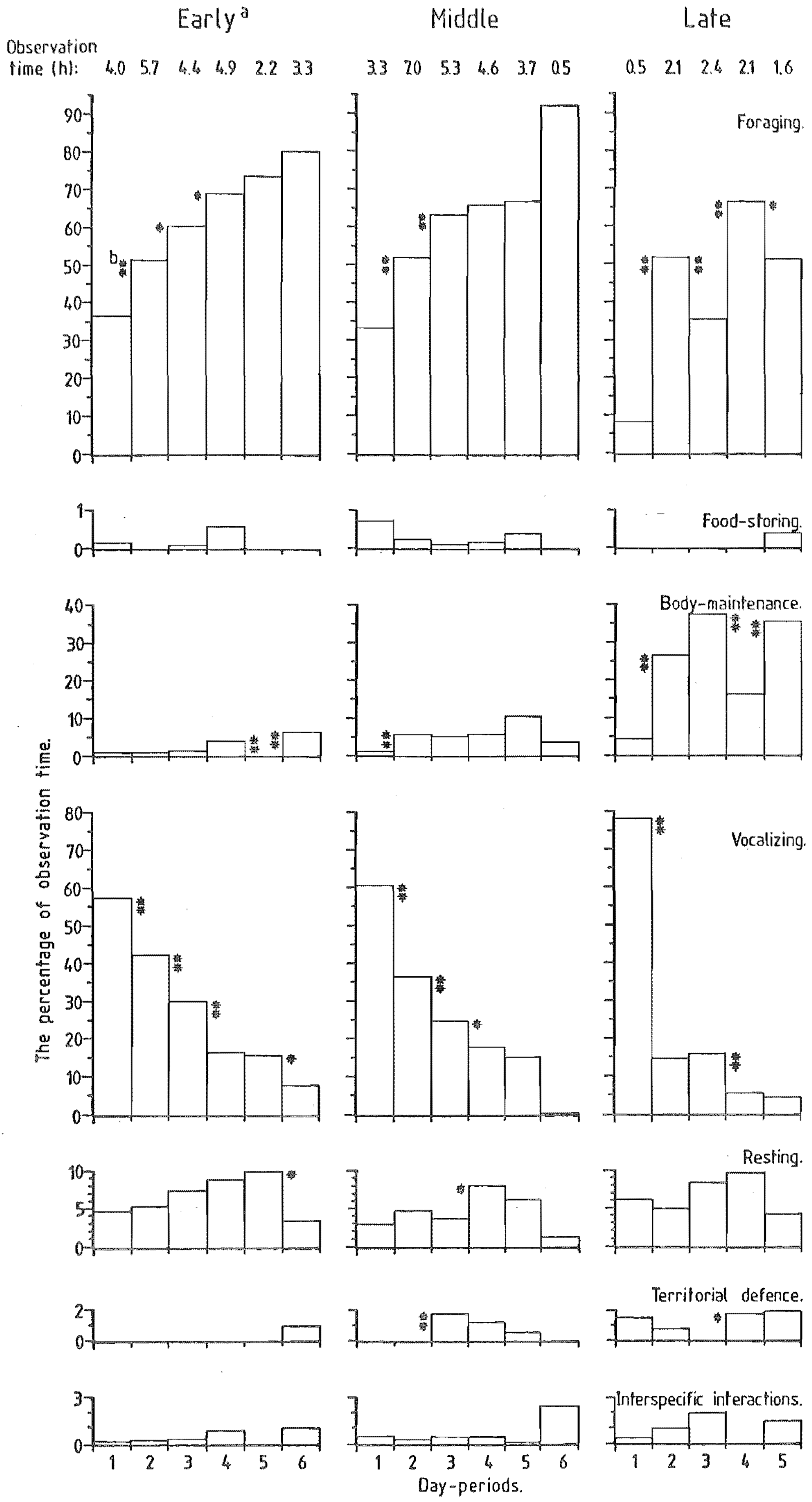
The diurnal pattern of territorial defence changed as the breeding season progressed. Early on, bachelors engaged in defence only in the late afternoon, but in the middle portion most territorial disputes occurred about midday. Late in the breeding season, disputes tended to occur throughout the day. For each part of the season, bachelors spent a similar time in interspecific interactions each day-period.

Figure 13.2. The diurnal patterns of behaviours for bachelor Robins during three portions of the breeding season.

The plotted values are given in Appendix 16.

[a] Early - August and September, Middle - October and November, Late - December.

[b] The asterisks indicate significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the percentage of observation time bachelors spent in a behaviour between adjacent day-periods.


Early a
Middle
Late
Observation time (h): 4.0 5.7 4.4 4.9 2.2 3.3
3.3 7.0 5.3 4.6 3.7 0.5
0.5 2.1 2.4 2.1 1.6
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Territorial defence.
Interspecific interactions.
b
90
80
70
60
50
40
30
20
10
0
1
0
40
30
20
10
0
80
70
60
50
40
30
20
10
0
10
5
0
2
0
3
0
The percentage of observation time.
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5
Day-periods.

13.3. Discussion

13.3.1. The monthly and total time-budgets

(a) Foraging

During the first four months of the breeding season, bachelors spent most of their time foraging and singing. Although several observers have noted that bachelors of various passerine species sang more than did paired males, only Pinkowski (1979) has shown this difference quantitatively. He found that unmated male Eastern Bluebirds in the breeding season fed for about half the time and sang three times as much as mated males. Similarly, bachelor Robins fed less and sang much more than did breeding males (Table 13.1).

The reduced foraging by bachelors from July to August ($P < 0.01$) was perhaps a consequence of the increased ambient temperature and daylength (Tables 2.1, p. 13 and 3.1, p. 20 respectively). In September 1977, when the monthly mean temperature declined compared with that for August (Table 2.1), bachelors foraged more during the former month (Appendix 15). In support of the suggestion that the overall increase in foraging for September (Fig. 13.1) was partly caused by the decline in temperature, in 1976 when the temperature rose from August to September, bachelors foraged less in the latter month (Appendix 15). A similar relationship between ambient temperature and foraging time was found by Verbeek (1964) for Brewer's Blackbird, and would be expected considering the approximately linear relationship between decreasing temperature and increasing standard metabolic rates for birds (King and Farner 1961).

The gradual reduction in foraging from September to November was probably related to increasing ambient temperatures, daylengths and, apparently, prey abundance. Combined with some or all of the above factors, the significant reduction in foraging from November to December may have also been related to the decline in singing then. Bachelors usually sang from song-perches in the tops of the tallest trees (Fig. 6.5, p. 64) and gave about 50 bouts of song each day (Section 6.4.1, p. 62). In December, the proportion of time spent singing was half that for November. This may have represented a significant saving in energy required for flights to song-perches so that less foraging would have been required in December.

Robins sun-bathed in December, but it seems unlikely that while doing so that they absorbed radiant energy as a supplementary energy source to reduce the time they spent foraging. Such energy can only be used by homoiotherms "when they are expending extra energy to maintain body temperature" (i.e. in conditions below their thermoneutral zone) (Morton 1967): Robins panted in the intense sunlight.

(b) Food-storing

Although the percentage of time bachelors spent storing food did not change significantly from month to month, it is of note that when they spent significantly less time foraging they also tended to spend less time storing food. From July to August, there was a significant decrease in food-storing behaviour, but the decrease from November to December was not ($P > 0.05$). These results agree with those for the non-breeding season (Section 10.4.1, p. 166), which show that Robins stored more food when they spent a greater proportion of time foraging.

(c) Body-maintenance

In keeping with the findings that body-maintenance was a low priority behaviour outside the breeding season (Chapters 9, 10 and 11), the proportion of time bachelors spent in body-maintenance during the breeding season was inversely correlated with that spent foraging. The time they spent in body-maintenance increased in August and December ($P < 0.01$) when they foraged less ($P < 0.05$), and *vice versa* in September.

(d) Vocalizing

Almost all the bachelor's vocalization time involved them singing full song (Fig. 6.2A, p. 60). The reduction in singing in September probably resulted because of the increased foraging they did then (Fig. 13.1). In agreement with this suggestion, in 1977 when bachelors foraged more in September than in August, they sang less in September, and *vice versa* in 1976 (Appendix 15). Therefore, from this negative correlation between foraging and singing, I concluded that singing was a lower priority behaviour for bachelors than was foraging.

I cannot explain why bachelors sang less in October than they did in September each year (Appendix 15), since they foraged less in October than in September and the monthly mean temperature was greater in October. The reduced singing in December was probably caused by a reduced secretion of sex hormones by the regressing testes and interstitial cells. Sex hormones have been shown to promote singing in some passerine species and for their secretion to decline once the birds began moulting (Lofts and Murton 1973). Bachelor Robins began to moult in December (Fig. 10.1, p. 145).

(e) Resting

Outside the breeding season, resting was a low priority behaviour for Robins. The time male Robins rested depended on time they spent foraging (Section 10.4.1, p. 166). Therefore, the increased resting in August ($P < 0.01$) probably occurred because bachelors foraged less then ($P < 0.01$). As the breeding season progressed bachelors spent a decreasing proportion of time foraging, but rested for a similar proportion of time each month. This was because the birds sang more rather than spent more time at rest.

(f) Territorial defence

The low proportion of time that bachelors devoted to territorial defence during August and September, compared with later months, arose because breeding Robins rarely strayed from their territories. Similarly, male Eastern Bluebirds (Pinkowski 1979), Dickcissels *Spiza americana* (Schartz and Zimmerman 1971) and Yellow-billed Magpies (Verbeek 1972) spent less time defending their territories once they began breeding. Juvenile and immature Robins straying into bachelors' territories caused the increased time bachelors spent in territorial disputes during October and December. I do not know why bachelors spent little time in territorial defence in November of both years (Appendix 15), because juveniles and immatures were also present then.

(g) Interspecific interactions

From month to month, bachelors were engaged in interspecific interactions for a fairly constant proportion of time. This was a consequence of the species that bachelors interacted with being present in Kowhai Bush throughout the breeding season, and possibly the interactions occurred with a similar frequency and duration each month.

13.3.2. The diurnal patterns

(a) Foraging

The diurnal patterns of foraging for bachelors in the early and middle portions of the breeding season were similar to that for winter (Fig. 10.9, p. 164), an increasing time was spent foraging as the day progressed. As discussed in Section 10.4.2 (p. 178), there were two likely reasons why bachelors foraged least in the early morning. It was probably less profitable for them to forage then, because cool temperatures would have restricted invertebrate activity decreasing their conspicuousness to Robins, and low light intensities may have reduced the ability of Robins to see prey (Kacelnik 1979). Therefore, when bachelors were able to meet their food requirements in less than the daylight hours, selection should favour those that carry out non-foraging activities in the early morning (Verner 1965).

The large proportion of time bachelors continued to spend foraging in the late afternoon, when the light intensity and temperature dropped, was caused by them having to "stock-up" with food to sustain them during the night. Small birds have high metabolic rates (Lasiewski and Dawson 1967), and therefore to store sufficient food in their bodies to meet their maintenance requirements at night, it seems necessary for them to concentrate on foraging just before going to roost. Very little foraging was carried out in the early morning towards the end of the breeding season, probably because the nights were short, temperatures at night and in the morning mild, and an abundance of prey was available in December. Robins readily caught slow flying March flies then, which were present in large numbers. With bachelors making fewer flights to high song-perches, except in the early morning, in contrast to earlier in the breeding season, the food needs of bachelors probably declined hence a little foraging was adequate for maintenance requirements around midday and mid-afternoon.

(b) Food-storing

That no distinct diurnal pattern of food-storing for bachelors occurred during any portions of the breeding season is of interest considering that they foraged for significantly different proportions of time in the course of the day. The results from the monthly time-budgets suggested that time spent storing food and foraging were directly related. However, on a diurnal basis this was not so; bachelors spent just as much time storing food from one day-period to the next. Similarly, the data for food-storing from the entire study show that Robins stored food mainly in the morning and early afternoon, with slightly less stored in the mid- to late afternoon (Fig. 5.1, p. 51). Probably, Robins that began the day with some bodily reserves - and bachelors have been included here since they foraged little and spent so much time singing in the early morning - readily meet their maintenance needs then and therefore found some surplus food to store. In the afternoon, bachelors stored food for a similar proportion of time as in the morning, presumably because their increased foraging during the former resulted in sufficient food being found to meet their energy needs of the afternoon, and enough to form bodily reserves for the forthcoming night as well as a surplus to store.

(c) Body-maintenance

Bachelors spent little time in body-maintenance in the early morning, because it was a low priority behaviour (Sections 9.4, p. 139 and 10.4.1, p. 166) and almost all time was then spent foraging and singing. During the early and middle portions of the breeding season, the small increase in body-maintenance after the early morning can probably be attributed to the increased foraging then. Associated with increased foraging was the likelihood that more time would have to be spent removing water, litter and bits of prey from plumage.

Sunning and its associated-preening bouts made up most of the body-maintenance time in the late portion of the breeding season. The diurnal rhythm of body-maintenance then partly reflects the presence or absence of suitable sunning conditions during the course of the day. In the early morning the sunlight's intensity seemed too low to stimulate sunning.

At this time a Robin occasionally assumed a preliminary posture for sunning and then switched to another behaviour. The decreased time spent in body-maintenance in the early afternoon ($P < 0.01$), when conditions for sunning were optimal, was correlated with a significant rise in foraging. Since the latter behaviour had priority over body-maintenance, I concluded that bachelors must have had to forage more in the early afternoon than they did previously, and so reduced their time spent sunning to compensate. Perhaps the birds foraged more then because it was a profitable time to do so. High ambient temperatures and light intensities in the early afternoon would have activated invertebrates and therefore made them most available to Robins.

(d) Vocalizing

In the breeding season, the diurnal pattern of vocalizing for bachelors was the same as in winter (Fig. 10.9, p. 164), i.e. singing decreased as the day progressed. As discussed earlier (Section 6.5.1, p. 76), this pattern of vocalizing reflects the lower profitability of foraging and the more favourable conditions for sound propagation early in the day. Thus, bachelors sang when it was least favourable for foraging. In so doing, their singing would have had least influence on the amount of food they found during the day than if they sang at any other time of the day.

I found no other studies describing the diurnal pattern of singing for bachelors of other insectivorous passerines. The diurnal patterns of vocalizing for paired male Robins differed from those for bachelors (Figs 14.2, p. 250, 14.5, p. 258, 15.4, p. 293, 16.5, p. 324 and 17.6, p. 361), except during the prelaying stage and when they were rearing juveniles (Figs 15.2, p. 284 and 18.2, p. 391 respectively). Paired males sang less early in the day than did bachelors, probably because the former did not need to attract a mate and instead spent the time in attracting their partners to nest sites, or in foraging to supply food to their partners or progeny.

(e) Resting

During each portion of the breeding season, bachelors generally rested most about midday and least in the early morning and late afternoon. This diurnal rhythm of resting is similar to that for Robins outside the breeding season (Sections 10.3.2, p. 158 and 11.3.2, p. 194). The data for male Robins involved in nest-site selection (Fig. 14.2), nest-building (Fig. 14.5), prelaying (Fig. 15.2) and incubation stages (Fig. 16.5), and while rearing juveniles (Fig. 18.2) show a similar diurnal pattern of resting. Bachelors rested mainly about midday, possibly because after carrying out all other behaviours of greater priority, there was more time to spend resting then than at other times of the day.

(f) Territorial defence

Two possible reasons why bachelors were involved in territorial disputes mainly in the afternoon were that the large amount of singing they did in the morning warned off likely intruders or because bachelors sang from perches in and above the canopy they did not see intruders. In the afternoon, when bachelors spent much time foraging, being below the canopy they were more likely to notice an intruder. In the early portion, breeding Robins were rarely seen off their territories and so most intraspecific interactions were boundary disputes between neighbours in the late afternoon. However, by the middle portion the first broods had fledged and these juveniles and immatures, which occasionally strayed into neighbouring territories, were vigorously evicted by bachelors. Late in the breeding season many immatures were roaming in Kowhai Bush. Perhaps because bachelors then sang less in the morning than they had previously, interactions between members of these two categories now occurred throughout the day.

(g) Interspecific interactions

While not significant, bachelors spent more time in interspecific interactions in the afternoon than they did in the morning. They foraged more in the afternoon and so were present in the lower understorey where such interactions most frequently took place. In the morning when bachelors sang most persistently, interactions between them and other species usually took the form of a bachelor fleeing from his song-perch at the approach of an avian predator. Thus, in the afternoon, interspecific interactions tended to be longer than those of the morning.

13.4. Summary

During the course of the breeding season, bachelors spent about 85% of their time foraging and singing. They foraged less ($P < 0.05$) and sang more ($P < 0.01$) than did breeding males. From the negative correlations between the changes in percentage of time bachelors spent foraging and singing from month to month, it seems that the time free for singing was after they had met their maintenance requirements. Therefore, like body-maintenance and resting, vocalizing was a low priority behaviour compared with foraging for bachelors. Their diurnal patterns of involvement in these behaviours tend to support this hypothesis. Since foraging was probably least profitable in the early morning (Kacelnik 1979, Verner 1965), singing then would have had least influence on the amount of food bachelors obtained during the day. Also, it was probably best for them to sing in the early morning because weather conditions are generally better for sound propagation then than later (Wiley and Richards 1978).

CHAPTER FOURTEEN

THE TIME-BUDGETS FOR ROBINS INVOLVED IN THE NEST-SITE SELECTION AND NEST-BUILDING STAGES OF THE BREEDING CYCLE

14.1. Introduction

Although several observers noted that nest-building was done solely by the female and that she was fed at intervals by her mate, none described the Robin's behaviour while selecting a nest-site (Falla *et al.* 1966, Flack 1973, Fleming 1950, Oliver 1955, Richdale 1941).

A description of the displays, calls and activities of male and female Robins associated with selecting a nest-site and nest-building is given here. Then follow monthly and total time-budgets for both sexes during the two stages. Comparisons are made between the total time-budgets for males involved in the two stages, as they are between those for females. Lastly, the diurnal patterns of the behaviours for both sexes engaged in the nest-site selection and nest-building stages are described.

From the analyses I anticipated answering the following questions:

1. Did males and females spend differing proportions of time in the reproductive behaviours (nest-site selection, nest-building, partner-interactions, feeding progeny)?

2. During the two stages, did the Robins devote more time to reproductive behaviours in the morning, as they did during the non-breeding season (Chapters 9, 10, 11)?

3. Was there evidence that the male's food-trips to his nest-building partner represented an important portion of the female's food supply?

4. Were females more protective of the nest against intruding Robins and other species of birds than were males?

14.2. Methods

Two factors combined to make it difficult to record the behaviour of Robins that were selecting nest-sites or building nests. First, neither stage lasted long. The selection of a nest-site usually took only a few hours so that with most pairs site selection was completed before I realised that another breeding cycle had begun. In addition, building usually started within 36 hours of the loss of eggs or nestlings. Nests were either old *Turdus* or Robin nests relined to a varying extent (an "old" nest) or were wholly made by Robins just before egg laying (a "new" nest) (Flack 1973). During the middle of the breeding season a new nest was usually completed within three days and the relining of an old nest sometimes took only a few hours. Second, females building nests were unusually secretive, or when I was present would either not collect material or would perch with it, but not return to the nest.

The singing of the male to attract his mate to be fed and his movements towards the nest were the main clues used to find a nest-building female. However, if the previous nesting had been successful, the male gave most prey to the juveniles and did not make frequent food-trips to the female while she was building the next nest. Therefore, after a pair had reared a brood finding their subsequent nest was often difficult.

For these reasons, only a few hours of observations were made of Robins selecting nest-sites or building nests. To avoid disturbing nest-building females and to augment the observations made while following the birds, I sat near their nests. Notes were taken of the frequency and duration of the female's trips to the nest with material and the frequency with which she was fed by her partner.

Where pairs seen selecting a nest-site or building a nest were also caring for progeny a behaviour "feeding progeny" (Fp) was defined. This included the time a parent with food in its beak spent calling juveniles, flying to them and giving them the food. Furthermore, it included time taken to retrieve and return food dropped by a juvenile.

As for previous chapters, the results and discussion sections are divided into two sub-sections: (1) the monthly and total time-budgets, and (2) the diurnal patterns of behaviours. Some of these sub-sections are further divided so that the data for each behaviour are described and discussed separately and in the sequence as shown on the figures.

14.3. Descriptions of nest-site selection and nest-building behaviours

14.3.1. Nest-site selection behaviour

Before a male induced his mate to visit a likely nest-site he attracted her to him by singing phrases of song and offering her food. Having fed her, he then flew towards a nest-site trying to attract her to it by singing. His flight was often slow and the wing-beats exaggerated, as in the "butterfly-flight" display (Section 8.3.1, p. 115). Once in a nest-site he began a continuous soft "siii, siii,....." call while shuffling about in a crouched posture. If the female did not move towards him he usually flew to a new site, singing as he went to attract her attention. When she moved to a nest-site which the male was squatting or standing in, he increased the frequency and volume of his call and vibrated a wing. If there was room for only one bird, the male left the site as the female entered. While she remained there the male perched nearby, flew to a new site or began another behaviour. Thus, the male's activities timed as nest-site selection behaviour (Nss) included the time spent attracting the female with his flight and song to a nest-site and the time he spent in a site.

Females were not seen attracting mates to sites. The activities of females timed as nest-site selection behaviour included the time they took to fly to the site and the time they remained there. While present, the females made nest-shaping movements and pulled at objects about them. Such movements seemed to involve the birds scratching with their feet and pushing out with their wings while in a crouched posture. Following such movements they stood up, rotated to face a new direction and then repeated the nest-shaping movements. Occasionally, a female returned to a site with material which she placed into it and then made nest-shaping movements. The time spent flying from a site or nest, gathering material, bringing it back to the site and pressing it into place was recorded as "nest-building" behaviour (Nb). Once several trips with material in quick succession had been made to a nest-site, the pair was considered to have started nest-building.

The nest-site selection behaviour of Robins proved similar to that described for several other species of passerines (Andrew 1957, 1961, Howard 1929, Nice 1943). In particular, the call, wing-vibrations of males and nest-shaping movements of females for *Emberiza* spp. when selecting a nest-site (Andrew 1957) seems to be very similar to that for Robins.

14.3.2. Nest-building behaviour

Three stages could be discerned in the building of a nest. First, the female brought coarse material (rootlets, twigs and strips of bark) and bound them together with cobwebs. After placing material into the site, she crouched in it and pressed it all into place with nest-shaping movements. She then stood up, turned clockwise or anticlockwise about 90 degrees and repeated the shaping movements. Any material that projected from the outer rim of the nest was pulled into the cup and pressed down into place. Occasionally, birds stood below the nest to remove material that was not bound into it.

Once the coarse layer had been completed, it was lined with finer material. During this second phase of building no cobwebs were used. As previously, shaping movements were made after each trip to the nest with material. Finally, a thin layer of very fine materials, not including cobwebs, (moss, fern scales, fine dried grasses and bark, leaf skeletons, and sometimes a few down feathers) were added. The cups of completed nests were often full of such material because it had been put into them, but not pressed into place.

When an old nest that was reasonably complete was used, little if any coarse material was placed in it. Thus, the use of an old nest represented a considerable saving in time and energy for a Robin, because less material had to be brought to the site and it often took only a few hours to complete, instead of several days. The added strength of these nests resulted in an increased survival of the nestlings (pers. obs., Flack 1973).

14.4. Results

14.4.1. The monthly and total time-budgets

14.4.1.1. Nest-site selection

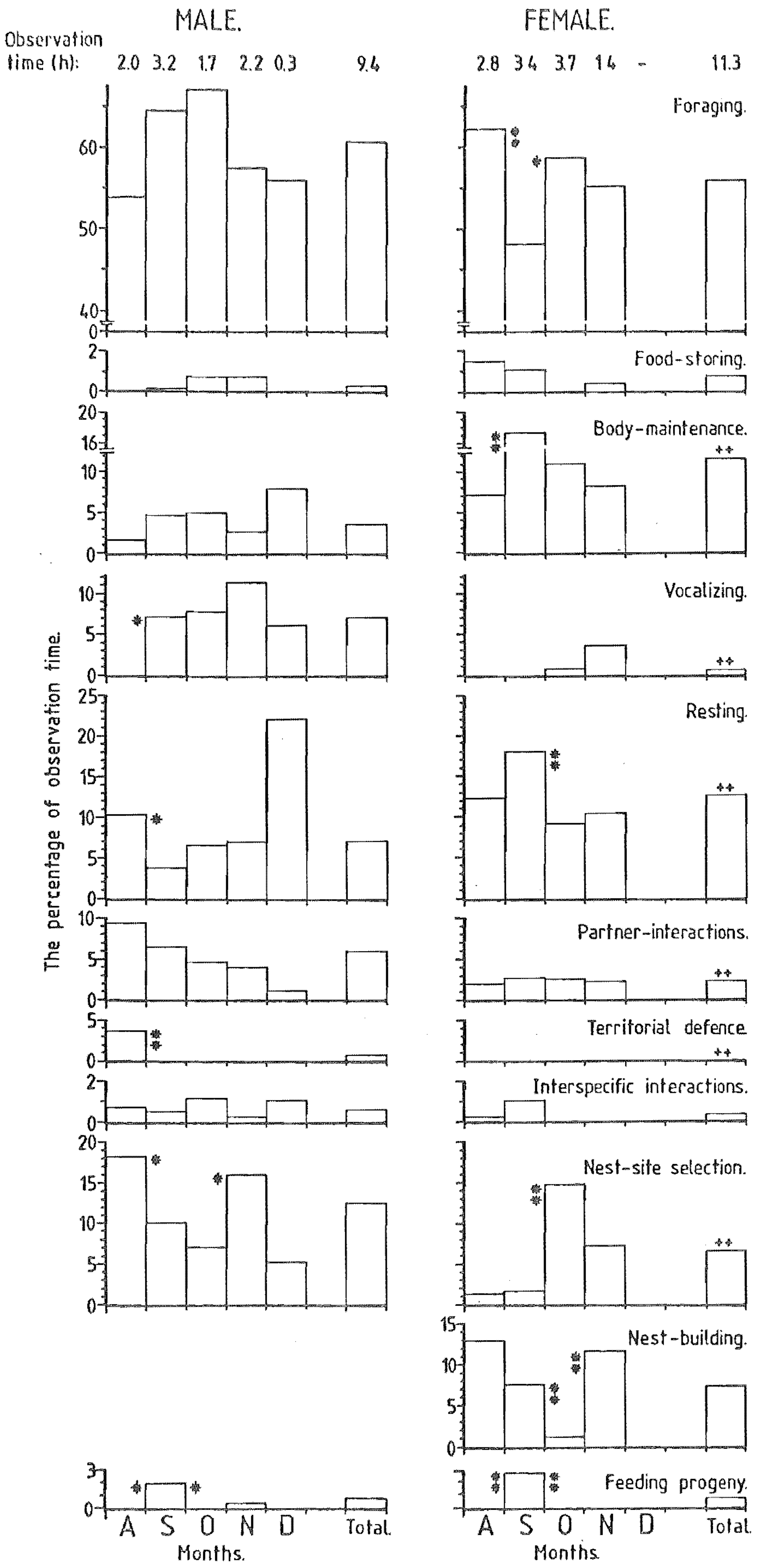
In total, males foraged for 61.8% and females 56.0% of time while selecting a nest-site, this difference is not significant ($P > 0.05$) (Fig. 14.1 and Appendix 17). Females spent more time in body-maintenance and resting than did their mates ($P < 0.01$). However, females spent less time vocalizing, interacting with their mates, and selecting nest-sites than did males ($P < 0.01$). Also, during this stage females took no part in territorial defence and they alone gathered nest-material and placed it into a nest-site (7.5% of their time). Both sexes spent a similar time storing food, interacting with other species and feeding progeny.

From the total time-budgets, males spent 26.5% of time in reproductive behaviours (vocalizing, partner-interactions, nest-site selection, nest-building and feeding progeny) compared with 18.2% for females.

Figure 14.1. The monthly and total time-budgets for male and female Robins selecting a nest-site.

See Appendix 17 for the plotted values.

[a]The asterisks and crosses indicate significance levels: * or + = $P < 0.05$, ** or ++ = $P < 0.01$. The asterisks at the sides of the columns indicate significant differences between the adjacent monthly samples. The crosses above the columns for the total time-budget of females show those behaviours in which males and females selecting a nest-site spent significantly different percentages of their time.


MALE.
FEMALE.
Observation time (h):
2.0 3.2 1.7 2.2 0.3 9.4
2.8 3.4 3.7 1.4 - 11.3
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
Nest-site selection.
Nest-building.
Feeding progeny.
The percentage of observation time.
A S O N D Total.
Months.
60
50
40
0
2
20
16
10
5
25
15
3
*
**
++

Males selecting a nest-site spent less time in body-maintenance and vocalizing then did bachelors ($P < 0.01$). This time was spent by the paired males visiting nest-sites and trying to attract their partners to them. Males selecting a nest-site and bachelors spent a similar time involved in each of the other behaviours.

14.4.1.2. Nest-building

A variety of nest-sites was used by Robins in Kowhai Bush with the common types being in trunk and branch forks, mistletoe *Loranthus micranthus*, the crowns of kanuka, and in old *Turdus* and Robin nests. The mean height for nests found during the 1977 and 1978 breeding seasons was 3.7 m ($n = 164$; canopy height 5-12 m) and of these nests 34% included parts of old nests. The mean time taken to build 27 new nests was 3.4 days, with some taking up to seven days in July and August. However, because some females spent up to two days trying to build in sites where the material fell out, the time to build a nest was sometimes longer than a week.

(a) Foraging

Overall, males spent 75.2% of time foraging while their partners were building a nest (Fig. 14.2 and Appendix 18). Although males foraged for a smaller proportion of time each month as the breeding season progressed (Fig. 14.2), owing to the increasing daylength, slightly more hours per day were spent foraging during the course of the season (Appendix 18). Nest-building females foraged for 37.5% of time, significantly less than their partners did ($P < 0.01$). Except for the significantly greater time spent foraging in November than in October and December, females tended to spend proportionately less time foraging per month as the season progressed.

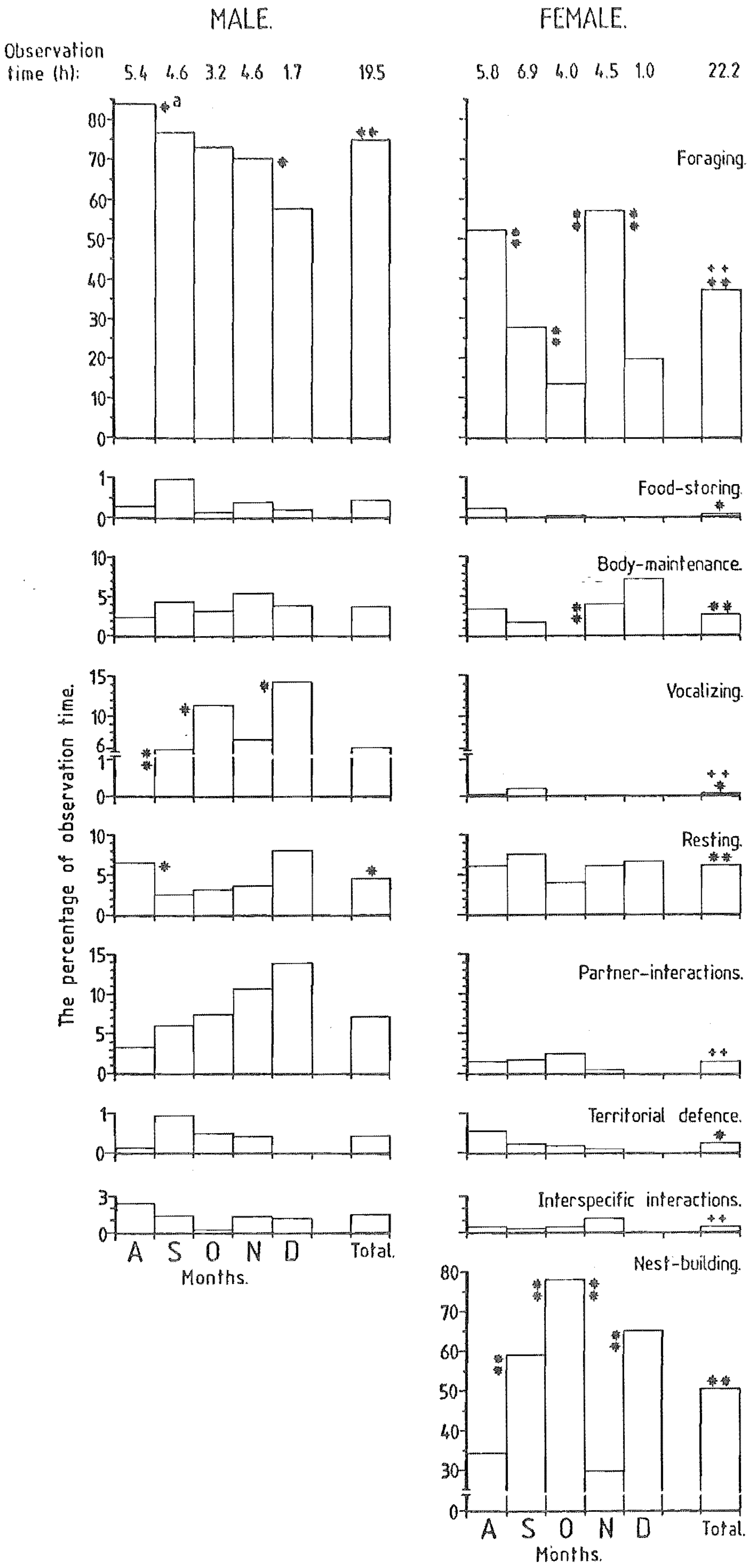
(b) Food-storing

Males spent a similar proportion of time each month storing food, as did females. From the combined months' data, males and females spent 0.45% and 0.08% of time respectively storing food, which is not significantly different.

Figure 14.2. The monthly and total time-budgets for male and female Robins involved in the nest-building stage.

Appendix 18 gives the plotted values.

[a]The asterisks and crosses indicate significance levels: * or + = $P < 0.05$, ** or ++ = $P < 0.01$. The asterisks at the sides of columns indicate significant differences between the adjacent monthly samples. Those above the "total" columns for males show those behaviours in which males selecting a nest-site (Fig. 14.1) and those involved in the nest-building stage spent significantly different proportions of time, and similarly for the asterisks above the "total" columns for females. The crosses above the "total" columns for females indicate those behaviours in which males and females involved in the nest-building stage spent significantly different proportions of time.


MALE.
FEMALE.
Observation time (h):
5.4 4.6 3.2 4.6 1.7 19.5
5.8 6.9 4.0 4.5 1.0 22.2
*a
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
Nest-building.
The percentage of observation time.
0
10
20
30
40
50
60
70
80
1
5
6
15
3
A S O N D
Total.
Months.

(c) Body-maintenance

For each month, males in the nest-building stage devoted a similar percentage of time to body-maintenance. Females spent longer in this behaviour during November and December than they did during October ($P < 0.01$), when very little time was spent in body-maintenance. Male and female Robins spent a similar time in body-maintenance during the nest-building stage in total.

(d) Vocalizing

Males were not heard singing each August of the three breeding seasons studied, but were during the other months. They tended to vocalize progressively more each month during the course of the breeding season, and in total vocalized for 6.3% of time. Nest-building females spent nearly 0.1% of time vocalizing, less than did their mates ($P < 0.01$).

(e) Resting

Males tended to rest for a similar proportion of time each month, as did females. Overall, the two sexes rested for a similar time during the nest-building stage.

(f) Partner-interactions

Males spent an increasing percentage of time interacting with their nest-building partners from month to month (Fig. 14.2). Similarly, the mean rate of food-trips per month by males to their partners tended to increase slightly from August to December (Fig. 14.3A). By comparison, females building nests spent a similar time each month interacting with their mates. From the combined monthly data, a male made an average of 3.2 food-trips per hour to his mate and spent 7.4% of time in partner-interactions. This degree of involvement in partner-interactions was significantly more than the 1.6% of time spent in this behaviour by females ($P < 0.01$).

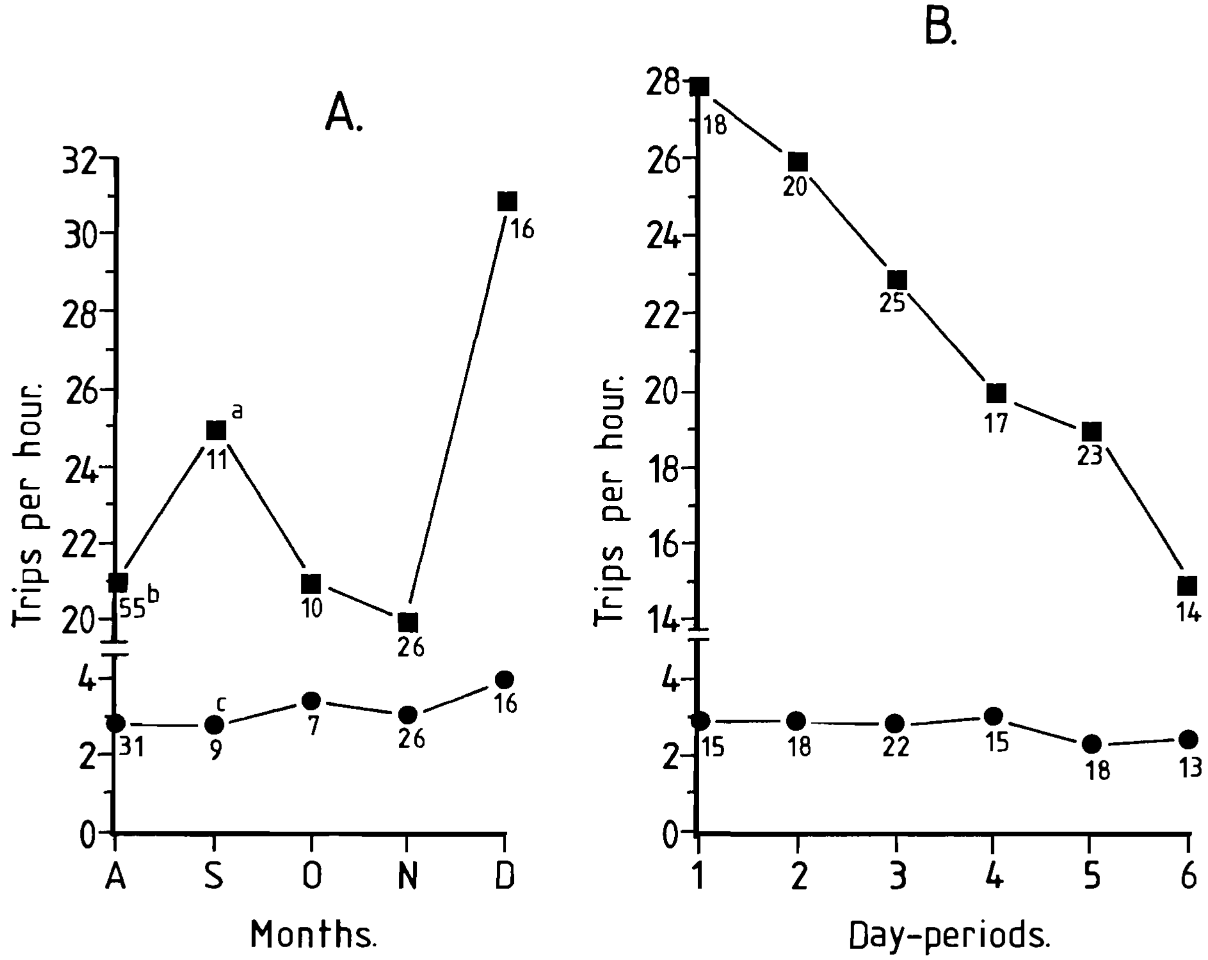


Figure 14.3 The monthly (A) and diurnal patterns (B) of the rate of trips with material to nests by females (number per hour), and food-trips by males to their partners (number per hour) while the latter were nest-building.

[a] ■–■, trips with material to nests by females.

[b] The number of hours of observation.

[c] ●—●, trips with food to partners by males.

(g) Territorial defence

The proportion of time males and females were engaged in territorial disputes during the nest-building stage showed no significant change from one month to the nest. Overall, males spent slightly more time engaged in this behaviour (0.5%) than did females (0.3%) ($P > 0.05$).

(h) Interspecific interactions

Males spent a similar proportion of time in interspecific interactions during the course of the breeding season, as did females. However, in total, males spent 1.6% of time in such interactions, significantly more than the 0.6% for females ($P < 0.01$).

(i) Nest-building

The proportion of time females devoted to building a nest varied significantly from month to month (Fig. 14.2). Similarly, their mean rate of trips with material to the nest varied each month (Fig. 14.3A). From the combined monthly data, I found that they spent 50.7% of time nest-building at a mean rate of 22.4 trips per hour.

Overall, females spent 52.3% of time in reproductive behaviours (vocalizing, partner-interactions and nest-building) compared with only 13.7% for males.

From the total time-budgets, males during the nest-building stage foraged more ($P < 0.01$) and rested less ($P < 0.05$) than did males selecting a nest-site (Fig. 14.2). However, males whose partners were building nests were not involved in nest-site selection, a behaviour that accounted for 12.5% of a male's time during the nest-site selection stage.

When nest-building, a female spent significantly less time foraging, storing food, preening, vocalizing and resting, and significantly more time in territorial defence and nest-building than when selecting a nest-site (Fig. 14.2). The only behaviour to which females devoted a similar time whether selecting a nest-site or building was partner-interaction.

14.4.2. The diurnal patterns of behaviours

14.4.2.1. The diurnal patterns of behaviours for Robins selecting a nest-site

Because Robin behaviour during the nest-site selection stage was recorded for few hours per day-period, and not at all in some day-periods, the diurnal pattern for each behaviour shown in Figure 14.4 and Appendix 19 can only be a guide to the bird's actual diurnal pattern of behaviour.

During early morning, males were occasionally seen displaying from sites, but females invariably took little interest in their mates' calls to attract them to sites then. Although many hours were spent in the forest during the late afternoon, Robins were not seen visiting nest-sites then.

Males attracting their partners to nest-sites spent more time foraging, selecting a nest-site and interacting with their partners in the morning than in the afternoon. Note that instead of singing mainly in the early morning, as bachelors did (Fig. 13.2), mated males sang more in the late morning than previously.

For the four day-periods for which information is presented, females spent less time as the day progressed visiting nest-sites and building in them, but spent more time in body-maintenance and resting. Males spent a similar time in interspecific interactions from one day-period to the next, as did females.

14.4.2.2. The diurnal patterns of behaviours for Robins during the nest-building stage

(a) Foraging

While their partners were building nests, males had a bimodal diurnal pattern of foraging with their peak times of foraging in the early morning and mid-afternoon (Fig. 14.5 and Appendix 20). However, there was no significant difference in the time they foraged between one day-period and the next. In contrast, their nest-building partners foraged least of all in the morning and significantly increased the time they devoted to this behaviour through the day.

Figure 14.4. The diurnal patterns of behaviours for males and females selecting a nest-site.

See Appendix 19 for the plotted values.

[a] The asterisks indicate significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the percentage of time Robins devoted to a behaviour during two adjacent day-periods.

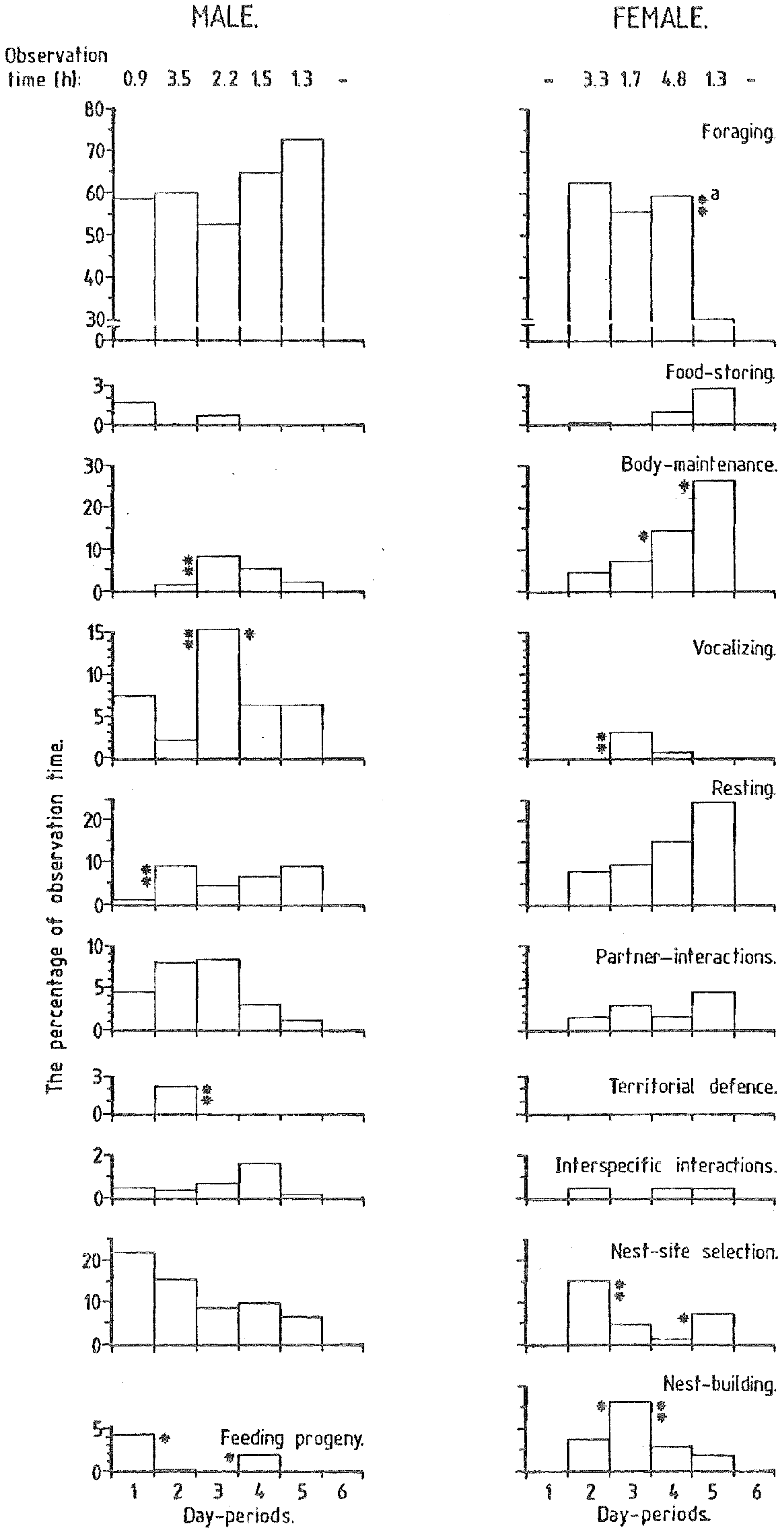
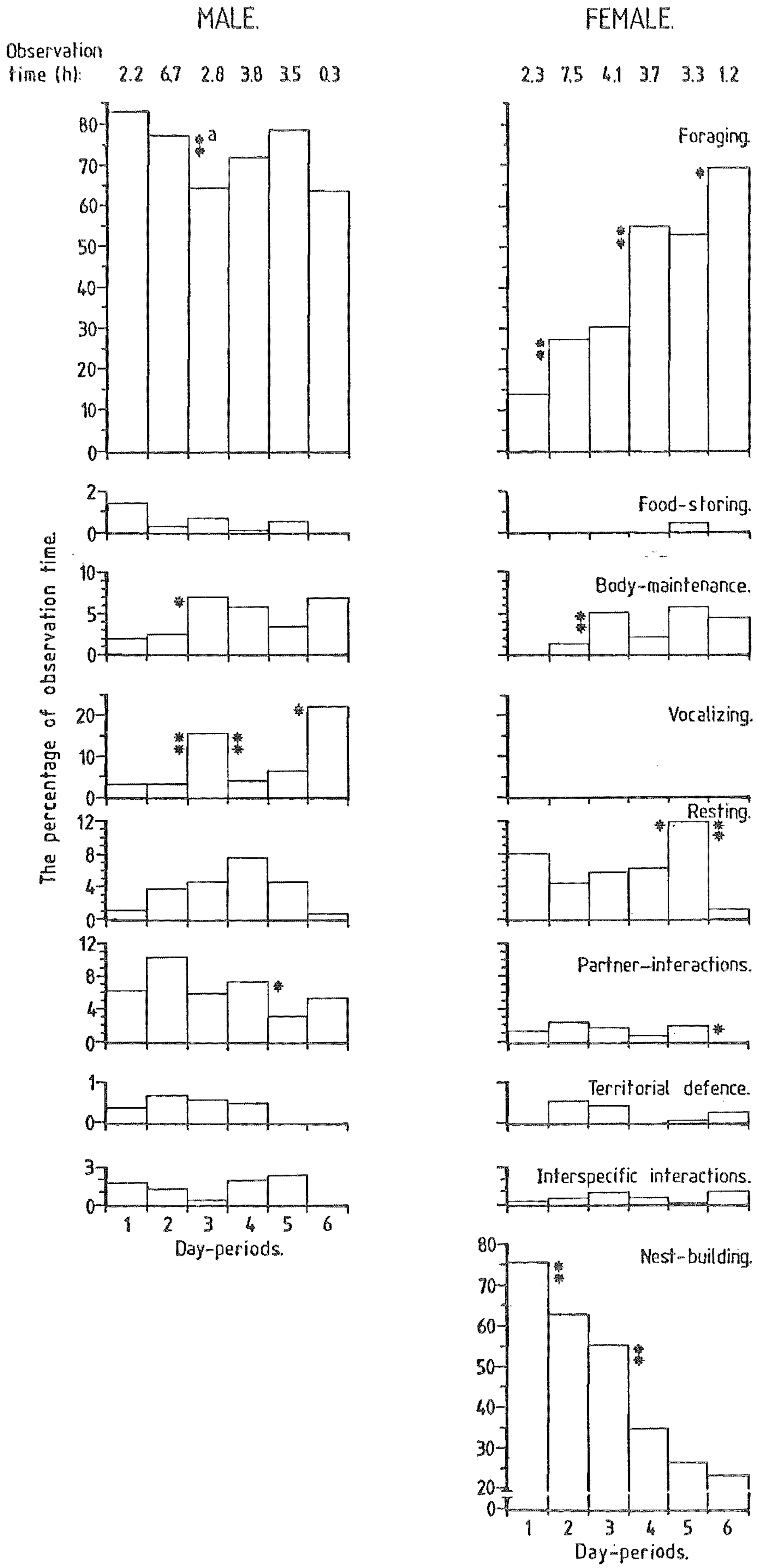

MALE.
FEMALE.
Observation time (h): 0.9 3.5 2.2 1.5 1.3 -
- 3.3 1.7 4.8 1.3 -
80
70
60
50
40
30
0
Foraging.
a
Food-storing.
3
0
Body-maintenance.
30
20
10
0
Vocalizing.
15
10
5
0
Resting.
20
10
0
Partner-interactions.
10
5
0
Territorial defence.
3
0
Interspecific interactions.
2
0
Nest-site selection.
20
10
0
Nest-building.
Feeding progeny.
5
0
1 2 3 4 5 6
Day-periods.
The percentage of observation time.

Figure 14.5. The diurnal patterns of behaviours for males and females involved in the nest-building stage.

Appendix 20 gives the plotted values.

[a] The asterisks indicate significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the percentage of time Robins spent in a behaviour during two adjacent day-periods.


MALE.
FEMALE.
Observation time (h): 2.2 6.7 2.8 3.8 3.5 0.3
2.3 7.5 4.1 3.7 3.3 1.2
Foraging.
80
70
60
50
40
30
20
10
0
a
Food-storing.
2
0
Body-maintenance.
10
5
0
Vocalizing.
20
10
0
Resting.
12
8
4
0
Partner-interactions.
12
8
4
0
Territorial defence.
1
0
Interspecific interactions.
3
0
Nest-building.
80
70
60
50
40
30
20
0
The percentage of observation time.
1 2 3 4 5 6
Day-periods.
1 2 3 4 5 6
Day-periods.

(b) Food-storing

Males spent a similar time storing food during each day-period, except the last, when no food was stored. By comparison, females stored food only in the mid-afternoon.

(c) Body-maintenance

Both sexes spent significantly more time in body-maintenance after the mid-morning than they did earlier, spending a similar time per day-period in this behaviour during the afternoon.

(d) Vocalizing

Females vocalized for 0.13% of time or less per day-period (Appendix 20), which was a similar proportion of time from one day-period to the next. In contrast, males had two peaks of singing activity. These arose in the late morning and late afternoon. They sang significantly less outside these day-periods.

(e) Resting

When involved in the nest-building stage, males and females rested mainly after the early morning and up until the late afternoon.

(f) Partner-interactions

Males interacted with their mates for a similar time each day-period up to and including the early afternoon, after which they spent less time in this behaviour (Fig. 14.5). Figure 14.3B shows that the rate of food-trips made by males to their nest-building partners had a similar diurnal pattern, nearly three trips per hour were made till the early afternoon, after which the rate declined to about 2.5 trips per hour. Females interacted with their mates for a fairly constant proportion of time throughout the day, except in the late afternoon when it declined significantly.

(g) Territorial defence

Both sexes spent slightly more time in territorial defence in the morning than they did afterwards.

(h) Interspecific interactions

Males spent a similar time each day-period interacting with mammals and other species of birds, as did females.

(i) Nest-building

The time per day-period that females spent building nests decreased during the day (Fig. 14.5). Their rate of trips to nests with material had the same diurnal pattern (Fig. 14.3B).

14.5. Discussion

14.5.1. The monthly and total time-budgets

14.5.1.1. Nest-site selection

To my knowledge, no published study has provided a time-budget for a passerine's behaviour during the nest-site selection stage of the breeding cycle. Therefore, this discussion deals largely with time-budgets for Robin behaviour.

(a) Foraging

Male and female Robins foraged for a similar time (about 58%) when looking for a nest-site. This was expected, because even though males gave some food to their partners, such courtship feedings were infrequent compared with later in the season. Bachelors foraged and sang for 57.4% and 27.9% of time respectively during the breeding season (Fig. 13.1, p. 229). The latter behaviour seemed to be mainly to attract a mate, a reproductive behaviour. By comparison, females selecting a nest-site devoted only about 15.1% of time to reproductive behaviours. Although the behaviours of selecting a nest-site and nest-building were probably more energy demanding than singing, a female presumably had time to find enough food to meet her requirements without her partner having to supplement her intake. There was no obvious cause for the significant reduction in foraging by females in September.

(b) Food-storing

Although the difference was not significant, females spent more than double the time storing food that males did. This arose because females sometimes stored food they received from their mates, rather than in storing more of the food they found themselves.

(c) Body-maintenance

The significantly greater time females spent in body-maintenance compared with males during this breeding stage may have been caused by females having to clean and order their plumage more after spending more time in nest-sites than males did. In support of this suggestion, during July before breeding began, adult females preened less than did adult males ($P < 0.01$) (Table 12.1, p. 213), which shows that a female's plumage did not previously require more care than a male's. Because body-maintenance tended to be a low priority behaviour for Robins, it is possible that males preened less than did females in order to devote more time to singing, interacting with their partners, and to selecting a nest-site.

(d) Vocalizing

Even though females gave more "chucks" and sub-song than did their partners, the time spent giving these vocalizations was much less than that spent singing full song by males during this stage (Fig. 6.2, p. 60). Therefore, overall males vocalized much more than their partners did (Fig. 14.1). This singing of full song by males probably had several functions during the nest-site selection stage. As well as announcing his possession of the territory and his willingness to defend it against intruders, the male seemed to use it to attract his mate when they were apart and he was ready to attract her to nest-sites.

(e) Resting

Females rested more than did their partners at a time when I would have expected them to devote any "spare" time to selecting a nest-site. In September, when females foraged significantly less than they did during the previous and subsequent months the extra time was spent in body-maintenance and resting. This seems to indicate that either they had to rest more than males for some unknown reason, or that they were not always ready to begin another nesting cycle when their partners were.

(f) Partner-interactions

Males spent more time in partner-interactions than did their mates, because males often spent several minutes carrying food about and singing, trying to find their partners. Sometimes a female did not respond immediately to her mate's song. For example, a female collecting or taking material to a nest-site responded to her mate's calling only after having placed the material in the site.

(g) Territorial defence and interspecific interactions

As expected for a species where females were dominated by their mates and some male intruders, females spent less time in territorial defence ($P < 0.01$) and interspecific interactions ($P > 0.05$) than did males. It was not unusual for two neighbouring males to be involved in a boundary dispute while their partners foraged or preened nearby. Male Robins interacted with other spccies more than did females because when a pair of Robins was visiting nest-sites it was more often the male that chased other birds that approached them. Thus, male Robins seemed more protective of prospective nest-sites against other birds than did female Robins.

(h) Nest-site selection and nest-building

Males spent more time in nest-site selection behaviour than did females, because the latter occasionally preened or foraged while their mates were trying to attract them to sites. However, if the time females spent nest-building is added to that which they spent investigating nest-sites, then they spent as much time as males did selecting a nest-site.

This summing of the time for the two behaviours also reveals a more even involvement per month by females in nesting activities during the course of the season. It is possible that by placing material into a site and trying to arrange it into place, a female was better able to determine the site's suitability.

(i) Feeding progeny

Some pairs selecting nest-sites were also caring for juveniles. Generally, they had only one juvenile and its food requirements were readily met so that males had time to also attract their partners to nest-sites.

While selecting nest-sites, males spent more time than did females in reproductive behaviours, 19.4% and 14.9% respectively ($P < 0.05$). If I had estimated the time males foraged to support the food-trips to females, males would have spent even more time than females in reproductive behaviours.

14.5.1.2. Nesting-building

(a) Foraging and partner-interactions

During the nest-building stage, males, as well as requiring food to meet their own energy demands, made frequent food-trips to their nest-building partners. The 75.2% of time spent foraging by males was more than they spent in this behaviour when looking for a nest-site ($P < 0.01$). However, they spent a similar time interacting with their partners during both stages, suggesting that the rate of food-trips by males to their partners was about the same for the two stages. This was not true because during the nest-site selection stage, males often spent several minutes trying to find their mates. In contrast, during the nest-building stage, males carrying food flew to the nest area where the female was usually present and she invariably responded quickly to his phrases of song by flying to him and begging vigorously.

The gradual reduction in the proportion of time spent foraging and the increased proportion of time spent in interactions with their mates by males as the breeding progressed, was possibly the result of increasing temperatures, daylengths and greater prey availability. These factors would have decreased the energy requirements per unit time for a male so that a greater proportion of his time would have been available to provide food for the female. As Figure 14.3A shows, the rate of male food-trips rose slightly from month to month during the breeding season. By comparison, male Eastern Bluebirds during the nest-building stage spent 47% of time feeding and 33% "idle" (Pinkowski 1979). Because the bluebirds were idle for so much time, spent less than 4% in courtship feeding, and reduced the time they were engaged in the latter activity once the females began building, it seems that courtship feeding in this species was mainly concerned with maintenance of the pair-bond and was not a means of providing the nest-building females with additional food to support the high energy demands of their building. A time-budget was not given for nest-building female Eastern Bluebirds so that it was not possible to determine what influence the likely lower rate of food-trips by male bluebirds had on their mates' behaviour.

Did the food provided by a male to his nest-building partner represent an important portion of her food supply? Female Robins building nests foraged for 37.5% of time, much less than did their partners ($P < 0.01$). Although no direct evidence was obtained to support the hypothesis, it would seem by comparison with other Robin time-budgets that this proportion of time spent foraging was insufficient to meet the energy demands of a nest-building bird, and that the food provided by the male was necessary to sustain the high rate of nest-building activity of females. In July, immature and adult females foraged for over 90% of time (Figs 11.1, p. 188 and 11.2, p. 190), significantly more than the 52.6% for nest-building females in August (Fig. 14.2). In addition, building females foraged less than did bachelors, 37.5% and 57.4% respectively ($P < 0.01$). From chapter 10 it seemed that bachelors foraged to find only sufficient food to meet their immediate maintenance requirements in order to sing as much as possible. This comparison therefore supports the suggestion that nest-building females did not forage for long enough to meet the high energy requirements of their building activities. The mean rate of food-trips by males to their mates in August was nearly three each hour and involved a large prey item being given to the latter each trip. It seems unlikely that such frequent food-trips functioned to maintain the pair-bond, because pair formation usually occurred during autumn and males did not start feeding their mates until breeding began. Even during the nest-site selection stage, food-trips to the female were infrequent and usually took place just before the male tried to attract her to nest-sites so that such food-trips may have been a method whereby the male found his mate to attract her to nest-sites. If a nest-building female had to find all her food she would have had to forage more than when selecting a nest-site, because the approximately 20 trips per hour to and from the nest with material would have required more energy to sustain it than the irregular trips when selecting a nest-site.

In support of the assumption that the food provided by males was necessary to enable nest-building females to maintain a higher rate of building than would otherwise have been possible, was the behaviour of the females when accepting it. After the male had given a few short phrases of song associated with his food-trips, the female, as long as she was not collecting material, immediately flew towards him and accepted the food while giving vigorous begging calls and wing vibrations. The food was quickly swallowed and only stored when the male made several food-trips in quick succession.

Robins in Kowhai Bush began breeding in late July-August each year, before other passerines. Perhaps the regular food-trips made by males to their nest-building partners made this early breeding possible. Early nestings were more successful than later ones (Flack 1973). Probably, the behaviour of males in feeding their nest-building partners enables a pair to carry out this and other stages in the cycle more quickly and therefore more successfully, and so has a strong selective value.

(b) Food-storing

That females spent less time storing food than did their partners during the nest-building stage and significantly less than did females involved in the previous stage suggests that the food they found plus that provided by their partners was needed for females' maintenance. Since stored food must be surplus to the immediate requirements of a bird, it is likely that nest-building females stored little food because most of the food from their partners was required to meet the high energy demands of nest-building.

(c) Body-maintenance and resting

Because males selecting nest-sites, and both sexes during the nest-building stage spent about 4% of time in body-maintenance, this proportion of time was probably sufficient for them to maintain their external surfaces. This suggests that the 12% of time devoted to this behaviour by females selecting nest-sites was because they were not hungry, did not require the time for other behaviours, and hence were able to spend it on a low priority behaviour. That females selecting nest-sites also rested more than when nest-building supports the above suggestion. I expected nest-building females to preen far more than when they were selecting nest-sites, because the former seemed more prone to fouling and disarranging their plumage when gathering, carrying and incorporating material into their nests. Why this did not arise I cannot explain. Presumably, both sexes rested significantly less during the nest-building stage than previously was because in the former males foraged and fed their partners more, and females spent most time foraging and nest-building so that neither had much time to rest.

(d) Vocalizing

During the nest-building stage, most of the vocalization time of males was spent in full song (Fig. 6.2A, p. 60). This seemed to function in proclaiming possession of the territory to prevent intruders interfering with the nesting of the pair. In addition, it may have helped to synchronise the reproductive states of the members of a pair (Dorst 1974, Lofts and Murton 1973, Welty 1975).

As was found by Nice (1943) for nest-building female Song Sparrows, female Robins vocalized less while building their nests than previously ($P < 0.05$), now tending to be quiet and secretive. "Chucks" were the main type of vocalization made by these females (Fig. 6.2B, p. 60). Because they were given more often early in the breeding season (Fig. 14.2), when days were shorter and food availability probably lower, the "chucks" were perhaps given to encourage their partners to bring them food. Juveniles made similar calls when hungry.

(e) Territorial defence

During the nest-building stage, males and females spent a similar time defending their territories. Little time was involved (< 0.5%) because intruders were vigorously driven from the territory and the chases seldom lasted more than a minute. Females, but not males, were more often engaged in such disputes when nest-building than when selecting nest-sites ($P < 0.05$), as was true of Yellow-billed Magpies (Verbeek 1972). Verbeek found that this was because the magpies often strayed onto neighbouring territories when collecting nest material. Similarly, this was probably the reason for the increased time female Robins spent in territorial disputes: they occasionally built nests near their territorial boundaries and hence attracted the attention of neighbouring Robins by their frequent trips to and from their nests with material.

(f) Interspecific interactions

Were females more protective of their nests against intruding Robins and other species of birds than were males? During the nest-building stage, males and females spent a similar time in disputes with intruding and neighbouring Robins. However, males spent more time in interspecific interactions than did females ($P < 0.01$). A male Robin seemed to defend a larger area around the nest against other birds than did his mate.

(g) Nest-building

The proportion of time females spent nest-building from month to month showed a reverse trend to that for foraging. Furthermore, these birds spent about 87% of time nest-building and foraging, and spent significantly less time in low priority behaviours (body-maintenance and resting) than did females selecting nest-sites. Together these features imply that females spent as much time nest-building as their food intake would allow. Although I am unable to explain why females in November foraged significantly more than they did in October and December, as expected the increased foraging resulted in their spending less time in nest-building, but not in those behaviours necessary for self-maintenance. Similarly, Schartz and Zimmerman (1971) found that when breeding Dickcissels reduced their involvement in reproductive activities (singing, territorial defence, courtship and maintenance of the female) because high ambient temperatures caused them to rest more to avoid heat stress, they did not reduce time spent in activities associated with self-maintenace.

Did males and females spend differing proportions of time in reproductive behaviours? In contrast to the result for Robins selecting nest-sites, nest-building females spent much more time in reproductive behaviours than did their partners, because the former spent a large proportion of time nest-building (50.7%). However, if the time males spent foraging to find food for the frequent food-trips they made to their partners had been accounted for, perhaps the time the two sexes spent in reproductive behaviours during the nest-building stage would have been similar.

14.5.2. The diurnal patterns of behaviours

14.5.2.1. The diurnal patterns of behaviours for Robins selecting a nest-site

(a) Foraging and nest-site selection

Nest-site selection by both sexes and nest-building by females during the nest-site selection stage formed a larger proportion of the birds' time-budgets in the early morning and decreased as the day progressed. Similarly, male Eastern Bluebirds spent more time inspecting nest-sites early in the day than they did later (Pinkowski 1979). That Robins carry out behaviours involved with reproduction mainly in the morning was shown by the time-budgets for non-breeding Robins (Chapters 9, 10 and 11) and by the pattern of singing for bachelors in the breeding season (Fig. 13.2, p. 232). As explained in previous chapters, Robins spent more time in non-maintenance behaviours in the early morning possibly because they foraged less efficiently then than later in the day, and they had to stock-up with food in the afternoon to sustain themselves at night. Although I spent many hours in the forest during the late afternoon, Robins were not seen visiting nest-sites then, indicating that they devoted little, if any, time to this behaviour then.

(b) Body-maintenance and resting

In agreement with their suggested low priority compared with other behaviours, resting and body-maintenance for Robins were much reduced in the morning when most time was devoted to foraging, partner-interactions, selecting a nest-site, and nest-building. Females spent more time resting and in body-maintenance in the afternoon than in the morning, while males spent similar or less time involved in these behaviours in the afternoon than in the morning. Perhaps this arose because females received occasional courtship feedings from their partners and so were able to forage less and devote the time to resting and plumage-care activities.

(c) Vocalizing and territorial defence

During the nest-site selection stage, males spent significantly more time singing in the late morning than they did earlier, as they did in winter (Fig. 10.7, p. 160). This suggests that selecting a nest-site was of a higher priority in the early morning than singing was. Because disputes to determine the location of territorial boundaries between neighbouring Robins took place mainly in the autumn (Section 10.4, p. 166) and fewer adult Robins died during the breeding season than at other times of the year (Fig. 12.1, p. 217), territorial boundaries were most stable during the breeding season. Presumably, therefore less time had to be spent singing in the morning to ward off intruders and so more time could be devoted to selecting a nest-site and related behaviours.

Overall, it seems that male and female Robins selecting nest-sites devoted slightly more time to reproductive behaviours (vocalizing, partner-interactions, nest-site selection, nest-building and feeding progeny) in the morning than they did in the afternoon. This diurnal pattern for reproductive behaviours can be best understood by considering when it is best to forage, because the most important behaviour of any organism is the accumulation of sufficient energy to exist (Verner 1965). Selection should favour those individuals that forage when it is most efficient to do so, since an equivalent amount of food can be acquired in less time leaving more time for other behaviours. Since foraging is probably least efficient for an insectivorous species in the early morning (Kacelnik 1979, Verner 1965), it seems best for those birds with some energy reserves left after the night to spend the early morning engaged in reproductive behaviours, as Robins did.

14.5.2.2. The diurnal patterns of behaviours for Robins during the nest-building stage

(a) Foraging

The probable reason why males spent much more time foraging in the early morning during the nest-building stage than they did when selecting nest-sites was because males had to maintain regular food-trips to their partners during the former stage. This is supported by the way in which males made more frequent food-trips and spent more time interacting with their mates in the morning than in the afternoon. The food provided by males probably helped to sustain females' high rate of building in the morning, especially considering that females foraged so little then.

The rate of food-trips did not decline until mid-afternoon, even though males foraged less after mid-morning. This may indicate that the large proportion of time spent seeking food before mid-morning was required to enable males to find sufficient prey then when conditions were possibly poor for finding insects. In the early morning, prey may have been difficult to see as a consequence of the low light intensities, and low temperatures probably would have reduced invertebrate activity, making detection difficult. The results from two other time-budget studies of insectivorous passerines tend to support the hypothesis that male Robins foraged for so long in the early and mid-morning in order to maintain a high rate of food-trips to their mates. Male Long-billed Marsh Wrens, which did not feed their nest-building partners, spent less time foraging in the early morning than later in the day (Verner 1965). Similarly, male Eastern Bluebirds, that spent less than 4% of their time feeding their nest-building mates, foraged less in the early morning than afterwards (Pinkowski 1979).

(b) Food-storing

That males spent slightly more time storing food in the morning than in the afternoon and females did not store any prey until the mid-afternoon suggests that males stored food that their partners would have eaten had the males given it to them. Maybe particular prey species, such as earthworms which were often stored, were readily available in the early morning, or that when maintenance costs were easily met, the birds stored some prey as a reserve.

(c) Body-maintenance

Both sexes spent significantly less time in body-maintenance during the first two day-periods than they did later in the day, because either their plumage was not disarranged or fouled by their activities or they chose to spend the time involved in other behaviours. The first suggestion seems less likely to be true because foraging and nest-building took up most of the morning and would have dishevelled the plumage. In the morning, body-maintenance behaviour involved the birds preening and scratching to remove sources of irritation or objects from their plumage.

Extended bouts of preening (Section 7.3.6, p. 94) took place mainly in the afternoon. Why Robins spent little time in body-maintenance in the morning is unclear; perhaps a certain level of plumage disarrangement and/or fouling had to occur before the birds would stop other behaviours to tidy and clean it.

(d) Vocalizing

During the nest-building stage, males sang mainly during lulls in foraging, as they did when selecting nest-sites (Fig. 14.4). Presumably, foraging to maintain themselves and their nest-building partners was more important in the early morning than was singing. Also, because breeding adults were probably able to recognise their neighbours' songs (Hay 1975) and they seldom encroached into neighbouring territories, presumably singing to announce territorial possession was not required in the early morning and could be intensified later in the day when foraging was less important.

(e) Resting

Nest-building females rested more in the early morning than did their partners possibly because the formers' frequent trips to and from the nest, involving much flight, caused females to tire sooner than did their foraging mates. In the late afternoon, both sexes rested less than earlier and devoted more time to other behaviours. Females foraged more in the late afternoon ($P < 0.05$), and males continued to forage as much as earlier, but sang more ($P < 0.05$).

(f) Partner-interactions

During the nest-building stage, most time Robins spent in partner-interactions involved the male feeding his mate. Therefore, the diurnal patterns of partner-interactions for both sexes reflect quite closely the diurnal pattern of the male's rate of food-trips, which were fairly constant during the course of the day. Similarly, Schartz and Zimmerman (1971) found that the time male Dickcissels spent in "female maintenance" behaviour was relatively constant through the day.

(g) Territorial defence and interspecific interactions

The percentage of time male and female Robins were involved in territorial defence and interspecific interactions was similar from one day-period to the next, presumably because such interactions arose randomly during the day and lasted about the same time in each day-period.

(h) Nest-building

The diurnal pattern of nest-building for females showed a gradual decline as the day progressed in both the time they spent nest-building and the rate of their trips to the nest with material. Several other studies of passerines have shown a similar diurnal pattern of nest-building activity: for example, the House Wren (Kendeigh 1952), Willow Warbler *Phyloscopus trochilus* (Kuusisto, *in* Palmgren 1949), Song Sparrow (Nice 1943), South Island Fantail (Ude Shankar 1977), and the Yellow-billed Magpie (Verbeek 1972). However, the Snares Fernbird *Bowlderia punctata* showed two peaks of nest-building activity, one in the early morning and another in the mid- to late afternoon (Best 1973).

Several factors may explain such a diurnal pattern for female Robins. Verbeek (1972) considered that when temperatures were favourable and with the day ahead of them, birds could limit the time they spent foraging in the morning to that which met their current physiological requirements so that time was available for non-maintenance activities. In the afternoon, more time would have to be spent foraging not only to meet current maintenance requirements, but also to stock-up with food to sustain them during the night. This hypothesis may partly explain why Robins spent much more time nest-building in the morning. However, a factor that probably influenced female Robins' diurnal pattern of nest-building was the diurnal pattern of their partners' food-trips. Because the rate of food-trips declined only slightly in the afternoon and females foraged more later in the day, possibly females obtained less food in the early morning than they used to sustain their high rate of building then. Perhaps the morning's building activity was sustained by food eaten or stored the previous afternoon that was not used during the night so that they began the day with an energy surplus. The birds may have operated at a negative energy balance in the early morning and therefore had to decrease their building activity later in the day to restore this. Furthermore, it is possible that they decreased their rate of building as the day progressed simply because they became fatigued. Gibb (1955) considered that fatigue caused parent Great Tits to lower their rate of food-trips to young during the afternoon.

Did Robins devote more time to reproductive behaviours in the morning than in the afternoon? As for Robins selecting nest-sites (Section 14.5.2.1, p. 268), nest-building females spent far more time in the morning in behaviours associated with reproduction (nest-building and partner-interactions) than in the afternoon. For males such a result is not so obvious. However, if the time they spent foraging to supply their partners with food could be determined I suspect that they too would have devoted more time to reproductive behaviours in the morning than they did in the afternoon.

14.6. Summary

14.6.1. Nest-site selection

When selecting a nest-site, both sexes spent a similar time foraging. Females spent more time in the low priority behaviours (body-maintenance and resting) than did males ($P < 0.01$). From these results it seems that the food given to females was offered as a reward so that males could then entice their partners to sites, rather than it comprising an important portion of the female's intake.

A pair of Robins selecting a nest-site did so mainly in the morning, possibly because it was a more efficient use of time to carry out non-maintenance behaviours then when foraging was probably less productive than later (Kacelnik 1979).

Instead of singing mainly in the early morning, as did bachelors during the breeding season and paired males in the non-breeding season, males involved in the nest-site selection stage sang more in the late morning than previously.

14.6.2. Nest-building

During this stage, males foraged much more than did their partners ($P < 0.01$), probably to find enough prey for both themselves and their partners. Overall, males made an average of 3.2 food-trips per hour and spent over four times as much time in partner-interactions as did their mates ($P < 0.01$). This latter result occurred because when a male took food to his mate, the female was sometimes gathering material or was some distance from where the male found the prey so that the male spent time finding his partner. In comparison, females usually flew only a short distance to accept the food once their mates had brought it to them.

Although both sexes spent a similar time in territorial defence during this stage, males interacted with other species more than did females ($P < 0.01$). Male Robins were more aggressive towards other species of birds and seemed to defend a larger area around their nests than did female Robins.

Nest-building was done solely by the female. In total, females spent 50.7% of time on building, making an average of 22.4 trips per hour with material to the nest.

During the nest-building stage, males foraged more ($P < 0.01$) and rested less ($P < 0.05$) than when selecting a nest-site. For the other behaviours, males involved in the two stages spent a similar time in them. By comparison, building females spent significantly less time foraging, storing food, preening, vocalizing and resting, and significantly more time in territorial defence and nest-building than when looking for a nest-site. During the two stages, females spent a similar time in partner-interactions, although this does not indicate that they received food from their mates at a similar rate during the two stages.

Because nest-building females in August foraged much less than during the previous month when not breeding, and less than did bachelors in August, it seems likely that the food supplied by their partners was necessary to supplement that females found for themselves to sustain their building activities.

The male's high foraging activity in the early morning, when conditions were probably least conducive to efficient foraging, possibly enabled them to maintain their rate of food-trips to their partners then. In the early morning, females spent more time building and less time foraging than later.

The data show that both males and females spent a similar time in partner-interactions from the early morning till the early afternoon, after which the time involved declined slightly for the rest of the day. Such a diurnal pattern arose because most partner-interactions involved the male feeding his mate, and the rate of the male's food-trips during the course of the day had a similar routine.

During the course of the day, females spent a decreasing time nest-building and made fewer trips per hour with material to their nests. They spent about 60% of time nest-building and 30% foraging in the morning, compared with about 75% of time spent foraging by males then. Thus, to sustain their nest-building activity in the morning, females probably relied to some extent on the food provided by their partners and hence reduced the time they spent nest-building in the afternoon to forage more and so restore their bodily reserves to cope with the night fast.

CHAPTER FIFTEEN

THE TIME-BUDGETS FOR ROBINS INVOLVED IN THE PRELAYING AND LAYING STAGES OF THE BREEDING CYCLE

15.1. Introduction

Although no time-budget studies for other *Petroica* species have been carried out that I can compare with these for the South Island Robin, several such studies of other birds involved in the prelaying and laying stages have been published. Some of these concerned species of Anatidae (Afton 1979, Dwyer 1975, Seymour and Titman 1978) and a member of the Recurvirostridae (Gibson 1978), but only generalizations can be made when comparing their time-budgets with those for Robins. The time-budget studies for prelaying and laying Eastern Bluebirds (Pinkowski 1979) and Long-billed Marsh Wrens (Verner 1965) were for males only. Verbeek (1972) provided time-budgets for both sexes of the Yellow-billed Magpies involved in the prelaying and laying stages of the breeding cycle.

Descriptions are given here of monthly and total time-budgets for male and female Robins, and their diurnal patterns of behaviours during the prelaying and laying stages. Statistical comparisons are made between the proportion of time Robins spent in each behaviour from month to month. Comparisons are also drawn between the total time-budgets for males and females during these stages. Also, statistical comparisons are made between the total time-budgets for males during the nest-building, prelaying and laying stages, and between those for females involved in these stages.

From these time-budgets and the comparisons between them I hoped to answer the following questions:

1. Was the time females foraged related to the rate of food-trips they received from their partners?

2. Was the time males spent in partner-interactions during these two stages related to their behaviour associated with copulations and/or their rate of food-trips to their partners?

3. Did Robins spend more time in interspecific interactions once an egg had been laid?

4. Did females' time-budgets reflect the energy demands of egg formation?

15.2. Methods

The notation on the figures is as in previous chapters. Asterisks and crosses denote the level of significant difference between two samples of the proportion of time Robins spent in a behaviour. Asterisks next to the vertical axes of columns indicate significant differences between the time Robins spent in a behaviour during two consecutive months or day-periods. Those above the columns of total time-budgets indicate the behaviours in which birds spent significantly different proportions of time during two breeding cycle stages. Crosses above the columns of the female total time-budgets denote those behaviours to which they devoted significantly different proportions of time compared with males during the same stage.

Observations in the 1976 breeding season showed that females spent more time in body-maintenance during the prelaying and laying stages than in previous stages. To determine whether this was related to the development of the brood patch for incubation, the number of preening movements the birds made to various body areas was scored. A preening movement consisted of the bird reaching down and drawing one or more feathers through its mandibles then lifting its head. A preening movement was scored each time the bird lifted its head, and I noted whether the brood-patch area or another part of the body had been preened.

Because many passerines are most susceptible to human interference while laying, I did not watch females while they were actually in the act of laying.

The results and discussion sections of this chapter are divided into two portions: (1) the monthly and total time-budgets and (2) the diurnal patterns of behaviours. Within these sub-sections, the information is further divided so that the data for each behaviour are treated separately and in the same sequence as shown on the figures.

15.3. Results

15.3.1. The monthly and total time-budgets

15.3.1.1. The prelaying stage

This stage was defined as beginning when less than one trip per hour with material was made to the nest, and finishing when an egg was laid. The length of the stage varied during the course of the breeding season, being longest in July and shortest in November (Table 15.1).

Table 15.1. The mean length (days) of the prelaying stage for Robins in each month from the combined observations of the 1977 and 1978 breeding seasons.

	Months						Mean length (all months)
	J	A	S	O	N	D	
Mean length of the prelaying stage:	6.8	5.1	4.8	3.6	2.9	3.6	4.2
Sample size:	4	12	5	5	13	5	44

Figure 15.1 shows the monthly and total time-budgets for male and female Robins during the prelaying stage. Appendix 21 provides the values plotted on Figure 15.1.

(a) Foraging

The proportion of time males foraged during the prelaying stage varied significantly from month to month. By comparison, females foraged for a similar proportion of time from September to December, which was less than they foraged for in August ($P < 0.01$). From the total time-budgets, females foraged more than did males ($P < 0.01$).

(b) Food-storing

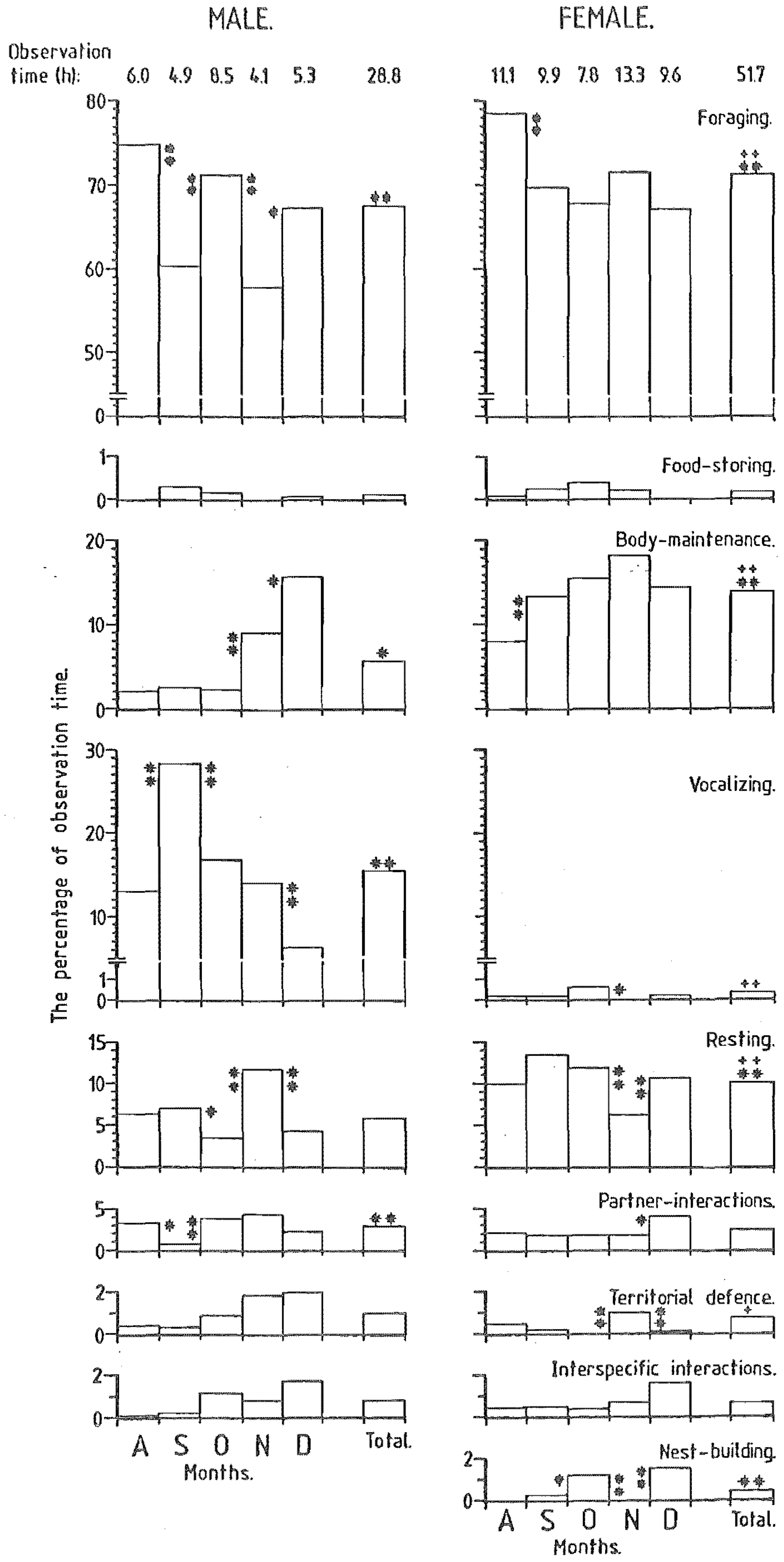
Males spent a similar proportion of time storing food from month to month during the breeding season, as did females. In total, both sexes spent a similar time storing food during the prelaying stage.

(c) Body-maintenance

Considering the total time-budgets, prelaying females engaged in body-maintenance more than did their partners ($P < 0.01$). Females spent more time in body-maintenance than did males from August to November, but in December the reverse was true.

Figure 15.1. The monthly and total time-budgets for male and female Robins involved in the prelaying stage of the breeding cycle. Appendix 21 provides the plotted values.

[a]The asterisks and crosses indicate significance levels: * or + = $P < 0.05$, ** or ++ = $P < 0.01$. Asterisks placed next to the sides of columns indicate significant differences between monthly samples. Those above the male total time-budget columns indicate significant differences between time males spent in a behaviour during the nest-building (Fig. 14.2, p. 250) and prelaying stages. Similarly, asterisks above the female total time-budget columns denote significant differences between the time females spent in a behaviour during the nest-building (Fig. 14.2) and prelaying stages. The crosses above the total time-budget columns for females show those behaviours to which males and females involved in the prelaying stage spent significantly different time.


MALE.
FEMALE.
Observation time (h):
6.0 4.9 8.5 4.1 5.3 28.8
11.1 9.9 7.8 13.3 9.6 51.7
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
Nest-building.
The percentage of observation time.
80
70
60
50
0
1
20
10
30
15
5
2
A S O N D
Total.
Months.

(d) Vocalizing

During the prelaying stage, males vocalized for about 16% of time per month, but with a greater proportion of time devoted to this behaviour in September ($P < 0.01$) and a lower proportion of time to it in December ($P < 0.01$). By comparison, females spent less than 1% of time each month vocalizing. Overall, females vocalized much less than did their partners ($P < 0.01$).

(e) Resting

The data show that for both sexes the proportion of time spent resting remained similar from month to month, except in November when there was a significant increase for males and a significant decrease for females. From the total time-budgets, females rested more than did males ($P < 0.01$).

(f) Partner-interactions

Generally, males spent a similar proportion of time each month interacting with their partners, as did females. Overall, males interacted with their partners slightly more than did females, although the difference was not significant. From 48.3 hours of observations of Robins involved in the prelaying stage, females received food from their mates at a mean rate of 1.5 times per hour.

(g) Territorial defence

The proportion of time males spent defending their territories increased gradually through the season. In December, males spent a significantly greater proportion of time in territorial disputes than during August and September ($P < 0.01$). The results for females do not show this seasonal trend. Except for a significant increase in November, females defended their territories against other Robins for a similar proportion of time each month. In total, males spent more time in territorial defence than did their mates ($P < 0.05$).

(h) Interspecific interactions

Overall, both sexes spent a similar time in interspecific interactions, and the time spent in this behaviour increased from month to month over the breeding season. The combined data for both sexes showed that during December they spent a greater proportion of time in this behaviour than over August and September ($P < 0.01$).

(i) Nest-building

The proportion of time prelaying females spent nest-building each month varied considerably. Over the breeding season, they devoted 0.6% of time to gathering nest material and incorporating it into their nests.

From the total time-budgets, males involved in the prelaying stage (Fig. 15.1) spent significantly less time foraging and interacting with their mates, and more time singing and in body-maintenance than during the nest-building stage (Fig. 14.2, p. 250). Prelaying females, by definition, spent less time nest-building than during the previous stage, 50.7% compared with 0.6% respectively. The time available after completing the nest resulted in prelaying females spending more time foraging, resting and in body-maintenance than did nest-building females ($P < 0.01$).

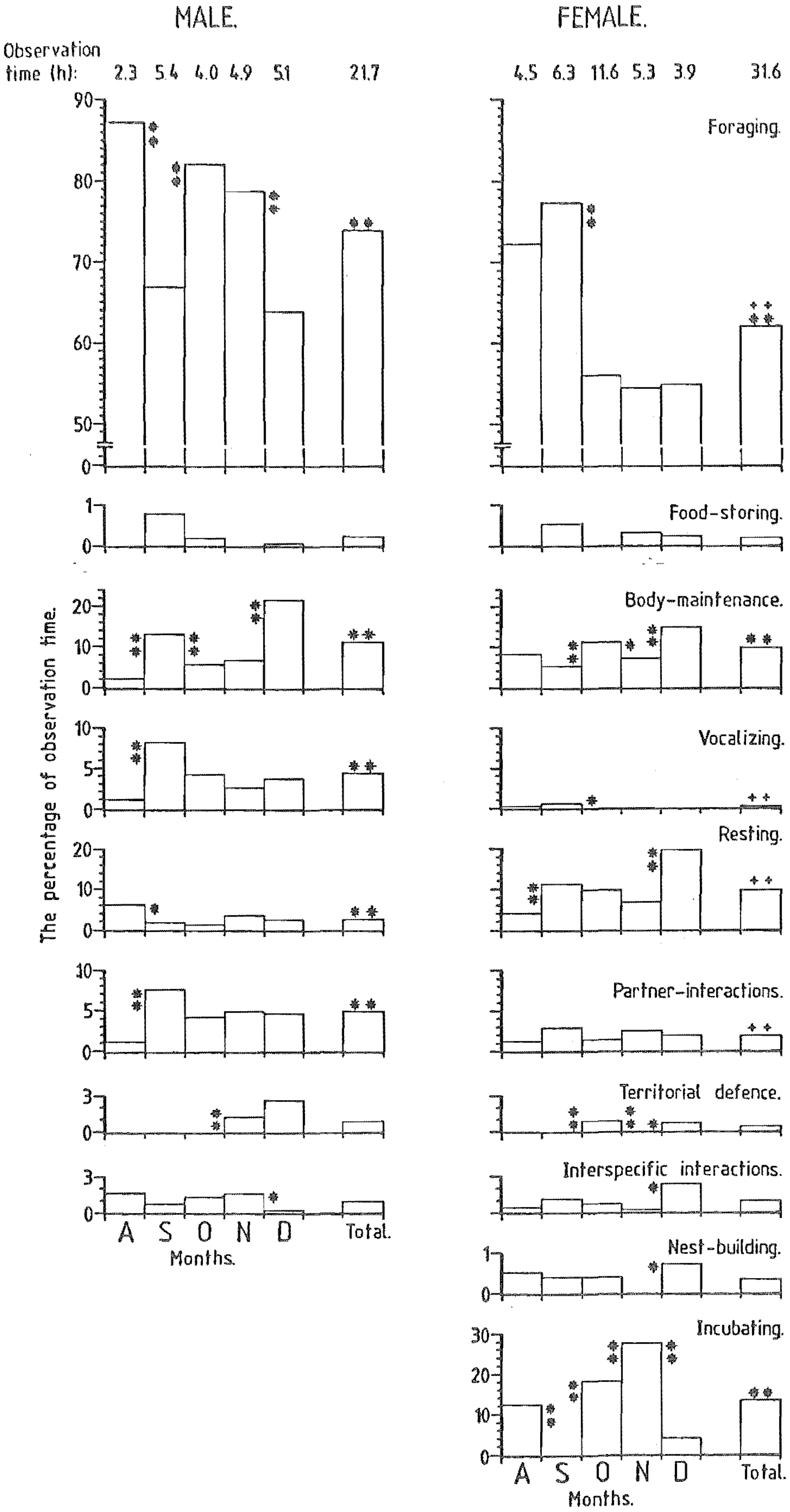
15.3.1.2. The laying stage

Although Flack (1979) recorded egg-laying from mid-May to early January, during this study the first Robin clutches were laid about late July and the last in early January. The laying stage includes those days on which an egg was laid and incubation attentiveness (the percentage of time spent covering the eggs) was less than 50%. Most clutches were of two or three eggs, eggs were laid at about 24 hour intervals, and full attentiveness was attained the day the last egg was laid, so that this stage lasted for one or two days only. Occasionally, with clutches of three or four eggs, full attentiveness began with the laying of the penultimate egg (pers. obs., Flack 1973).

Figure 15.2 shows the monthly and total time-budgets for male and female Robins involved in the laying stage. Appendix 22 gives the results on which Figure 15.2 is based.

Figure 15.2. The monthly and total time-budgets for male and female Robins involved in the laying stage of the breeding cycle. Appendix 22 gives the plotted values.

[a]The asterisks and crosses denote significance levels: * or + = $P < 0.05$, ** or ++ = $P < 0.01$. Asterisks placed next to the sides of columns indicate significant differences between adjacent monthly samples. Those above the male total time-budget columns indicate significant differences between the time males spent in a behaviour during the prelaying (Fig. 15.1) and laying stages. Similarly, asterisks above the female total time-budget columns denote significant differences between the time females spent in a behaviour during the prelaying (Fig. 15.1) and laying stages. The crosses above the total time-budget columns for females show those behaviours in which males and females during the laying stage spent significantly different time.


MALE.
FEMALE.
Observation time (h): 2.3 5.4 4.0 4.9 5.1 21.7
4.5 6.3 11.6 5.3 3.9 31.6
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
Nest-building.
Incubating.
The percentage of observation time.
90
80
70
60
50
0
1
20
10
5
3
30
A S O N D Total.
Months.

(a) Foraging

During the laying stage, the proportion of time males foraged changed significantly from month to month, except from October to November. Overall, they foraged for 74% of time, significantly more than the 62% for laying females ($P < 0.01$). Laying females foraged significantly more in August and September (about 75% of time) than during the following three months (about 55% of time). However, because of the increasing daylengths during the course of the breeding season, they foraged for a similar number of hours per day throughout the season (Appendix 22).

(b) Food-storing

Males spent a similar proportion of time storing food from one month to the next, as did females. From the total time-budgets it is evident that males and females spent a similar time storing food during the laying stage.

(c) Body-maintenance

The proportion of time both sexes devoted to body-maintenance changed significantly between some successive months. However, they tended to spend gradually more time in this behaviour as the breeding season progressed. Overall, both sexes spent a similar time in body-maintenance.

(d) Vocalizing

Except for the significant increase in September, males sang for a similar proportion of time each month. Over the breeding season, males sang for 4.5% of time, significantly more than the 0.2% of time their partners spent vocalizing.

(e) Resting

Males rested for a similar proportion of time each month, except for a significant decrease from August to September. Females tended to spend more time resting from month to month, and in total rested much more than did their partners ($P < 0.01$).

(f) Partner-interactions

In general, males spent a similar proportion of time interacting with their partners from month to month, as did females. However, from the total time-budgets, males spent more time in this behaviour than did females ($P < 0.01$). From 35.0 hours of observations, males fed their partners at a mean rate of 2.5 times per hour during the laying stage.

(g) Territorial defence

Although males spent twice as much time defending their territories against intruding conspecifics compared with females, this difference was not significant. Territorial disputes involving Robins engaged in the laying stage took place only after September.

(h) Interspecific interactions

Male Robins spent a similar time per month interacting with other species from August to November inclusive, as did female Robins. In December, males spent less ($P < 0.05$) and females more ($P < 0.05$) time in such interactions than in November. In total, male and female Robins interacted with other species for a similar time.

(i) Nest-building and incubating

Laying females spent about 0.5% of time building their nests each month, except in November when they were not seen nest-building. The time they spent incubating changed significantly from month to month, but overall they devoted 13.8% of time to this behaviour.

From the total time-budgets, males involved in the laying stage (Fig. 15.2) sang and rested significantly less ($P < 0.05$) and spent much more time in foraging, body-maintenance and partner-interactions ($P < 0.01$) than during the previous stage (Fig. 15.1). From the prelaying to the laying stage their rate of food-trips to their partners increased from 1.5 to 2.5 per hour.

Laying females spent less time in foraging ($P < 0.01$) and body-maintenance ($P < 0.01$), and more time incubating ($P < 0.01$) than did females during the prelaying stage. Table 15.2 shows that during both stages females directed a similar proportion of preening movements to their brood-patch areas. However, the combined data for females involved in the prelaying and laying stages shows they directed significantly more preening movements to their brood-patch areas than they did outside the breeding season ($P < 0.01$).

Table 15.2. The percentage of preening movements made by females to their brood-patch areas during the prelaying and laying stages of the breeding cycle and during the non-breeding season.

	Total number of preening movements	Percentage of preening movements to the brood-patch area	
Prelaying stage:	1687	28%	Not significant
Laying stage:	615	24%	
Breeding season (prelaying and laying stages only):	2302	27%	$P < 0.01$
Non-breeding season:	652	16%	

Male Robins spent a similar time interacting with other species during the prelaying and laying stages, as did females. The combined data for both sexes involved in these two stages (133.8 hours of observation time, Appendices 21 and 22) show that they spent 0.87% of time in interspecific interactions. Similarly, the combined data for paired adult and immature Robins of both sexes during June and July (182 hours of observation time, Appendices 5, 6, 11 and 12) show that they spent 0.52% of time in interspecific interactions, significantly less than those involved in the prelaying and laying stages ($P < 0.01$).

15.3.2. The diurnal patterns

15.3.2.1. The prelaying stage

(a) Foraging

Males foraged least of all in the early morning (Fig. 15.3, Appendix 23). The time they spent foraging from mid-morning to mid-afternoon was significantly higher than for the early morning, but significantly less than for the late afternoon. Prelaying females spent much of the early morning foraging and then reduced their foraging significantly for the rest of the morning. In the afternoon, females foraged for a similar time each day-period, which was greater than the time they spent foraging in the mid- to late morning ($P < 0.01$).

(b) Food-storing

The data show that males spent a similar time storing food from one day-period to the next, as did females.

(c) Body-maintenance

The diurnal pattern of body-maintenance for the two sexes differed during the prelaying stage. Although the time males spent in body-maintenance did not change significantly during the course of the day, they spent slightly more time in this behaviour about midday than at other times. Females spent a similar time in body-maintenance as the day progressed, except for spending less time in this behaviour in the early morning than later in the day ($P < 0.05$).

(d) Vocalizing

Males sang less per day-period during the course of the day. In comparison, females vocalized for a similar time each day-period.

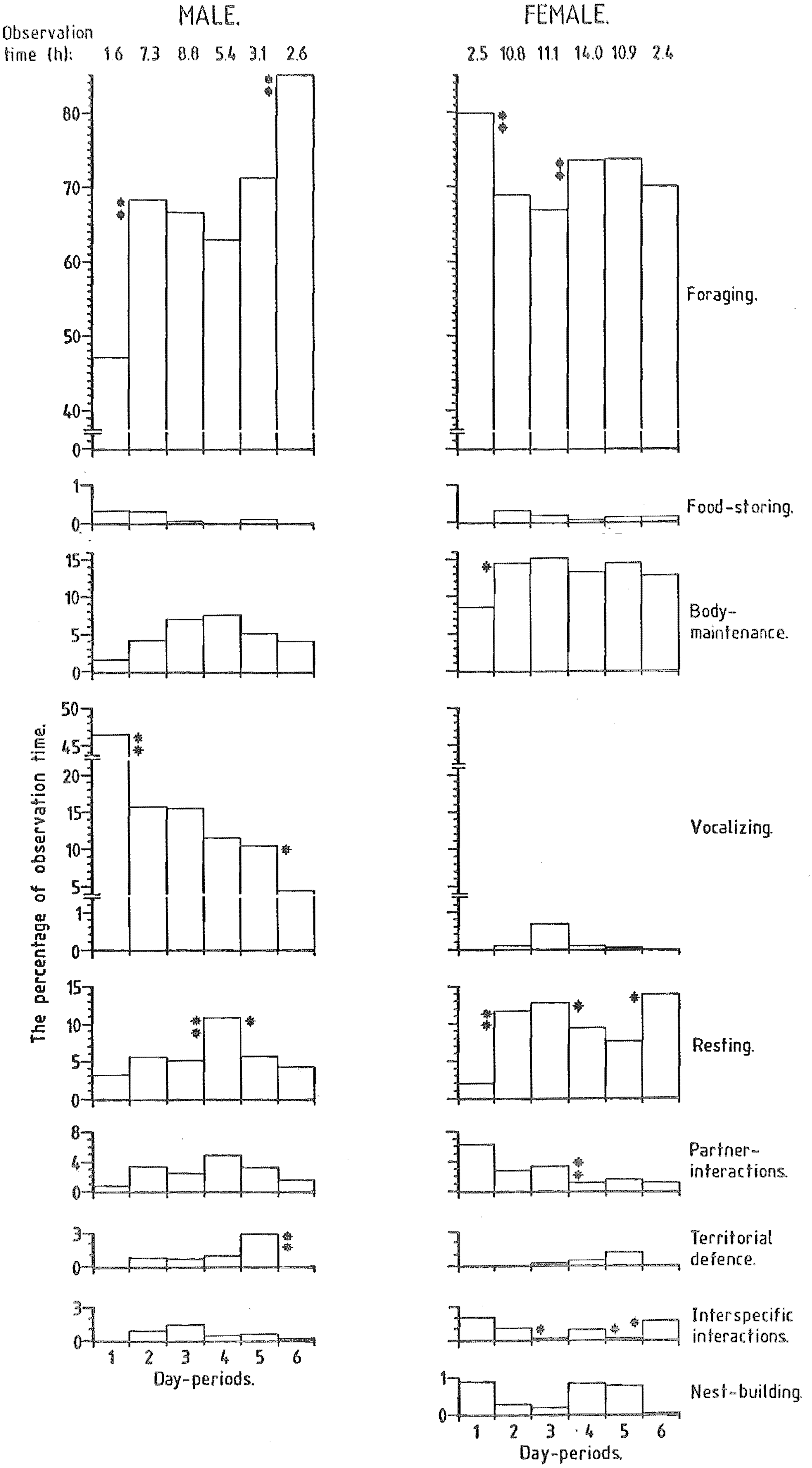
(e) Resting

The proportion of time males rested per day-period remained fairly constant throughout the day, except for a significant increase in the early afternoon. Prelaying females had a bimodal diurnal pattern of

Figure 15.3. The diurnal patterns of behaviours for male and female Robins involved in the prelaying stage.

Appendix 23 gives the plotted values.

[a]The asterisks indicate significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the time Robins spent in a behaviour between two successive day-periods.


MALE.
FEMALE.
Observation time (h): 1.6 7.3 8.8 5.4 3.1 2.6
2.5 10.8 11.1 14.0 10.9 2.4
80
70
60
50
40
0
Foraging.
1
0
Food-storing.
15
10
5
0
Body-maintenance.
50
45
20
15
10
5
1
0
Vocalizing.
15
10
5
0
Resting.
8
4
0
Partner-interactions.
3
0
Territorial defence.
3
0
Interspecific interactions.
1
0
Nest-building.
The percentage of observation time.
1 2 3 4 5 6
Day-periods.
1 2 3 4 5 6
Day-periods.

resting, and rested most in the mid- to late morning and late afternoon. They rested least of all in the early morning.

(f) Partner-interactions

The diurnal pattern of partner-interactions for males shows a gradual increase to about midday and then a decrease through the afternoon. In contrast, prelaying females spent significantly more time interacting with their partners in the morning than in the afternoon.

(g) Territorial defence

Both sexes spent slightly more time in territorial disputes in the afternoon than in the morning.

(h) Interspecific interactions

Males spent a similar time each day-period in interspecific interactions. However, females spent more time in this behaviour in the early morning and late afternoon than during the rest of the day.

(i) Nest-building

Although the time prelaying females spent building their nests did not change significantly from one day-period to the next, they devoted slightly more time to this behaviour in the early morning and early to mid-afternoon.

15.3.2.2. The laying stage

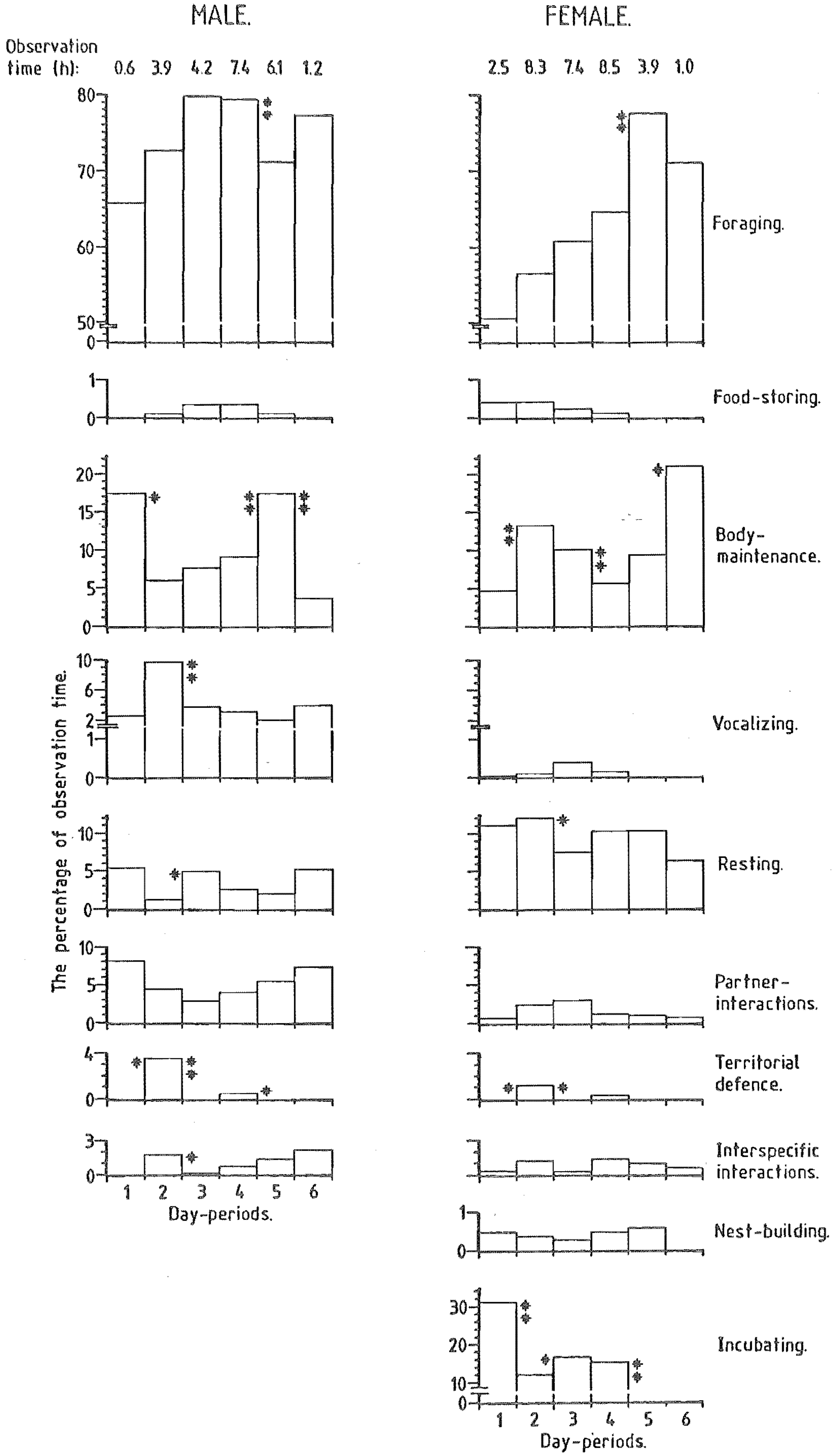
(a) Foraging

The diurnal pattern of foraging for males during the laying stage (Fig. 15.4, Appendix 24) showed an increase, though not significant, in time devoted to this behaviour from the early to late morning, followed by a significant decline in the mid-afternoon and a slight increase in the late afternoon. By comparison, female foraging increased each day-period till the late afternoon, when it declined slightly.

Figure 15.4. The diurnal patterns of behaviours for male and female Robins involved in the laying stage.

Appendix 24 shows the plotted values.

[a]The asterisks indicate significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the time Robins spent in a behaviour between two successive day-periods.


MALE.
FEMALE.
Observation time (h):
0.6 3.9 4.2 7.4 6.1 1.2
2.5 8.3 7.4 8.5 3.9 1.0
80
70
60
50
0
Foraging.
1
0
Food-storing.
20
15
10
5
0
Body-maintenance.
10
6
2
1
0
Vocalizing.
10
5
0
Resting.
10
5
0
Partner-interactions.
4
0
Territorial defence.
3
0
Interspecific interactions.
1
0
Nest-building.
30
20
10
0
Incubating.
The percentage of observation time.
1 2 3 4 5 6
Day-periods.
1 2 3 4 5 6
Day-periods.

(b) Food-storing

The data show no diurnal pattern in this behaviour by either sex.

(c) Body-maintenance

Both sexes had a bimodal diurnal pattern of body-maintenance during the laying stage. The peaks in such behaviour for males took place in the early morning and mid-afternoon, but for females they occurred in the mid- to late morning and late afternoon.

(d) Vocalizing

Males spent a similar time singing each day-period, except for a significant increase in the mid-morning. Females did not have a marked diurnal pattern of vocalizing.

(e) Territorial defence

Both sexes spent little time in territorial defence, except during the mid-morning and early afternoon.

(f) Incubating

Laying females were not seen incubating in the mid- to late afternoon. They spent about twice as much time incubating in the early morning as during the mid-morning to early afternoon ($P < 0.01$).

In general during the laying stage, neither males nor females had a diurnal pattern of resting, partner-interactions or interspecific interactions. Similarly, laying females spent a similar time from one day-period to the next adding material to their nests.

15.4. Discussion

15.4.1. The monthly and total time-budgets

15.4.1.1. The prelaying stage

(a) Foraging

The reduction in foraging by males during the prelaying stage compared with that during nest-building arose partly because they provided less food to their partners than previously - only 1.5 food-trips per hour to their prelaying partners compared with 3.2 per hour to nest-building partners. Furthermore, the lower rate of food-trips made by males in the prelaying stage would have resulted in them flying back and forth to their partners less than in the nest-building stage. Hence, because of the high energy demands of flight, in the prelaying stage males would have needed to forage less to find sufficient food to maintain themselves than previously.

Prelaying female Robins foraged more than did their partners ($P < 0.01$). Similarly, it seems that during the prelaying stage female Yellow-billed Magpies fed more than did their partners (Fig. 1, Verbeek 1972). Also, females of several *Anas* species spent more time foraging and foraged at a faster rate than did their mates during this stage of the breeding cycle: for example, *Anas clypeata* (Afton 1979), *A. strepera* (Dwyer 1975) and *A. rubripes* (Seymour and Titman 1978). Gibson (1978) found that prenesting female American Avocets spent more time feeding than did males.

Did the female's time-budget reflect the energy requirements of egg formation? Females foraged more than did their partners probably to meet the high energy requirements of egg formation. Provisional estimates for passerines by King (1973) suggested that the maximum daily cost of egg production was a substantial fraction of the female's energy budget, equalling about 13 to 16% of the daily energy intake of normal function without a gain or less of body weight. Flack (in prep.) found that female Robins had steady weights throughout the year, except in spring when their weights fluctuated markedly, perhaps because of egg formation and laying. This suggests that egg formation in Robins was mainly supported by an increased food intake rather than the use of endogenous reserves. Several studies suggest that egg formation takes place during the prelaying stage (see reviews by King 1973, Ricklefs 1974). This was supported by the results of an experiment in which a beetle pupa containing dye was fed to a female Robin a known time before egg laying and the eggs were analysed using the yolk fixing and staining methods of Grau (1976) (Appendix 25). Therefore, the significantly greater time spent foraging by females in the prelaying stage compared with when selecting a nest site (Fig. 14.1, p. 247) or building a nest (Fig. 14.2, p. 250) was probably to find sufficient food to meet the requirements of egg formation. Thus, it seems that the female's time-budget does reflect the energy requirements of egg formation.

Although prelaying females foraged for a similar proportion of time from September to December, they gradually spent more hours per day foraging during the season as daylength increased. This increase in foraging time would have allowed females to find more food and receive more from their partners each day. Perhaps this resulted in their eggs forming more quickly and was the reason for the shortening of the mean length of the prelaying stage during the course of the breeding season (Table 15.1).

(b) Food-storing

Since food-storing seemed to take place only when Robins found more than enough food to meet their immediate energy needs, stored food can presumably be considered as a surplus. Therefore, because Robins spent a similar time from month to month storing food, and both sexes spent as much time doing this, it seems that they were able to meet their food requirements fairly readily during the prelaying stage. It should be remembered that this was not the case in the nest-building stage when females spent less time storing food then than did their partners ($P < 0.05$).

(c) Body-maintenance

A possible reason why prelaying females spent more time in body-maintenance than did males ($P < 0.01$) was the development of the brood patch for incubation. Perhaps the loss of feathers and increased blood circulation to the area resulted in it requiring more preening than outside the breeding season. This greater involvement in body-maintenance by females compared with males, seems to have arisen out of necessity and not because females had more time to spend in such a low priority behaviour, since females foraged more than did their partners during this stage ($P < 0.01$).

In December, males spent more time in body-maintenance than did females, instead of *vice versa* as in previous months. This was because males sun-bathed in December, but prelaying females did not.

(d) Vocalizing

Males sang more in the prelaying stage than in the nest-building stage ($P < 0.01$), partly because they had more time to do so. In the prelaying stage males foraged less than when their partners were building nests ($P < 0.01$). Observations of other male passerines have shown a similar increase in singing activity once the nest had been completed: for example, Eastern Bluebirds (Pinkowski 1979) and Long-billed Marsh Wrens (Verner 1965). Verner considered that this increased singing by polygamous male wrens, as well as attracting more mates and repelling other males, served the added function of increasing the female's receptivity to approach by the male, making it possible for copulation to occur. The appropriate displays between members of a pair "are often essential to stimulate final oocyte development, ovulation and insemination" (Lofts and Murton 1973). Robins copulated during the prelaying stage and members of a pair probably had to achieve a rapport not only in their reproductive physiology, but in their social relations as well. This would have been most important for Robins because males invariably dominated their mates. An important feature of a male's behaviour during the prelaying stage was the change from a dominant to a submissive role during partner-interactions, such as seen in the "butterfly-flight" display (Section 8.3.1, p. 115). The increased singing by males during the prelaying stage, as well as having other functions, may have helped to signal to the female his submissiveness and readiness to copulate (Section 8.4.1, p. 123). During this stage, a singing male often gave a "butterfly-flight" display when approached by his partner.

(e) Resting

Except in November, males rested for a similar proportion of time each month, as did females. Although the reason for the marked reduction in foraging for males during November over the October result is unknown, presumably it allowed them to devote significantly more time to such a low priority behaviour as resting. The significant decrease in resting for females in November seems to have been a consequence of the birds spending slightly more time in foraging and body-maintenance, and significantly more time in territorial defence than during the previous month. These behaviours were probably important for the maintenance of females and their territories, and more time was spent in them at the expense of resting, a low priority behaviour. Overall, females rested more than did males ($P < 0.01$), possibly because females vocalized much less than did males - 0.2% and 15.6% of their time respectively.

(f) Partner-interactions

Was the time males interacted with their partners related to the male's rate of food-trips? The lower rate of food-trips to prelaying females compared to nest-building females was probably largely responsible for males interacting significantly less with prelaying partners (Fig. 15.1) than with partners building nests (Fig. 14.2, p. 250.

Since egg formation took place during the prelaying stage and it "evidently places a tremendous energetic strain on the female" (Ricklefs 1974), why did males reduce their food-trip rate to prelaying partners? Observations of Great Tits and Blue Tits revealed that courtship feedings were infrequent before egg-laying (Hinde 1952, Krebs 1970, Rayoma 1966a). However, studies of other birds have shown that males increased the frequency of food-trips (courtship feedings) to their mates during the prelaying stage. Courtship feedings by male Lesser Black-backed Gulls *Larus fuscus* and Black Noddies *Anous tenuirostris* were almost confined to the prelaying stage (Brown 1967, Cullen and Ashmole 1963 respectively). These authors suggested that the timing of the courtship feedings and the amount of food provided supported the extra food requirements of females during the period of accelerated ovary development. Nisbet (1977) studied the courtship feeding of Common Terns *Sterna hirundo*, and his findings suggested that these feedings by the male made a substantial contribution to the nutritional requirements of the female when egg formation was occurring and was one of the factors limiting the egg number and size.

Two factors may be important in explaining why female Robins received fewer food-trips in the prelaying stage than in the nest-building stage. First, the female Robin's style of foraging mostly involved them hopping over the ground and scanning from branches (Section 4.3.2, p. 33), activities which would be little hindered by the extra weight of developing eggs. This contrasts with the precise flight manoeuvres required for terns to dive and catch fish (Nisbet 1977). Second, female Robins *had* time to forage for the extra food required. The time-budget shows that prelaying females stored surplus food and spent significantly more time resting and in body-maintenance than while nest building, which suggests that they were able to find enough food to meet their requirements each day. Furthermore, the time females rested and preened was significantly greater than that spent by males on these behaviours ($P < 0.01$). Previous results showed that resting and body-maintenance were low priority behaviours with time spent in them being inversely related to that spent foraging (Chapters 9, 10 and 11). Since pair-members often foraged apart, food-trips by the male were not initiated immediately beforehand by the female signalling her hunger. Presumably, the frequency of food-trips was controlled by the vigour with which the female begged for food during previous feedings. Therefore, males made fewer food-trips to their partners in the prelaying stage than during the nest-building stage, probably because females begged less vigorously when fed by their partners. I conclude that females found much of the food they needed to meet their increased energy requirements of egg formation. However, it is also possible that during this stage males were reluctant to take food to their mates because of a need to become submissive, temporarily, towards their mates in readiness to copulate.

(g) Territorial defence

Females spent less time than did males in territorial defence because when a female encountered an intruder, she gave alarm "chucks" to which her mate responded by coming to her and evicting the intruder. Usually, a female took no further part in such a dispute. Vigorous flight is an energy-demanding activity (Tucker 1969) and such behaviour on the female's part would have used up energy better used for egg formation. It has been shown that chick size is positively correlated with egg size and that larger chicks have a higher survival rate than small chicks (Nisbet 1978, Parsons 1970, Schifferli 1973). Therefore, females would be expected to spend as little time as possible chasing intruders, leaving this behaviour to the male so that as much of the female's energy as possible could be put into forming large eggs. Perhaps gravid female Robins were less proficient at the rapid and sudden manoeuvres in flight seen during territorial disputes. Furthermore, it may have been related to the greater investment in time and energy by males in territorial defence than by females, and the inability of some females to dominate male intruders.

(h) Interspecific interactions

Both sexes spent more time in interspecific interactions later in the breeding season, probably because of the presence of increasing numbers of juveniles of many species. A similar situation was known to cause breeding Robins to spend more time in territorial defence during the course of the season. Greater numbers of immature Robins were present as the season progressed and these birds moved about the forest causing adults to spend more time evicting them.

(i) Nest-building

The significant variation in time spent in nest-building from month to month by prelaying females arose because not all females engaged in this behaviour, and those that did devoted considerably different proportions of time to it. The material gathered and incorporated into their nests by prelaying females was found while they foraged on the ground or included down feathers obtained when they were preening.

15.4.1.2. The laying stage

(a) Foraging

There was no obvious cause for the abrupt decreases in the proportion of time males spent foraging in September and December, and for females after September. But as expected from previous results, these decreases in foraging time were correlated with increased time spent resting and in body-maintenance. During the laying stage, males foraged more than they did during the prelaying stage ($P < 0.01$), probably to find enough food to make more frequent food-trips to their partners. Males made 2.5 food-trips per hour during the laying stage, but only 1.5 per hour in the prelaying stage. Similarly, male Eastern Bluebirds spent more time foraging during the laying stage than previously (Pinkowski 1979).

Was the time females foraged related to the rate of food-trips by their partners? Yes, a laying female foraged less than did a prelaying one ($P < 0.01$), presumably because a greater proportion of the female's energy requirements were met in the laying stage by the food supplied by her partner (2.5 food-trips/h) than was the case in the previous stage (1.5 food-trips/h). In addition, perhaps the energy required for egg formation was lower in the laying stage when fewer yolks were being formed than during the prelaying stage (King 1973).

(b) Food-storing

Even though laying females foraged less than did their mates, the two sexes spent a similar time storing food in the laying stage. Thus, the food females found themselves plus what they received from their mates was sufficient to create a surplus for storing. Most of the prey items stored by females were those from their partners when the latter made several food-trips in quick succession so that the females became satiated.

(c) Body-maintenance

Prelaying and laying females directed a similar proportion of preening movements to their brood-patch areas, but laying birds spent less time in body-maintenance than did prelaying birds ($P < 0.01$). Thus, laying females presumably preened all their plumage areas less than did prelaying females. Also, both sexes spent a similar time in body-maintenance during the laying stage, so possibly the development of the brood patch was complete by this stage and/or it did not need preening any more than the corresponding area on males. Nice (1937) found that the brood patch of Song Sparrows was bare and liberally supplied with blood vessels by the time the first egg was laid. Thus, I conclude that the increased proportion of time female Robins spent in body-maintenance later in the breeding season was related to the longer daylengths and higher ambient temperatures indirectly resulting in them having to forage less so that they had more time for body-maintenance, rather than as a result of the development of the brood patch.

(d) Vocalizing

Male Robins, like male Eastern Bluebirds (Pinkowski 1979) and Long-billed Marsh Wrens (Verner 1965) sang less once their mates began laying. It seems unlikely that this reduced singing was an attempt by the birds to prevent predators using the songs to locate Robin nests, because the birds sang well away from their nests. More likely once an egg had been laid, singing was no longer necessary to increase the female's receptivity to approach and copulation by the male or to stimulate ovulation because copulation should have occurred before laying began. Possibly the main reason for this decline in singing was so that males could spend more time finding and taking food to their partners. This would be a means whereby a male could reduce the chance of his mate abandoning the nest when she began incubating, thereby protecting his investment in time and energy into the pair's reproductive effort to that stage. Laying females spent so little time vocalizing because they gave mainly contact "chucks" to locate their mates and these calls lasted only a second or two.

(e) Resting

Males rested less in the laying stage than they did while involved in the prelaying stage ($P < 0.01$), because they had to spend significantly more time in foraging, body-maintenance and partner-interactions, and resting was a low priority behaviour they could reduce their involvement in presumably without affecting their chances of survival. However, contradictory to this explanation, males rested for a greater proportion of time in August than they did in September, but spent significantly more time foraging in August, a result for which I have no explanation.

Laying females rested more than did their mates, presumably because females foraged less than males ($P < 0.01$) and so the former had more time to spend resting. Possibly, when females were satiated it was better for them to rest and so conserve their energy for egg formation rather than engage in an energy demanding behaviour.

(f) Partner-interactions

Was the time males interacted with their partners related to the male's rate of food-trips? Yes, males interacted more with their partners once an egg had been laid because they then made more frequent food-trips to their partners than in the prelaying stage. In addition, during the laying stage, females often remained near their nests to receive food, rather than flying towards their partners as did prelaying females. Thus, males spent more time per food-trip finding and feeding their laying mates than previously.

Laying females often attracted their partners to their nests after being fed by slowly flapping one or both wings, giving a soft twittering call and flying towards the nest. This behaviour may have been to show males that laying had begun and so signal to them that incubation was about to start, when more frequent food-trips were made to females. Overall, females spent a similar time interacting with their mates during the prelaying and laying stages. The time they spent in sexual chases, copulating and "chucking" at their singing mates during the prelaying stage was in the laying stage spent receiving food more frequently and in attracting their mates to their nests.

As for Robins, the rate of food-trips to female Great Tits and Blue Tits increased once they had laid their first eggs (Royama 1966a). Royama estimated that the extra food female tits needed for egg production, but were unable to collect for themselves because they did not have time, was supplied by their mates. Female Great Tits and Blue Tits laid clutches of about 8-13 eggs (Witherby *et al.* 1938), suggesting they were engaged in both egg formation and laying over several days. With about an hour spent laying each morning and the nest still being completed (Kluijver 1950), females had insufficient time to find enough food for egg formation as well as self-maintenance so that the food supplied by their partners was essential (Royama 1966a).

Although probably not so essential to Robins as for tits, the increased food-trips received by laying female Robins perhaps occurred because Robins spent time laying and incubating and so had less time than previously to forage while still incurring the high energy demands of albumen and shell formation.

(g) Territorial defence

As happened during the prelaying stage, Robins involved in the laying stage spent more time in territorial disputes during the later months of the breeding season. This was a consequence of increasing numbers of young becoming independent and moving about in search of mates and/or areas of forest uninhabited by conspecifics. Although not a significant difference, males spent twice the time ousting intruders that their mates did. This result arose because compared with female Robins, males were more aggressive, investigated sounds that were likely to come from intruders and supplanted their mates when females were interacting with intruders.

(h) Interspecific interactions

During the laying stage, most time a pair of Robins were engaged in interspecific interactions involved them protecting their nests and eggs by chasing other birds from the vicinity of Robin nests. Did Robins spend more time in interspecific interactions once an egg had been laid? In total, male Robins spent a similar time in such interactions during the prelaying and laying stages, as did females. Thus, Robins were as much involved in interspecific interactions whether their nests were empty (prelaying stage) or contained an egg (laying stage). That these interactions involved Robins protecting their nests is supported by the fact that Robins involved in the prelaying and laying stages of the breeding cycle spent more time in interspecific interactions than did paired Robins in winter (June and July) ($P < 0.01$).

(i) Nest-building

Like Robins, Great Tits occasionally brought material to their nests during the laying stage (Kluijver 1950). What elicited the Robin's response to collect nest material is unknown, but they devoted little time to this behaviour (0.4%) and it always involved the addition of material to the nest lining.

(j) Incubating

Most female Robins were not seen incubating until they had laid the last egg, but some began incubating with partial attentiveness (less than 50% of time spent incubating) before the clutch was completed. Thus, in some cases, their involvement in incubation increased gradually over a day or two. Several other passerines have been found to spend more time incubating as their clutches were completed: for example, the Goldcrest *Regulus regulus* (Haftorn 1978), Great Tit (Kluijver 1950), Yellow-billed

Magpie (Verbeek 1972) and the Tree Sparrow *Spizella arborea* (Weeden 1966). Female Robins were not seen to start incubating when only one egg had been laid; there had to be two or more. This was probably why they incubated significantly less in December than they did in November. Several two-egg clutches were laid in December, but almost all clutches in November were of three eggs.

It seems unlikely that the partial attentiveness of laying females resulted in any appreciable warming of the eggs, and embryo development, because eggs that were partially incubated hatched at about the same time as those that were laid when full attentiveness (more than 50% of time spent incubating) had begun. This suggests that during the laying stage, incubation resulted in insufficient heat being applied to the eggs to allow embryo development, as was the case during partial incubation by Great Tits (Kluijver 1950). Perhaps laying female Robins spent this time covering their eggs because they were stimulated hormonally or visually to do so, but did not have enough time to begin full attentiveness. Also, on two occasions laying females sat over their eggs when Bellbirds came near their nests. Bellbirds took feathers from Robin nests when females were inattentive, and perhaps female Robins covered their eggs when time permitted to protect their nests and eggs from such interference from other birds. No eggs were seen being damaged or eaten by other birds, although this may have happened.

15.4.2. The diurnal patterns

15.4.2.1. The prelaying stage

(a) Foraging and vocalizing

As described previously, it would seem advantageous for Robins to sing in the early morning because weather conditions are more favourable for sound propagation then (Richards and Wiley 1978), and least favourable for foraging (Kacelnik 1979). These seem to be the main reasons why male Robins at the prelaying stage foraged less and sang more in the early morning than later in the day. They foraged significantly more after the early morning, probably because it became more profitable to do so, so that the birds were able to make up for the energy reserves used at night and their likely low food intakes in the early morning. The increased foraging by males in the late afternoon compared with earlier was probably to find enough food to last them throughout the night. This is supported by the fact that males interacted with their partners less in the late afternoon than earlier so that the extra food the males found in the afternoon was not given to them.

Yolk formation continues at night (Appendix 25, Grau 1976), so that most food in the alimentary tract of females would probably have been digested and used for self-maintenance and egg formation by the morning. Therefore, they probably had little, if any, energy reserves by morning. This is supported by the diurnal patterns of body weights for several passerines (Baldwin and Kendeigh 1938). This was probably the main reason why prelaying females, in contrast to their mates, foraged for most of the early morning. I am unable to explain why females foraged less than did males in the late afternoon because the former would have had higher energy requirements during the course of the night as a consequence of egg formation.

(b) Food-storing

Although neither male nor female Robins stored food to a distinct diurnal pattern, they tended to do so more when they spent least time foraging per day-period. Presumably, the amount of foraging Robins carried out was related to their food requirements. When the birds spent little time foraging they probably had adequate food reserves and therefore were able to store more prey than when they spent a large proportion of time foraging.

(c) Body-maintenance and resting

Did Robins spend more time in body-maintenance and resting when they foraged less? Yes, in general, when Robins at the prelaying stage foraged less during a day-period they then spent more time in body-maintenence and resting. However, males spent little time in body-maintenance in the early morning, even though they did not forage much then, because they spent most of their spare time singing. For females, time spent resting per day-period was inversely correlated with that spent foraging, but this was not true for body-maintenance. Perhaps the development of the brood patch required females to preen it for at least some time each day-period independent of the time they spent foraging.

(d) Partner-interactions

During the course of the day males carried food at a fairly steady rate (Fig. 14.3B, p. 252) and interacted with their mates for a similar time each day-period (Fig. 14.5, p. 258) when involved in the nest-building stage, but this no longer seems to have been the case during the prelaying stage. Prelaying females interacted with their partners significantly more in the morning than they did in the afternoon, because interactions other than those involved with the acceptance of food from their partners occurred more often in the morning, such as "butterfly-flight" displays, sexual chases and copulations. This was not reflected in the diurnal pattern of partner-interactions for males because my movements while observing females sometimes seemed to attract their mates which led to interactions between the partners. When following males, females were not usually attracted to the male or myself, possibly because the former tended to remain near their nests.

(e) Territorial defence

Both sexes spent more time in territorial defence in the afternoon than they did earlier, probably because males sang less in the afternoon. Krebs (1977) demonstrated that singing by resident Great Tits helped to deter intruders, and from previous results this seems to have been true of singing by Robins (Figs 10.7, p. 160, 10.8, p. 162 and 10.9, p. 164). Therefore, the reduced singing of full song in the afternoon may have contributed to the increased time males spent in territorial defence then. Possibly because there was little singing in the afternoon a non-territorial immature bird was unaware when it was intruding into a breeding pair's territory.

(f) Interspecific interactions

As for most other times of the year, males involved in the prelaying stage spent a similar time as the day progressed interacting with other species. I am unable to explain why prelaying females interacted with other species significantly less in the late morning and mid-afternoon compared with other times of the day. There was no obvious feature in female Robins' behaviour that seems to have contributed to this result.

(g) Nest-building

Prelaying females spent more time adding material to their nests in the early morning and early to mid-afternoon, possibly because they foraged more then. Most of the material collected by these birds was fine dried grasses and moss from the ground. Perhaps, because in some cases prelaying birds had only completed the nest-building stage the previous day, once they stopped foraging and were on the ground where nest material was readily available, they collected material rather than beginning another behaviour.

During the prelaying stage, males spent more time in reproductive behaviours in the morning than in the afternoon, mainly because of their increased singing of full song in the early morning. It seems likely that this singing functioned more in relation to interactions between members of a pair than to advertise territorial possession. Females' involvement in reproductive behaviours took place only slightly more in the morning than it did in the afternoon. Some types of interactions between pair-members, such as copulations, sexual chases and "butterfly-flight" displays, occurred predominantly in the morning during this stage of the breeding cycle, as they did outside the breeding season (Sections 8.3.1, p. 115 and 11.4.2, p. 207).

15.4.2.2. The laying stage

(a) Foraging and food-storing

During the nest-building stage, when males foraged more and made more frequent food-trips to their partners than during the laying stage, males spent most of the early morning foraging (Fig. 14.5, p. 258). In contrast, during the laying stage males foraged slightly less in the early morning than they did later in the day. This suggests that they found enough food for their own and their partners' requirements without foraging for as long in the early morning as they did in the nest-building stage. Similarly, laying females spent much of the morning laying, resting, incubating and in body-maintenance, and this suggests they too were readily able to meet their food requirements. This hypothesis is supported by the fact that laying females spent more time storing food in the morning, when they foraged least of all. In contrast to their partners, males spent more time storing food when they foraged most of all during the day. Males stored little food in the early to mid-morning, presumably because most surplus prey they captured then was given to their partners.

(b) Body-maintenance

The diurnal patterns of body-maintenance for male and female Robins at the laying stage tended to be the reverse of those for foraging, showing that even during this stage of the breeding cycle most body-maintenance was carried out when time was not required for foraging.

(c) Vocalizing

Since male vocalizations during this stage consisted largely of full song (Fig. 6.2A, p. 60) and since sound propagation over long distances and through dense vegetation is best achieved in the early morning (Wiley and Richards 1978), it was not surprising that males sang most of all in the morning. Females had no diurnal pattern of vocalizing because they gave contact "chucks" at a similar rate throughout the day and the calls were of only one to two seconds duration.

(d) Resting

As the day progressed females tended to spend a similar time resting, as did males. These results suggest that whatever the birds did each day-period, they had to spend a certain minimum time resting.

(e) Partner-interactions

Even though there was no significant change in the time males or females spent in partner-interactions during the day, females spent most time in such interactions in the late morning, the time of day when males spent least time in this behaviour. Why the two sexes had slightly different diurnal patterns of involvement in partner-interactions I cannot explain.

(f) Territorial defence

It is not known why both sexes spent significantly more time chasing conspecifics during mid-morning than they did in the early and late morning, because males sang most in mid-morning. From the results of the diurnal patterns of vocalizing and territorial defence during the prelaying stage, it seemed that singing helped to ward off intruders.

(g) Interspecific interactions

In general, males spent a similar time in interspecific interactions each day-period, as did females. Possibly, this was because the behaviour of Robins involved in the laying stage and that of other species resulted in such interactions arose randomly during the day.

(h) Nest-building

The diurnal pattern of nest-building for laying females was the same as when they were prelaying, a similar time being spent on nest-building from one day-period to the next. If stimuli from the nest were responsible for eliciting this behaviour, I would have expected laying females to add material to their nests mainly in the early morning, when they laid and incubated more than they did later in the day. It does not seem that when foraging, laying females were stimulated by the sight of nest material to collect it, as prelaying females appeared to be. Laying females foraged significantly more in the mid- to late afternoon than earlier, but spent a similar time nest-building each day-period. What governed the diurnal pattern of nest-building behaviour of laying females is not obvious.

(i) Incubating

As did female Robins, female Goldcrests incubated their incomplete clutches mainly before noon (Haftorn 1978). Perhaps the time spent and the act of laying, which took place in the morning, stimulated the birds to spend more time incubating then than in the afternoon. With the day ahead of them for foraging and with some stored food available, female Robins had time to incubate in the morning. But, in the mid- to late afternoon, when they foraged more than they did earlier in the day

($P < 0.01$), perhaps there was not enough time to incubate. From the monthly time-budgets (Section 15.4.1.2), it was suggested that females sometimes incubated during the laying stage to protect their eggs from other birds. However, because female Robins spent a similar time in interspecific interactions each day-period and not mainly in the morning when they incubated most, perhaps the main reason they incubated was not to prevent other birds damaging their eggs.

In the laying stage, males spent slightly more time in the morning than in the afternoon in behaviours related to reproduction (vocalizing, partner-interactions, and foraging to supply food to their partners). Females devoted much more time in the morning to reproductive behaviours (incubating and laying) than they did in the afternoon. A possible reason for this diurnal pattern of reproductive behaviour relates to the efficiency of foraging during the day. Foraging by insectivorous birds is probably least efficient in the early morning (Kacelnik 1979, Verner 1965). Therefore, when possible it is better for the birds to carry out reproductive behaviours then.

15.5. Summary

15.5.1. The prelaying stage

Males foraged less during the prelaying stage than during nest-building ($P < 0.01$). This difference arose mainly because males made fewer food-trips per hour to their prelaying partners (1.5/h) than when their partners were building nests (3.2/h), and therefore they did not have to find as much food for their partners during the prelaying stage.

Prelaying females foraged more than did their partners ($P < 0.01$), partly because females received fewer food-trips from their mates than previously. However, the main reason was probably that these birds had to meet the high energy requirements of egg formation (King 1973).

Even though females were forming eggs, they received fewer food-trips per hour from their partners than when building a nest. It seems that a male reduced his rate of food-trips to his prelaying partner because the female's foraging was not hindered by her increased weight associated with egg formation and she had sufficient time to find enough food to meet the energy requirements of egg formation, whereas nest-building significantly affected their foraging opportunities. Perhaps males did not supply more food to their prelaying females than they did because it was more important for males to sing. During the prelaying stage males spent less time in partner-interactions than when their mates were nest-building, because of the lower rate of food-trips made in the former stage.

During prelaying, males foraged least in the early morning, probably because this was a less favourable time to forage and weather conditions generally made it a more favourable time for sound propagation (singing). Males sang much more in the early morning than afterwards ($P < 0.01$). During the late afternoon, males foraged more than at other times of the day ($P < 0.01$), presumably to find food for their partners as well as to increase their own bodily reserves for the night. Prelaying females foraged most in the early morning, presumably because they had little energy reserves left after the night when most may have been used up in self-maintenance and egg formation.

In general, the diurnal patterns of body-maintenance and resting for males and females were the reverse of their patterns of foraging. Males devoted most time to body-maintenance and resting about midday even though they foraged least in the early morning, because most "spare" time was spent singing in the early morning.

Prelaying females interacted with their partners more in the morning than they did in the afternoon, because interactions other than those involved with the acceptance of food from their partners occurred more often in the morning.

15.5.2. The laying stage

During this stage, males foraged more than did their partners ($P < 0.01$), the reverse of the situation in the prelaying stage. This arose because males foraged more in the laying stage than during the prelaying one, while laying females foraged less than before. The increased foraging of males was probably related to the need to find enough food to make more frequent food-trips to laying partners (2.5/h) than to prelaying females (1.5/h). Laying females foraged less than previously, either because they had less time to do so, the food supplied by their partners met more of their requirements than formerly, and/or the energy required for egg formation was lower in the laying stage when fewer yolks were being formed.

Males sang less once their partners had laid an egg (4.5% of time) than previously (15.7% of time) ($P < 0.01$). Possibly the main reason for this decline was that males spent more time finding and taking food to their partners.

Males spent more time interacting with their partners after the first egg had been laid than before, because males made more food-trips during the laying stage and spent more time per food-trip finding and feeding their mates then. Males made more food-trips to laying females than to prelaying ones probably because the former had less time to forage, but were still incurring the high energy requirements of egg formation. Females interacted with their partners for a similar time during the two stages. This occurred because the time they spent in sexual chases, copulating and "chucking" at their singing partners during the prelaying stage was replaced in the laying one by time spent receiving food more frequently and attracting their mates to their nests.

Robins did not spend more time in interspecific interactions once their nests contained eggs: they were just as protective of their nests whether they contained eggs or not. However, Robins involved in the prelaying and laying stages spent more time interacting with other species than did paired Robins in winter ($P < 0.01$). This suggests that some of the increased time the former spent in this behaviour was the result of attempts to protect their nests.

Overall, laying females incubated their incomplete clutches for 13.8% of time. This incubating did not result in embryo development.

Since both sexes foraged less in the early morning than later in the day, and females incubated and stored food more so in the early morning, probably the birds were readily able to meet their food requirements then, in contrast to prelaying females.

The diurnal patterns of body-maintenance for Robins during the laying stage tended to be the reverse of their patterns of foraging, as it was during other stages of the breeding cycle.

Males sang mainly in the early to mid-morning, probably because at that time of day weather conditions were better for sound propagation than afterwards (Wiley and Richards 1978). As during the prelaying stage, laying females followed no clear diurnal pattern of vocalizing.

CHAPTER SIXTEEN

THE TIME-BUDGETS FOR ROBINS INVOLVED IN THE INCUBATION STAGE

16.1. Introduction

Many comparisons have been made between the various types of involvement by members of a pair of passerines in incubation and on the influences of environmental factors (food availability, ambient temperature, and rain) on the time spent warming the eggs (reviews by Drent 1975, Kendeigh 1952, Skutch 1962, White and Kinny 1974). In recent years several investigators have tried to determine the energy requirements of incubating birds to discover whether incubation requires an increased level of energy expenditure compared with that for non-incubating birds (King 1973, Mertens 1977, Ricklefs 1974, Walsberg and King 1978). Nevertheless, little quantitative information has been published about how incubating passerines use their time. Verbeek (1972) gave time-budgets for both sexes of a species where the male supplied food to his incubating mate. Similarly, Pinkowski (1979) gave budgets for both sexes of a species, but in this case the incubating female foraged for all her food. Verner (1965) and Schartz and Zimmerman (1971) each gave a time-budget for polygamous males which neither incubated nor fed their incubating mates.

Only the female Robin incubated. The male frequently brought her food (Flack 1973, Fleming 1950, Richdale 1941, Soper 1976). Incubation began with the laying of the first egg for a pair that bred in captivity (Richdale 1941). However, in a large sample of nests at Kowhai Bush most females began full incubation with the laying of the last egg and occasionally when the penultimate egg had been laid (Flack 1973, 1979). The incubation stage (Section 3.3, p. 19) lasted 17-18 days (Flack 1973, 1979).

Descriptions and comparisons of the monthly and total time-budgets for male and female Robins involved in the incubation stage are given here. The influence of ambient temperature, day of incubation, and the rate of the male's food-trips on the female's attentiveness (the proportion of time they spent on the eggs) are described. The total time-budgets for males and females involved in the incubation stage are compared both with each other and with the total time-budgets for Robins involved in the laying stage. The diurnal patterns of each behaviour are compared between the early, middle and late portions of the breeding season. As well as providing a quantitative description of the time-budgets for both sexes when involved in the incubation stage, I hoped to determine which factors, if any, influenced the female's attentiveness.

16.2. Methods

The behaviour of Robins involved in the incubation stage was timed during the 1976 and 1977 breeding seasons. The time females spent on turning their eggs, preening and moving about while in the nest was recorded as incubation time. Some females could not be followed while they were off their eggs (inattentive) without influencing their behaviour. Therefore, to obtain sufficient observation time of incubating females I sat near their nests and recorded their attentive and inattentive periods, and whether they were fed by their mates while off the nest. During the 1977 season, the ambient temperature (°C) near the nest during each observation was recorded a metre from the ground in the shade. The maximum and minimum temperatures were averaged to give a mean temperature for the observation.

Male behaviour during the incubation stage was recorded only for those not feeding juveniles from the pair's previous nesting. However, the behaviour of incubating females was timed whether or not their partners were feeding juveniles.

The results and discussion sections are divided into two sub-sections: (1) the time-budgets, and (2) the diurnal patterns of behaviours. Each of these sub-sections is further divided so that the data for each behaviour are described and discussed separately, and in the sequence shown on the figures.

16.3. Results

16.3.1. The monthly and total time-budgets

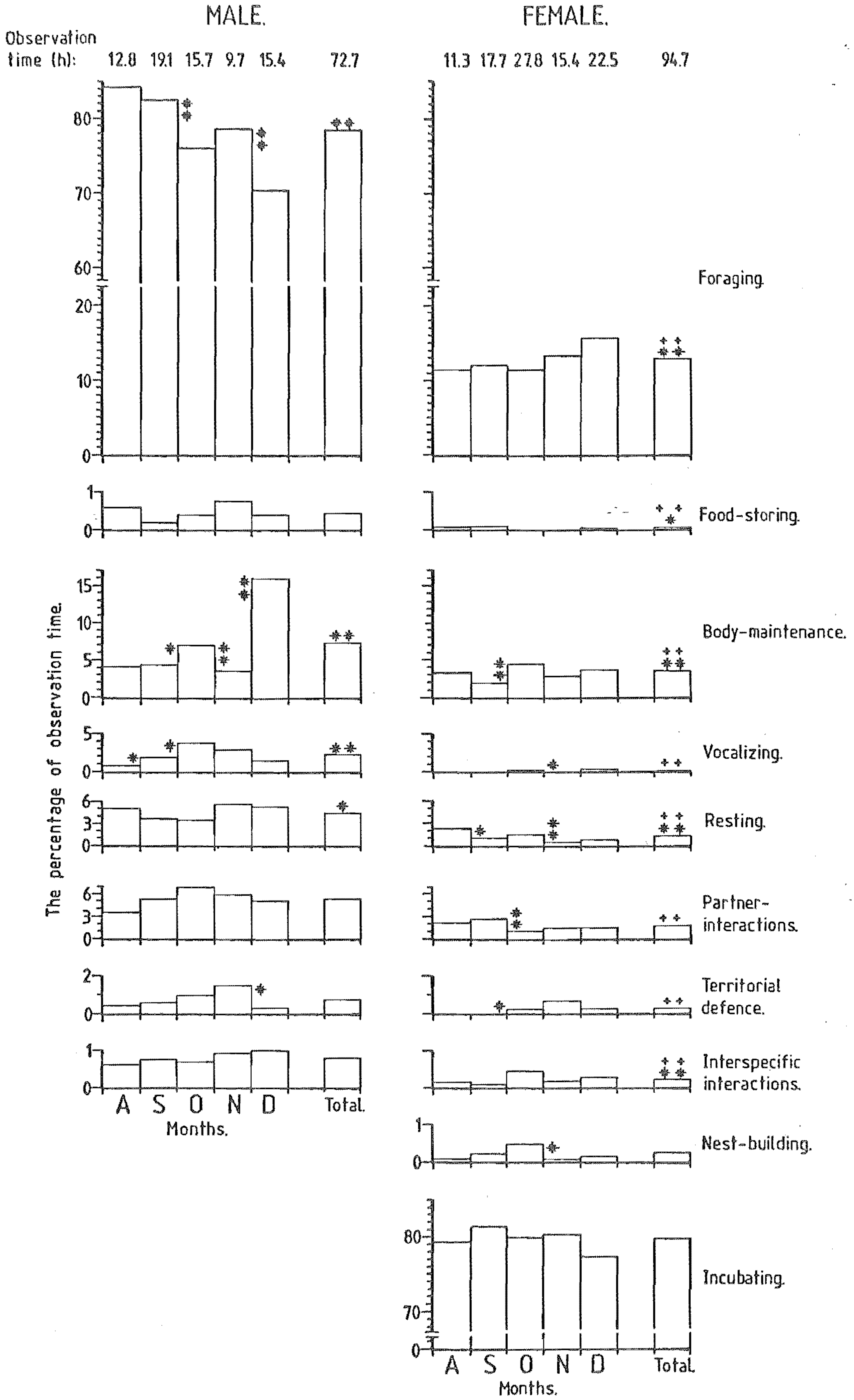
(a) Foraging

During the incubation stage males spent 78.5% of time foraging (Fig. 16.1), significantly more than the 74.0% they devoted to foraging in the laying stage ($P < 0.01$). In the course of the season, the proportion of time that males with incubating partners foraged decreased, the differences being significant in October and December. However, as a result of increased daylength, the hours per day males foraged tended to

Figure 16.1. The monthly and total time-budgets for male and female Robins involved in the incubation stage.

Appendix 26 gives the plotted values.

[a]The asterisks and crosses indicate significance levels: * or + = $P < 0.05$, ** or ++ = $P < 0.01$. The asterisks placed next to the sides of columns denote significant differences between adjacent monthly samples. Those above the male totals columns show significant differences between the time males were involved in particular behaviours during the laying (Fig. 15.2, p. 284) and incubation stages, likewise for females. The crosses indicate those behaviours in which males and females involved in the incubation stage spent significantly different percentages of time.


MALE.
FEMALE.
Observation time (h): 12.8 19.1 15.7 9.7 15.4 72.7
11.3 17.7 27.8 15.4 22.5 94.7
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
Nest-building.
Incubating.
The percentage of observation time.
A S O N D Total.
Months.
80
70
60
20
10
0
1
15
5
6
3
2

increase from month to month (Appendix 26). Incubating females foraged for 12.9% of time (Fig. 16.1), much less than did their partners ($P < 0.01$) and laying females ($P < 0.01$) (Fig. 15.2, p. 284). In contrast to males, incubating females foraged for a slightly greater proportion of time from month to month.

(b) Food-storing

Males spent about 0.4% of time on storing food in total and each month. Females devoted only 0.03% of time to this behaviour, significantly less than did their partners (Fig. 16.1) and laying females.

(c) Body-maintenance

About 7.4% of the male's time was spent in body-maintenance, less than during the previous breeding stage ($P < 0.01$). During October and December, the proportion of time spent by males in this behaviour increased significantly compared with that in the previous months. These monthly increases in body-maintenance were correlated with significantly decreased foraging. Females spent 3.5% of time in body-maintenance, less than half that of their partners and much less ($P < 0.01$) than spent by laying females. Incubating females preened more in October than September ($P < 0.01$), otherwise they devoted a similar proportion of time to this behaviour during each month of the breeding season.

(d) Vocalizing

While their partners were incubating males spent about 2.2% of time vocalizing, which was mainly full song (Fig. 6.2A, p. 60). The proportion of time per month they vocalized increased significantly till October, then gradually decreased. Comparing total time-budgets, males sang less in the incubation stage than in the laying one ($P < 0.01$), and vocalized more than did their incubating partners ($P < 0.01$). Females spent less than 0.1% of time vocalizing, which mainly involved giving "chuck" calls (Fig. 6.2B, p. 60).

(e) Resting

During the incubation stage, both sexes rested significantly less than in the laying stage, and incubating females rested less than did their partners ($P < 0.01$). Males rested for a similar proportion of time each month, but females tended to spend a decreasing proportion of their time per month resting as the season advanced.

(f) Partner-interactions

From the total time-budgets (Fig. 16.1), males interacted with their partners more than did females ($P < 0.01$). Males devoted a similar time to such interactions during the laying and incubation stages: the same was true of females. Males spent an increasing proportion of time per month until October interacting with their partners, after which it decreased. By comparison, females interacted with their partners more in August and September than afterwards ($P < 0.01$). Most of the time pair-members interacted with each other involved the male feeding his mate. From data for the entire breeding season, males not feeding juveniles brought food to their incubating partners 2.9 times per hour, slightly more often than the 2.5 times per hour during the laying stage. However, males that were feeding juveniles fed their incubating partners only 1.1 times per hour.

(g) Territorial defence

During the incubation stage, territorial defence against conspecifics took up 0.7% of the male's time. Males spent a similar time defending their territories during the laying stage. The percentage of time males were seen ousting intruders and engaged in boundary disputes increased each month to November, then declined in December. Females spent less time in territorial defence than did their partners and were involved in such behaviour only after September.

(h) Interspecific interactions

Whether they were involved in the laying or incubation stages, male Robins interacted with other species for a similar time. During the latter stage, males spent a similar proportion of time in interspecific interactions from month to month as the breeding season progressed, as did females. The total time-budgets show that incubating females spent nearly 0.3% of their time involved in interactions with interspecifics (Fig. 16.1), less than half that of their partners (0.7%) ($P < 0.01$) and the 1.0% for laying females ($P < 0.01$).

(i) Nest-building

Incubating females occasionally collected lining material and incorporated it into their nests. This behaviour took up 0.25% of their time, which was slightly less than laying females spent in nest-building.

(j) Incubating

Females incubated for about 80% of their time during each of the months studied.

From October to December, males feeding juveniles of the previous brood made 1.1 food-trips per hour to their incubating partners, compared with 2.6 per hour for those males without juveniles (Fig. 16.2A). Males which did not have juveniles to feed fed their partners on 82% of the occasions females left the nest (Fig. 16.2B). In contrast, females whose partners were feeding juveniles, received food on only 34% of the occasions when they left their nests. Females whose partners were feeding juveniles incubated less each month than did those whose partners had no juveniles to care for ($P < 0.01$) (Fig. 16.2C).

Two females whose mates disappeared continued to incubate, but the loss of the mates had a marked effect on the attentiveness of the females. One of these females, observed for 16.3 hours in September 1977, spent 72.8% of time incubating, much less ($P < 0.01$) than the 84.0% for females that were incubating in the same month and had partners. The other, watched for five hours in early January 1978, incubated for 62.8% of time compared with 74.9% for females with partners ($P < 0.01$).

With each 10°C rise in ambient temperature within the range of 1.0°C to 20.9°C, females significantly decreased their attentiveness (Fig. 16.3). Above 21.0°C the female's attentiveness increased slightly. However, when intense sunlight shone on their nests their attentiveness increased markedly to 93.9% during a total of 2.3 hours of observation

Figure 16.2. The influence of the male's rate of food-trips to his partner on her attentiveness (% time spent incubating) for each month and combined months of the breeding season.

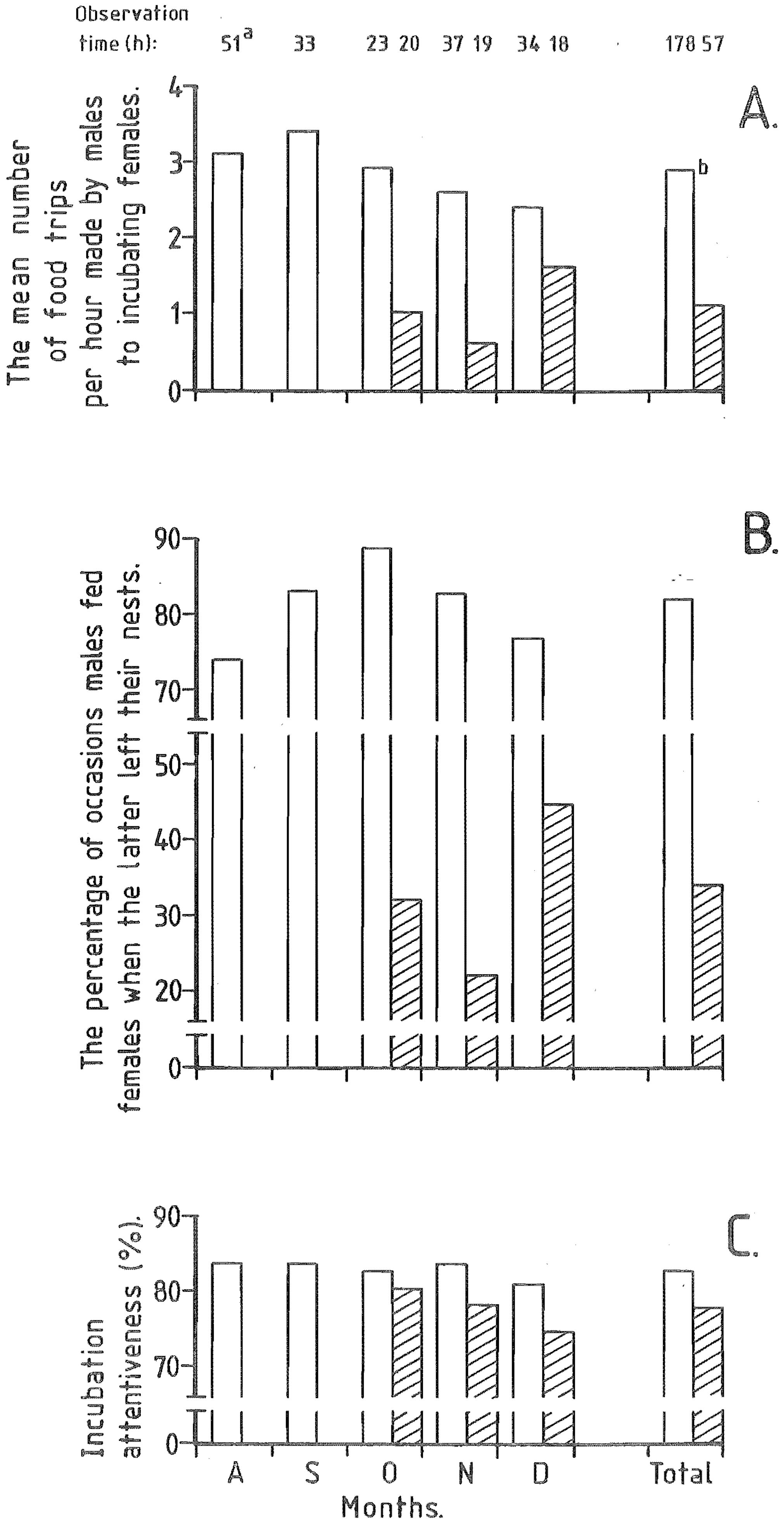
A The mean number of food-trips per hour by males to their partners.

B The percentage occasions males fed their partners when the latter left their nests.

C The incubation attentiveness of females.

[a] The number of hours of observation time per month are the sample sizes for all three graphs.

[b] Unshaded columns are for pairs that did not have dependent juveniles and the shaded columns are for those that did.


Observation time (h):
51a
33
23 20
37 19
34 18
178 57
A.
The mean number of food trips per hour made by males to incubating females.
0
1
2
3
4
b
B.
The percentage of occasions males fed females when the latter left their nests.
0
20
30
40
50
70
80
90
C.
Incubation attentiveness (%).
0
70
80
90
A
S
O
N
D
Total
Months.

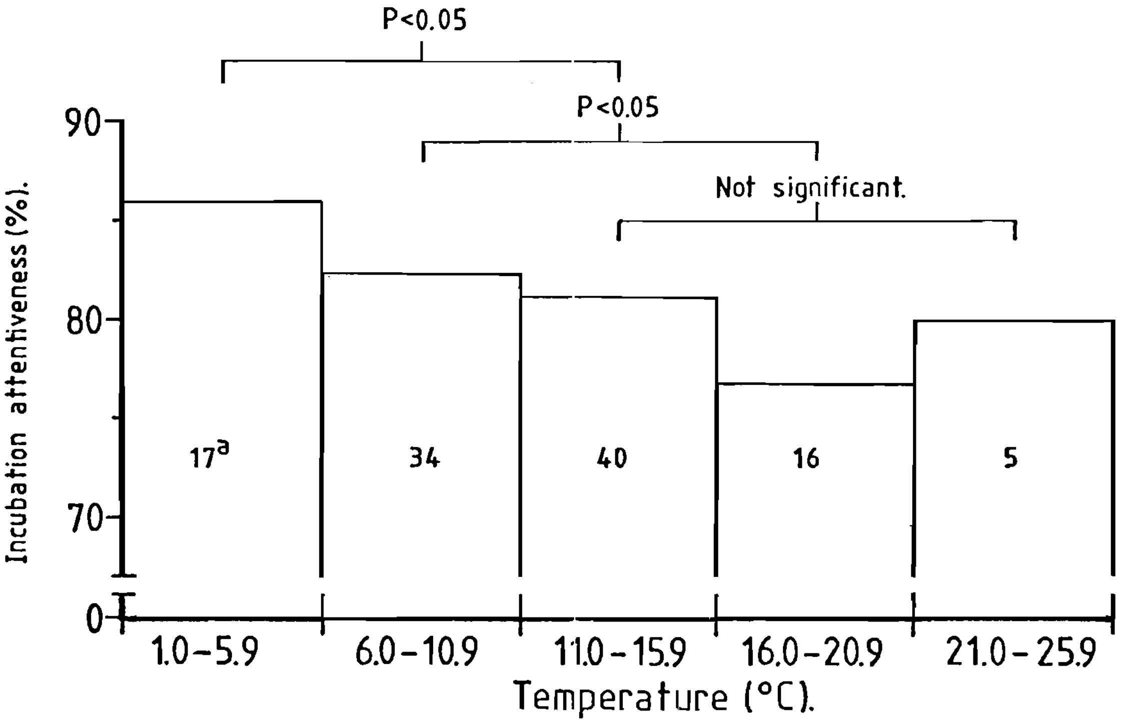


Figure 16.3 The influence of ambient temperature (°C) on incubation attentiveness (% of time spent incubating).

[a]The number of hours of observation time.

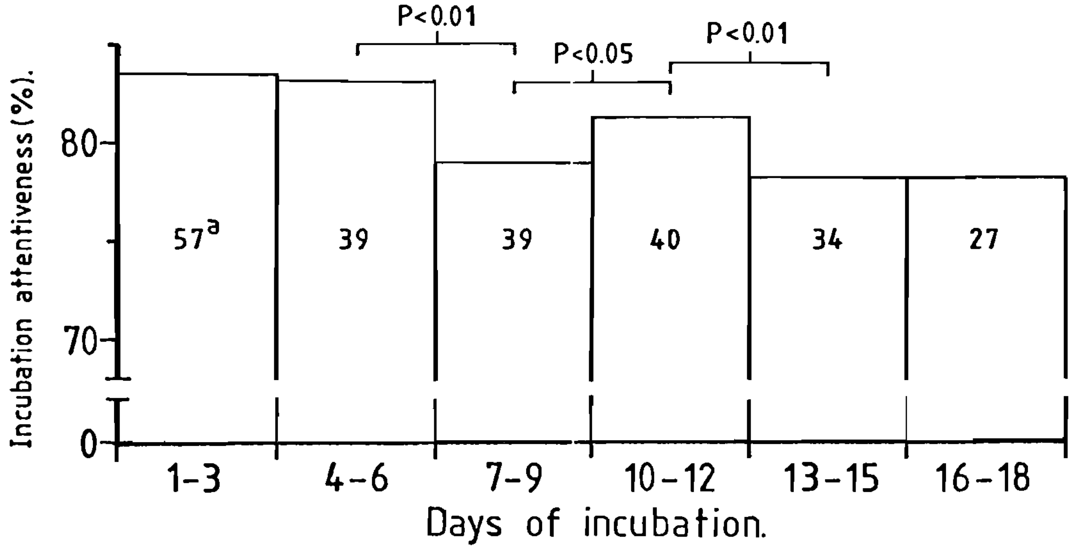


Figure 16.4 The influence of the day of incubation on incubation attentiveness (% of time spent incubating).

[a]The number of hours of observation time.

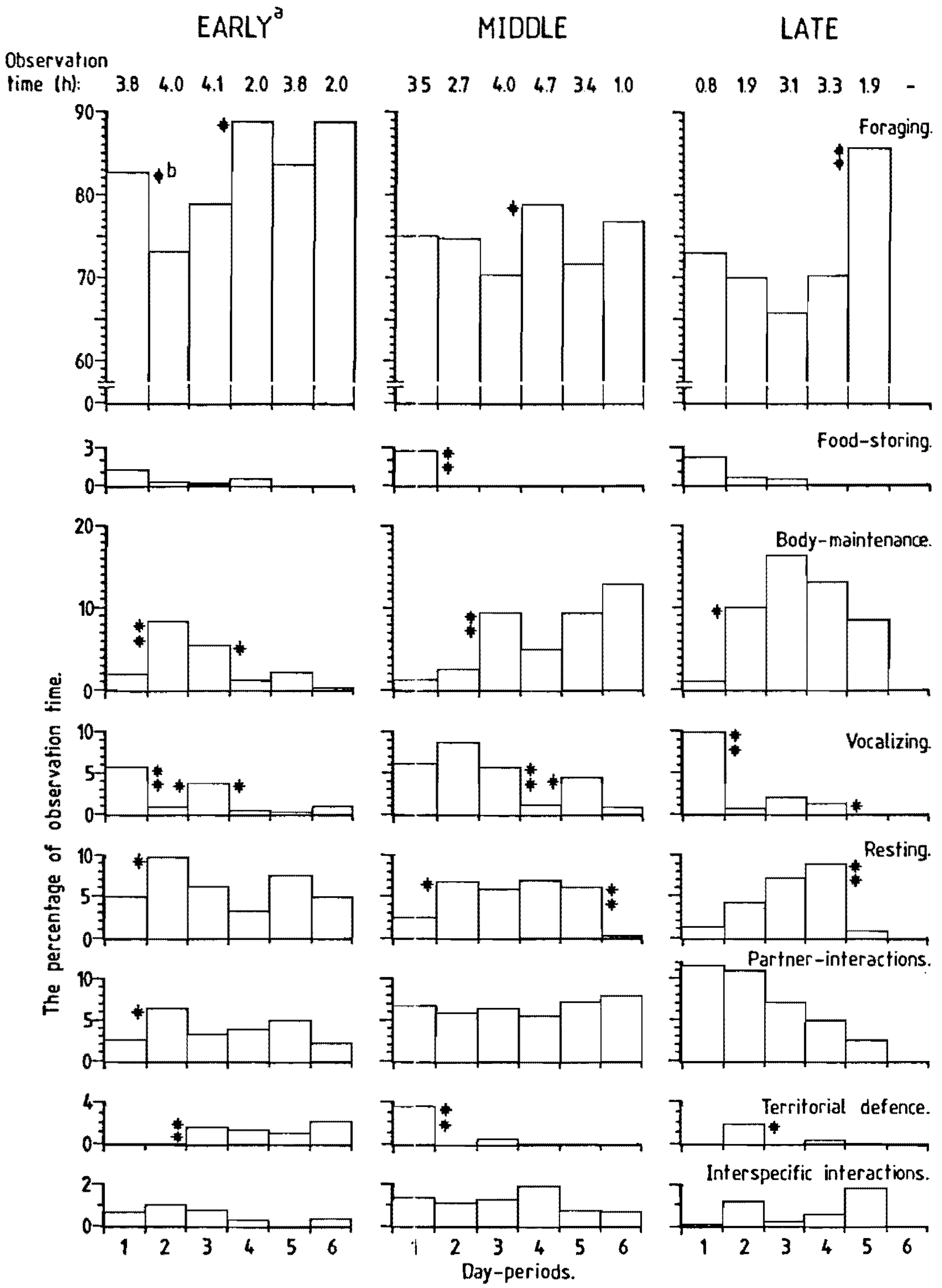


Figure 16.5 The diurnal patterns of behaviours during three portions^a of the breeding season for males involved in the incubation stage. Appendix 27 gives the graphed values.

^{a}Early - August & September, Middle - October & November, Late - December.

^{b}The asterisks denote significant differences (×=P<0.05, × ×=P<0.01) in the percentage of time males spent on a behaviour between two successive day-periods.

time. Incubating females watched during heavy rain that had been falling for over half an hour when observations were begun incubated for 86.3% of a total of 21.1 hours of watching under these conditions.

In the first six days of incubation the female spent an average of 83% of the day incubating, but this dropped to about 78% for the rest of the incubation period, except for a significant rise to 82% for days 10 to 12 (Fig. 16.4).

16.3.2. The diurnal patterns

16.3.2.1. The diurnal patterns of male behaviours

(a) Foraging

During the early and middle portions of the breeding season, the male's times of increased foraging occurred in the early morning, and early and late afternoon (Fig. 16.5). Late in the season, however, male foraging peaked in the early morning and possibly the mid-afternoon.

(b) Food-storing

Throughout the breeding season, males whose partners were incubating stored food mainly in the early morning.

(c) Body-maintenance and resting

The diurnal rhythm of body-maintenance for males varied seasonally, but in each case the peak tended to occur when least time was spent foraging. Likewise, males tended to rest more per day-period when they foraged least: this usually took place in the mid-morning to early afternoon.

(d) Vocalizing

Males vocalized most in the early and late morning, except in the middle of the breeding season when much singing took place in the mid-morning and mid-afternoon.

(e) Partner-interactions

During the first two portions of the breeding season males spent a similar time each day-period interacting with their partners, but late in the season the time devoted to this behaviour gradually declined in the course of the day.

(f) Territorial defence

Although the diurnal pattern of territorial defence of males differed for each portion, they usually spent more time interacting with conspecifics other than their mates in the afternoon.

(g) Interspecific interactions

Generally, males spent a similar time each day-period in interspecific interactions.

16.3.2.2. The diurnal patterns of female behaviours

(a) Foraging and incubating

Although their diurnal pattern of foraging differed for each portion of the breeding season (Fig. 16.6), the time females foraged and incubated per day-period was inversely related. A significant increase in foraging was correlated with a significant decrease in incubation, but not necessarily *vice versa*.

(b) Food-storing

In contrast to the diurnal pattern of food-storing for males, females spent more time storing food after the early morning.

(c) Body-maintenance

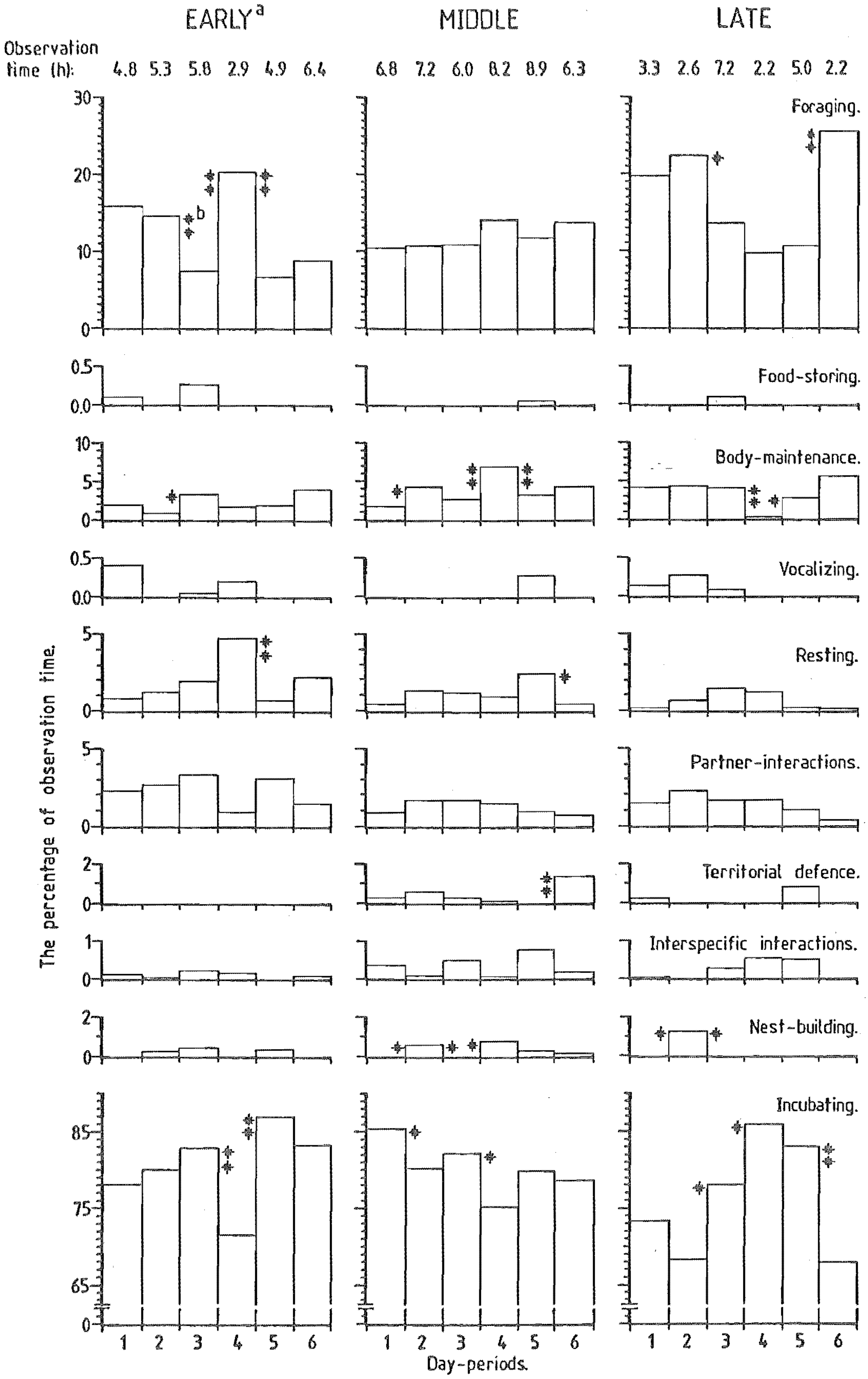
Incubating females spent a similar time during the course of the day in body-maintenance. Exceptions to this trend occurred in the early afternoon for the middle and late portions of the breeding season (Fig. 16.6).

Figure 16.6. The diurnal patterns of behaviours during three portions of the breeding season for incubating females.

Appendix 28 provides the plotted values.

[a] Early - August and September, Middle - October and November, Late - December.

[b] The asterisks indicate significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the percentage of time females spent in a behaviour between two successive day-periods.


EARLY^a
MIDDLE
LATE
Observation time (h):
4.8 5.3 5.8 2.9 4.9 6.4
6.8 7.2 6.0 8.2 8.9 6.3
3.3 2.6 7.2 2.2 5.0 2.2
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
Nest-building.
Incubating.
b
30
20
10
0
0.5
0.0
10
5
0
0.5
0.0
5
0
5
0
2
0
1
0
2
0
85
75
65
0
The percentage of observation time.
1 2 3 4 5 6
1 2 3 4 5 6
1 2 3 4 5 6
Day-periods.

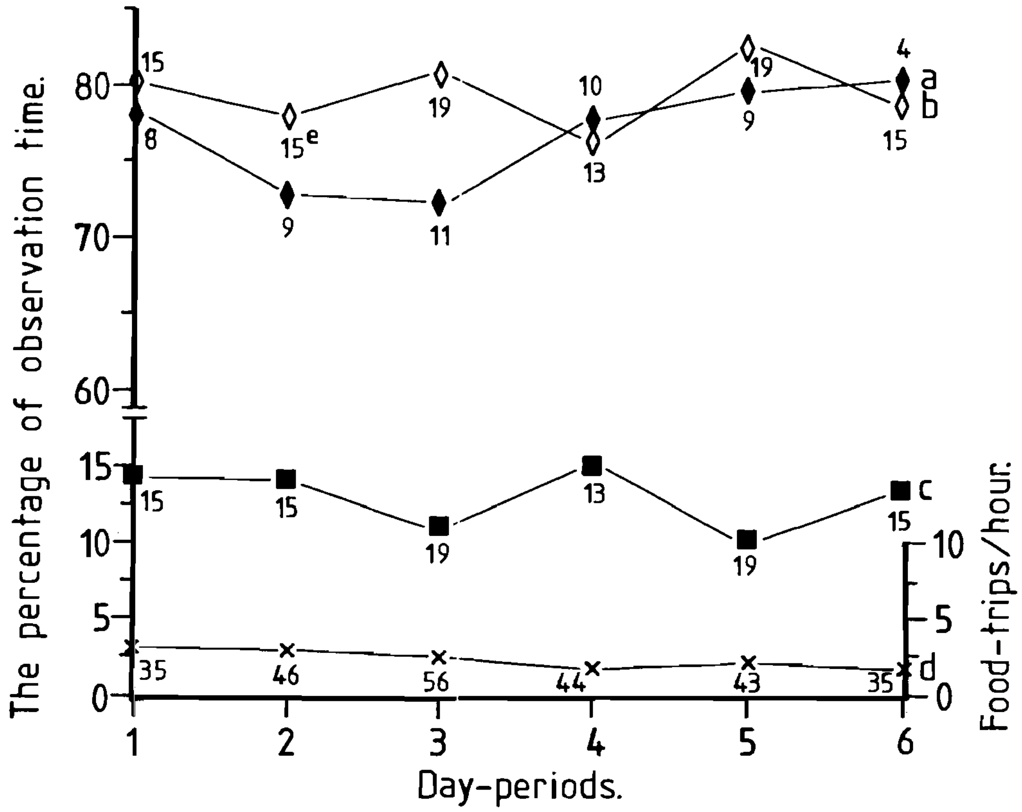


Figure 16.7 The diurnal patterns of foraging (◆—◆) and food-trips (×—×) of males, and foraging (■—■) and incubation (◊—◊) of females during the incubation stage.

a - the percentage of time males foraged.
b - the percentage of time females incubated.
c - the percentage of time females foraged.
d - the mean number of food-trips per hour males made to their partners.
e - the number of hours of observation time per day-period.

(d) Vocalizing

There was no significant change in time females vocalized from one day-period to the next for any portion of the breeding season.

(e) Resting

Incubating females rested mainly about midday and least in the early morning and late afternoon.

(f) Partner interactions

Although the time females interacted with their mates did not change significantly from one day-period to the next, they tended to spend more time in this behaviour during the mid- to late morning, and least just before sunset.

(g) Territorial defence

Incubating females did not engage in territorial defence in the early portion of the breeding season. In the other portions they spent more time in such disputes in the afternoon than the morning.

(h) Interspecific interactions

The time females spent in interspecific interactions was similar for each day-period.

(i) Nest-building

Nest-building by incubating females was largely carried out in the mid- to late morning, not in the early morning.

The male's diurnal pattern for food carrying to partners differed from their diurnal pattern of foraging: the peak time of foraging was in the afternoon, but fewer food-trips per hour were made then than in the morning (Fig. 16.7). In the afternoon when females received fewer feeds per hour from their mates, overall they foraged ($P > 0.05$) and incubated ($P > 0.05$) for a similar time as in the morning.

16.4. Discussion

16.4.1. The monthly and total time-budgets

(a) Foraging

The increased foraging of males during the incubation stage over that for the laying stage was related mainly to the more frequent food-trips made to incubating partners than to laying ones. A similar situation was found to exist in Yellow-billed Magpies (Verbeek 1972). In contrast, male Eastern Bluebirds, that did not feed their incubating partners, foraged less during the incubation stage than previously (Pinkowski 1979). However, this positive correlation between the time spent in foraging and the rate of food-trips does not explain why male Robins foraged longer per day each month as the breeding season progressed (Appendix 26) because over this period they gradually decreased the rate that they fed their incubating partners (Fig. 16.2A). I expected males to forage less later in the season since the rising mean monthly temperatures (Table 2.1, p. 13) and shortening nights (Table 3.1, p. 20) should have resulted in lower self-maintenance costs. Some evidence indicates that rearing a brood affects the parent's bodily reserves and even their survival. Body weights and fats or protein reserves of both males and females in some passerines decreased while they reared young (Fogden 1972, Morton and Welton 1973, Payne 1974, Ward 1969). Hussell (1972) found weights of female buntings rearing large broods were less than those rearing small broods. Thus, it is possible that the increased daily feeding time enabled males to accumulate bodily reserves in preparation for the high demands of feeding a brood or to replace energy reserves used up feeding a previous brood.

There are two main reasons why incubating females foraged much less than did either sex during the other stages of the breeding cycle. Firstly, the frequent food-trips by the male would presumably have met a considerable proportion of the female's food requirements. Secondly, the reduced activity of incubating birds compared with that of non-incubating birds would probably have contributed to the former having a lower energy demand and consequently a lower food intake than non-incubating Robins. Other than the process of finding food, incubating Robins would probably have spent most energy re-warming their eggs after an inattentive period (King 1973). Mertens (1977) estimated that the metabolic rate of an incubating Great Tit at night, averaged over the whole incubation period, was about 1.5 times the basal metabolic rate compared with 2.5 times for non-incubating birds. The only extra energy needed to be expended during incubation would be in rewarming the eggs after inattentive periods (King 1973). However, Walsberg and King (1978), working with Mountain White-crowned Sparrows *Zonotrichia leucophrys*, estimated that the energy required to re-warm eggs and for the resting metabolism of incubating sparrows was still lower than that of non-incubating birds exposed to the same microclimate. Another factor which reduces the need for an energy input by an incubating bird is that the developing embryos provide warmth (King 1973, Mertens 1977, Walsberg and King 1978). It has been demonstrated for the avian egg that heat production was positively correlated with the day of incubation (Needham 1931) and the weight of the developing embryo (Drent 1975). At an incubation temperature of 38°C heat production from the Herring Gull's *Larus argentatus* egg exceeded heat loss after day 13 and by day 27 a gradient of +2.69°C was evident (Drent 1975). Thus, embryonic heat production facilitated heating and retarded cooling. King (1973) considered that because of the heat generated by the embryos the major functions of the incubating parent during the late stages of incubation was to re-warm the eggs, to supply insulation, to protect the eggs from lethal heating, and to protect them from predators.

That incubating passerines require less food than do non-incubating birds is supported by the findings considered above and those of Pinkowski (1979). He noted that incubating female Eastern Bluebirds, that did not receive food from their mates, spent 28% of time foraging compared with 42% spent by their mates. This indicates that if female bluebirds did incur additional energetic expenses during incubation these were not compensated for by an immediate increase in foraging time. Therefore, it seems likely that incubating female Robins foraged for only 13% of their time because (a) their energy requirements were lower than those of non-incubating Robins, (b) they received much food from their partners, (c) they spent little time in energetically-expensive activities, and (d), towards the end of incubation, some egg warmth would have been supplied by the embryos.

Incubating females spent more time foraging in November and December than previously (Fig. 16.1), because their partners were feeding juveniles and as a result these females received fewer feedings than did those whose partners were not caring for juveniles (Fig. 16.2). Thus, females whose mates were feeding former broods spent more time foraging for themselves and to do so had to reduce the time spent incubating. Increasing ambient temperatures late in the breeding season probably allow females which are not being adequately fed by their partners more time off the nest without serious egg cooling. However, this does not seem to be the main reason for their decreased attentiveness because, had the temperature been the major cause, I would have expected the females to spend more time resting and preening rather than foraging. In addition, that females spent so little time storing food suggests that they had only enough time while inattentive to meet their immediate food requirements. The few occasions when a female was seen storing food were when her mate made several food-trips to her in quick succession so that she became satiated and had an excess to store.

(b) Body-maintenance and resting

Body-maintenance and resting were shown to be of low priority for Robins outside the breeding season; increased foraging was correlated with a decrease in resting and body-maintenance (Chapters 9-11). The same relationship occurred in the incubation stage. During this stage males foraged significantly more than previously and the behaviours of females were confined mainly to self-maintenance foraging and incubation. Both sexes rested and preened significantly less than during the laying stage. When males foraged significantly less in October and December than in previous months ($P < 0.01$), the only change in behaviour was an increase in body-maintenance activities. Similarly, both sexes of Yellow-billed Magpies spent less time resting and preening once the female began incubating (Verbeek 1972). Incubating female Robins were noted as spending less time in body-maintenance than their partners, but this may not be a true reflection since the former often preened while incubating and in the recording of field data the activity was simply recorded as incubation.

The proportion of time males rested each month remained fairly similar, perhaps as the large proportion of time spent on foraging necessitated their spending at least some time resting to recuperate. As the season progressed incubating females gradually spent less time resting because they had to do more food collecting for themselves, having received food less frequently from their partners. Bent (1964) postulated a similar response in that when environmental conditions required incubating birds to forage more and to maintain their degree of attentiveness, the reserve of inattentive time spent doing non-foraging activities had to decrease. However, the proportion of time incubating females were recorded as resting is probably not a true indication of how much they rested. It has been shown for some species, such as the Willow Ptarmigan *Lagopus lagopus*, and Mountain White-crowned Sparrow, that during incubation metabolism did not increase over the resting level of non-incubating birds (West 1968, Walsberg and King 1978). Therefore, much of the time female Robins incubated may have been similar energetically to resting.

(c) Vocalizing

The need for males to forage more during the incubation stage probably was a factor contributing to their singing less than during the laying stage. This suggestion is supported by the results for August to November, but in December when the proportion of time spent foraging decreased ($P < 0.01$), vocalizing time also decreased. At this time instead of singing the males sun-bathed and preened, as they did when involved in the prelaying and laying stages in December (Fig. 15.1, p. 280, and 15.2, p. 284). It would have been expected that since males spent more time in defence of their territories against immature birds as the season progressed proportionately more time would have also been spent on singing late in the season to warn off these intruders. Perhaps adult males sang less in December than previously because the secretion of hormones controlling singing had begun to decline with the regression of their testes and interstitial cells at the onset of the moult (Lofts and Murton 1973). As applied during the laying stage, incubating females spent very little time vocalizing, giving infrequent and short duration "chuck" calls only.

(d) Partner-interactions

The proportion of time males interacted with their incubating partners each month largely reflected the rate at which males made trips with food to them. A female sometimes remained on the nest until her mate had flown within 10 metres of her even though he had begun calling her to be fed long before. As a result males spent more time in interactions with their mates, than the expected result of both sexes spending a similar time in this behaviour. After September, females spent less time in partner-interactions than previously ($P < 0.01$), because by

October some females were incubating their second clutches after their first broods had fledged. Such females, whose mates were feeding the pair's progeny from the previous nesting, received food less frequently from their mates (about 1.0 times/h) than did females incubating their first clutches (about 3.2 times/h) or those whose previous nesting attempts had been unsuccessful (about 2.6 times/h) (Fig. 16.2A).

Even though food-trips by males were more frequent during the incubation stage (2.9 times/h) than the laying stage (2.5 times/h), males spent a similar time in interactions with their mates for both stages. This resulted because laying females were not always near as their mates carried food towards their nests. Such females did not respond to their calling mates so quickly as did those incubating.

(e) Territorial defence

Incubating females did not engage in territorial disputes until October because most interactions between conspecifics before this month involved neighbouring males displaying at their common boundaries. Even when an intruder came near an incubating female, the latter usually crouched low instead of chasing the intruder away. By October both sexes spent more time defending their territories against intruding Robins because nestlings reared from the first nesting cycle, now independent of their parents, often intruded into the territories of breeding pairs. Furthermore, some pairs had by then hatched a second brood and so were evicting the juveniles from their previous nesting, behaviour I recorded as territorial defence.

(f) Interspecific interactions

Male Robins spent a similar time interacting with other avian species and mammals during the laying and incubating stages because male Robins displayed their frontal spots to and chased other species just as often whether their mates were incubating or laying. However, incubating females spent less time in such interactions than when laying. When incubating, a female did not leave her nest to chase an approaching bird until it came quite close. Also, incubating females crouched low into their nests or gave frontal-spot displays when approached by other birds. These activities did not involve Robins leaving their nests and so the females were recorded as incubating during such interactions. By comparison, laying females usually stayed near their nests and chased most other birds away when intruders were still several metres from a Robin nest.

(g) Nest-building

Skutch (1962) found that species of the genera *Synallaxis, Platypsaris, Pachyramphus* and *Psaltriparus* added material to their nests after incubation had begun. Female Robins were observed doing the same, but overall very little time was devoted to this behaviour, except during the first and last two days of incubation and after heavy rain. All material was added to the lining of nests and this often included down feathers found when foraging or that came loose as they preened.

(h) Incubating

Information about the attentiveness for other populations of South Island Robins and the other subspecies are not available for comparison with that determined in this study. However, Kearton (1979) found that female Yellow-breasted Tits, another member of the genus *Petroica*, that did all the incubating and were fed at intervals by their mates, spent 72.7% of 8.6 hours of observation time on their eggs. By comparison, female Robins, whose mates were not feeding juveniles, were attentive for 82.9% of time (Fig. 16.2C). Male tits fed their incubating partners about twice each hour. This rate of food-trips was lower than that of nearly three times per hour for male Robins and may be a reason for the female tit's lower attentiveness compared with the Robins.

Females spent a slightly lower proportion of time incubating in December than previously (Fig. 16.1), but considering the influence of male food-trips and ambient temperatures on attentiveness, I expected the females to have a gradually declining attentiveness earlier in the breeding season. This arose partly because the behaviour of females whose mates were feeding juveniles formed a small proportion of the sample in Figure 16.1.

As for the Robin, in studies of other species it has also been found that female's attentiveness during incubation was influenced by the rate of food provision by the male to his partner (see Kendeigh (1952) and Skutch (1962)). Female Pied Flycatchers *Ficedula hypoleuca*, which normally receive about half their food from their mates (Curio *in* Royama 1966b), spent much longer off the nest feeding themselves and even then lost weight when neglected by their partners (von Haartman *in* Royama 1966b).

The decrease in attentiveness as the ambient temperature increased has also been reported in several other studies: for example, the Zebra Finch *Taeniopygia guttata* (Burley 1968), Goldcrest (Haftorn 1978), Village Weaverbird *Ploceus cucullatus* (White and Kinney 1974), and Dead Sea Sparrow *Passer moabilicus* (Yom-Tov *et al.* 1978). At Kowhai Bush the temperature recorded in direct sunlight on hot days often exceeded 36°C (Section 7.4.3, p. 102). Under these conditions incubating females were more attentive than on rainy days standing over their eggs and shaded them with out-spread wings. The same response has been reported in Yellow-headed Blackbirds (Fautin 1941) and Village Weaverbirds (White and Kinney 1974). This protection is related to the fact that avian embryos tolerate overheating less well than cooling (Yom-Tov *et al.* 1978).

Like female Robins, females of several other species have been found to reach their full attentiveness the day the last egg was laid: for example, the House Wren (Kendeigh 1952), American Goldfinch *Spinus tristis*, American Robin and Yellow Warbler *Dendroica petechia* (Skutch 1962). This pattern is not universal because some other passerines gradually increase their attentiveness over the first three days of incubation. If heat production of the Robin egg is positively correlated with the weight of the developing embryo, as has been demonstrated in the Herring Gull egg (Drent 1975), it would explain why attentiveness was highest during the first few days of incubation and lowest just before hatching. As a result of the increasing heat production by the embryo, the release temperature (the temperature at which the eggs were maintained) would be reached progressively faster as embryonic development proceeded. Also, if the eggs cooled slower as the embryos developed this would enable females to spend longer off their nests late in the incubation stage than is possible earlier. Because attentiveness declined as the ambient temperature increased and the ambient temperature increased during the course of the breeding season (Table 2.1, p. 13), it is therefore possible that this factor also contributed to the gradual decrease in attentiveness as incubation progressed. I do not know why females incubated more during days 10-12 of the incubation stage than in the previous three-day period ($P < 0.05$). Attentiveness may have been influenced by other conditions prevailing at the time the data was recorded and not directly to the day of the incubation stage.

Which factors, if any, influenced the time females spent incubating? It was found that a lower rate of male food-trips, increased ambient temperatures and, in general, as the incubation stage proceeded female Robins incubated less. Extremes of weather, such as intense sunlight shining directly on to the nest and heavy rainfall, led to very high attentiveness.

16.4.2. The diurnal patterns of behaviours

(a) Foraging

Generally, both sexes foraged more early than later in the morning, probably to replace energy reserves depleted at night and to provide energy for the day's activities. In the early morning males stored more food than at any other time of the day. This would tend to indicate that food was readily available or that they were able to capture more than their immediate needs. In addition, the large proportion of time males foraged in the early morning was positively correlated with their more frequent trips with food to their partners then than later in the day. In view of the fact that during the early morning females were fed more frequently by the male than at any other time of the day and that they foraged for themselves more then than later in the morning and seldom stored food early in the morning suggests that the female had little energy after the night. In the middle of the breeding season females received less food from their partners than previously. This suggests that the milder night-time temperatures and shorter nights were less of a drain on their energy reserves then than earlier in the season.

The peak foraging activity of males took place in the early and late afternoon, at a time when the rate of food-trips to their mates was low. Thus, the foraging of males in the afternoon contributed more to their self-maintenance than foraging in the morning. Since incubating females also foraged more and stored little food in the early and late afternoon, they probably did so to make up for the slightly lower rate of food-trips by their mates then and to accumulate bodily food reserves to sustain them through the night. In the late portion of the breeding season the afternoon peak of foraging activity of both sexes occurred later than during the previous portions of the season. Possibly this was because the warmer temperatures, shorter nights and (likely) greater prey availability allowed them to postpone "stocking-up" with food until later in the afternoon.

(b) Body-maintenance and resting

The negative correlation between the time males foraged and spent on resting and body-maintenance activities arose because the latter behaviours were given lower priority than foraging; males rested and preened most when less time was required for foraging. This diurnal pattern of preening and resting was not so evident with incubating females presumably because most of their inattentive time was required for foraging, with much preening and resting being carried out while the birds were incubating.

(c) Vocalizing

Males did most of their singing in the morning because that was the best time to do so (Section 6.5.1, p. 76). The vocalizations of incubating females were mainly "chucks" given to attract their mates. These calls were given most frequently in the morning when females were foraging, presumably to entice their partners to bring them food. In support of this explanation, females during the middle portion of the breeding season did not have an early morning peak of foraging activity, nor did they give "chuck" calls then.

(d) Partner-interactions

Like male Robins, male Great Tits took food to their incubating partners most frequently in the early morning (Hinde 1952, Kluyver 1950, Royama 1966b). The diurnal pattern of time male Robins interacted with their partners reflected the males' rate of food-trips and how quickly females reached them to accept the food. In the early morning males made food-trips most frequently and females responded quickly to their partners' phrases of song and left their nests to be fed. During the afternoon, males spent a similar proportion of time in partner-interactions as in the morning, because although males made fewer food-trips per hour females reacted more slowly to their mates' phrases of song when approaching with food. I am unsure why males spent gradually less time interacting with their mates during the course of the day in the late portion. Perhaps it reflects the male's lower frequency of food-trips in December.

(e) Intraspecific and interspecific interactions

Both sexes tended to defend their territories against intruding Robins less in the morning because males sang more then which probably helped to warn off intruders. In the afternoon, when males sang very little, immatures were unable to recognise the territorial boundaries of breeding pairs. This resulted in adults having to spend time chasing immature intruders from their territories. This was not as common an event in the morning. Robins involved in the incubation stage spent a similar time throughout the day interacting with other species, presumably because the frequency and duration of such interactions did not change from one day-period to the next.

(f) Nest-building

Nest-building by incubating Robins tended to take place after the early morning and before the late afternoon, as Skutch (1962) found for several other incubating passerines. He considered they gathered material mainly about midday because the eggs could be left longer then when ambient temperatures were highest. Little nest-building was carried out in the early morning and late afternoon because at these times incubating Robins had to forage for most of the time they were inattentive.

(g) Incubating

The attentiveness of female Robins was influenced by the ambient temperature, day of incubation, rainfall, and the rate of food-trips by their mates. Therefore, the diurnal pattern of attentiveness would be expected to be related to more than one factor. Considering the influence of ambient temperature, attentiveness should have been highest in the early morning and late afternoon when temperatures were lowest (Fig. 7.3, p. 98). However, only in the early morning of the middle portion was attentiveness higher than at midday. Similarly, Haftorn (1978) found a lack of correlation between attentiveness of female Goldcrests and temperature during the last few hours of the day. Because female Robins spent much time foraging when they were inattentive in the early morning and late afternoon, presumably they spent so much time off their nests to find enough food even though temperatures were low then. The females were most attentive about midday late in the breeding season when they were expected to be least attentive while temperatures were high. This high attentiveness may have been caused by my sample including a few nests exposed to direct sunlight whose birds shaded their eggs to prevent over-heating.

The female's diurnal pattern of attentiveness was partly related to the pattern of their partner's food-trips. Males brought food to incubating females least frequently in the early and late afternoon, times when females were least attentive. However, the changes in attentiveness were not as great as expected considering the much lower rates of male food-trips in the afternoon than in the morning. High afternoon temperatures may have led to the females having lower energy requirements then than in the morning and therefore having to forage less. Also, the warmer afternoon temperatures would have increased invertebrate activity and made them more available to Robins, thus decreasing the time taken to find the same amount of food in the afternoon than in the morning.

16.5. Summary

16.5.1. The monthly and total time-budgets

Males foraged more in the incubation stage (78.5%) than during the laying stage (74.0%) probably because they made more frequent food-trips to their partners in the former. It seems likely that incubating females foraged for only 13% of their time because (a) their energy requirements were lower than those of non-incubating Robins (Mertens 1977, Walsberg and King 1978), (b) they received much food from their partners, (c) spent little time in energetically-expensive activities and (d), towards the end of incubation, some of the heat required to keep the eggs warm would have been supplied by the embryos. The proportion of time males foraged decreased each month during the course of the breeding season. In contrast, females foraged for a slightly greater proportion of time from month to month mainly because the rate of food-trips they received from their mates decreased over the same period.

Males spent less time in body-maintenance during the incubation stage than in the laying one ($P < 0.01$). Significant increases in the monthly proportion of time males devoted to body-maintenance were correlated with significant decreases in foraging. They rested for a similar time per month during the course of the breeding season. Incubating females preened and rested less than did their partners ($P < 0.01$). However, females preened and rested more than was recorded because any time they spent in these behaviours while attentive was clocked as incubating time.

Most of the time pair-members interacted with each other involved the male feeding his partner. Males spent more time interacting with their incubating mates ($P < 0.01$) rather than both sexes spending a similar time in this behaviour. This apparent anomaly arose because when a male sang phrases of song to attract his mate to be fed and flew towards her, partner-interaction behaviour, females often continued incubating until the male was within a few metres of the nest before leaving to accept the food he brought. Both sexes spent less time interacting with each other after October than formerly because by this time many pairs had juveniles which the males fed while the females incubated the next clutch. Such females received fewer food-trips from their mates (1.1 times/h) than did those whose mates were not tending for juveniles (2.9 times/h).

Females incubated for about 80% of time each month. Those whose partners were feeding juveniles incubated less than did those whose partners were not so engaged ($P < 0.01$) owing to the slower rate of male food-trips to females in the former situation. Similarly, the two females whose partners died during the incubation stage were less attentive than those with partners. Each 10°C rise in ambient temperature within the range of 1.0 to 20.9°C was accompanied by a significant decrease in time females incubated. However, above 21.0°C and especially when intense sunlight shone on the nest or heavy rain fell female attentiveness increased. In general, females were most attentive at the start of the incubation stage and least towards the end.

16.5.2. The diurnal patterns of behaviours

Males either had two or three peaks of foraging activity in the day when involved in the incubation stage, whereas incubating females had one or two. For both sexes the major peak usually occurred in the late morning or early afternoon.

For males during the first two portions of the breeding season and females throughout the season no diurnal pattern of interacting with their partners was evident, but in the late portion males spent gradually less time during the course of the day in this behaviour.

The diurnal pattern of incubating by females was inversely related to that for foraging; a significant increase in foraging was correlated with a significant decrease in incubating in the same day-period. Also, when females received fewer food-trips per hour from their mates for a day-period, they incubated less and foraged more.

CHAPTER SEVENTEEN

THE TIME-BUDGETS FOR ROBINS REARING NESTLINGS

17.1. Introduction

Much has been written concerning the influence of parental behaviour on the growth and survival of nidicolous nestlings, such as how feeding rates vary with nestling age, brood size, size of prey items and the timing of the breeding season (Balen 1973, Finlay 1971, Gibb 1950, 1955, Gibb and Betts 1963, Kendeigh 1952, Kirkham and Morris 1979, Klomp 1970, Kluijver 1950, Moreau 1947, Royama 1966b). Although time-budgets for birds rearing nestlings are available for a few passerines (Pinkowski 1979, Post 1974, Verbeek 1972, Verner 1965), little has been published, to my knowledge, about how these budgets differ for male and female parents. A description and statistical comparison of the time-budgets for such Robins is given here. In addition, the influence of brood size, nestling age and time of day on the time-budgets is described.

From the analyses and comparisons of the time-budgets I hoped to answer questions like the following:

1. Did the time-budgets for both sexes differ between the incubation and nestling-rearing stages?

2. Did an increase in nestling age result in parent Robins spending more time feeding their broods and cleaning the nests?

3. Did adults spend less time in resting and body-maintenance when more time was used to forage and care for progeny?

4. Were adults more protective of their nestlings than they were of eggs when other species came near Robin nests?

5. Was the time females spent brooding related to their nestlings' age and the number of nestlings present?

6. Did the rate of food-trips (parental effort) vary according to the brood size and the nestlings' age?

Generally, the hatching of a Robin clutch took from a few hours to a day. Both parents fed the nestlings and removed faecal sacs, but only the female brooded. At nine to ten days the nestling's eyes opened and when 13 days old they were within the adult weight range (Flack 1979). From hatching to fledging, the rearing of nestlings took about 21 days (pers. obs., Flack 1979).

17.2. Methods

Three behaviours of Robins rearing nestlings not previously described in this thesis are brooding (Brd), feeding progeny (Fp) and nest sanitation (Ns). Females were timed as "brooding" when sitting over their nestlings whether the former remained still or preened. "Feeding progeny" involved the time a parent spent flying directly to the nest with food and offering it to the nestlings. It could be readily determined whether a parent was carrying food to its young or was continuing to forage with prey in its beak by making flights between perches (scanning) (Section 4.2, p. 27). The removal of faecal sacs and a probing action into the nest cup was defined as "nest sanitation". As well as the time taken to grasp a faecal sac as it was voided and to take it away from the vicinity of the nest, nest-sanitation time included that spent by a parent waiting for a nestling to defecate. Allard's (1940) description of a parent Starling "standing astride the nestlings or among them and jabbing its beak" into the nest cup aptly describes the action of female Robins. This was such a vigorous activity that nests in vines or among thin branches shook as the female probed into the nest. Nest probing was usually carried out just before the female began to brood.

The day the first nestling hatched was designated as day 1. In almost all cases, all eggs of a clutch hatched the same day. Since both parents could not be watched simultaneously, to determine their rate of food-trips to a brood observations were made while seated about seven metres from the nest. During such watches, the number of food-trips made and faecal sacs removed by each parent was scored, and the percentage of time the nestlings were brooded was recorded. Sometimes when the female was brooding or if the nestlings did not gape when offered food by the male, he gave it to the female who then fed it to the nestlings. Such food transfers were recorded as male food-trips.

Instead of providing monthly time-budgets as in previous chapters, the time-budgets for Robins rearing nestlings are given according to the brood size and age of the nestlings the adults were rearing. The nestlings were divided into four age-classes; 1-5, 6-10, 11-15, and greater than 15 days old. The data for these time-budgets were amalgamated to give "total" time-budgets.

The results and discussion sections are divided into two sub-sections: (1) the time-budgets, and (2) the diurnal patterns of behaviours. Each of these sub-sections are further divided so that the data for each behaviour are described and discussed separately and in the sequence as shown on the figures.

17.3. Results

17.3.1. The time-budgets for males

Figure 17.1 and Appendix 29 give the time-budgets of males rearing nestlings for each of four age-classes of one brood size, there being three brood sizes.

(a) Foraging

The proportion of time males foraged did not change significantly as the nestlings aged for each brood size, except for the increase from the first (1-5 days) to the second (6-10 days) age-class for males feeding three nestlings. Overall, males foraged for 83.3% of time when rearing nestlings, more than the 78.4% of time they spent in foraging during the incubation stage ($P < 0.01$).

(b) Food-storing

Males stored food mainly when their nestlings were less than six days old. In total, they spent only 0.1% of time storing food, which was significantly less than the 0.4% of time they devoted to this behaviour during the incubation stage ($P < 0.05$).

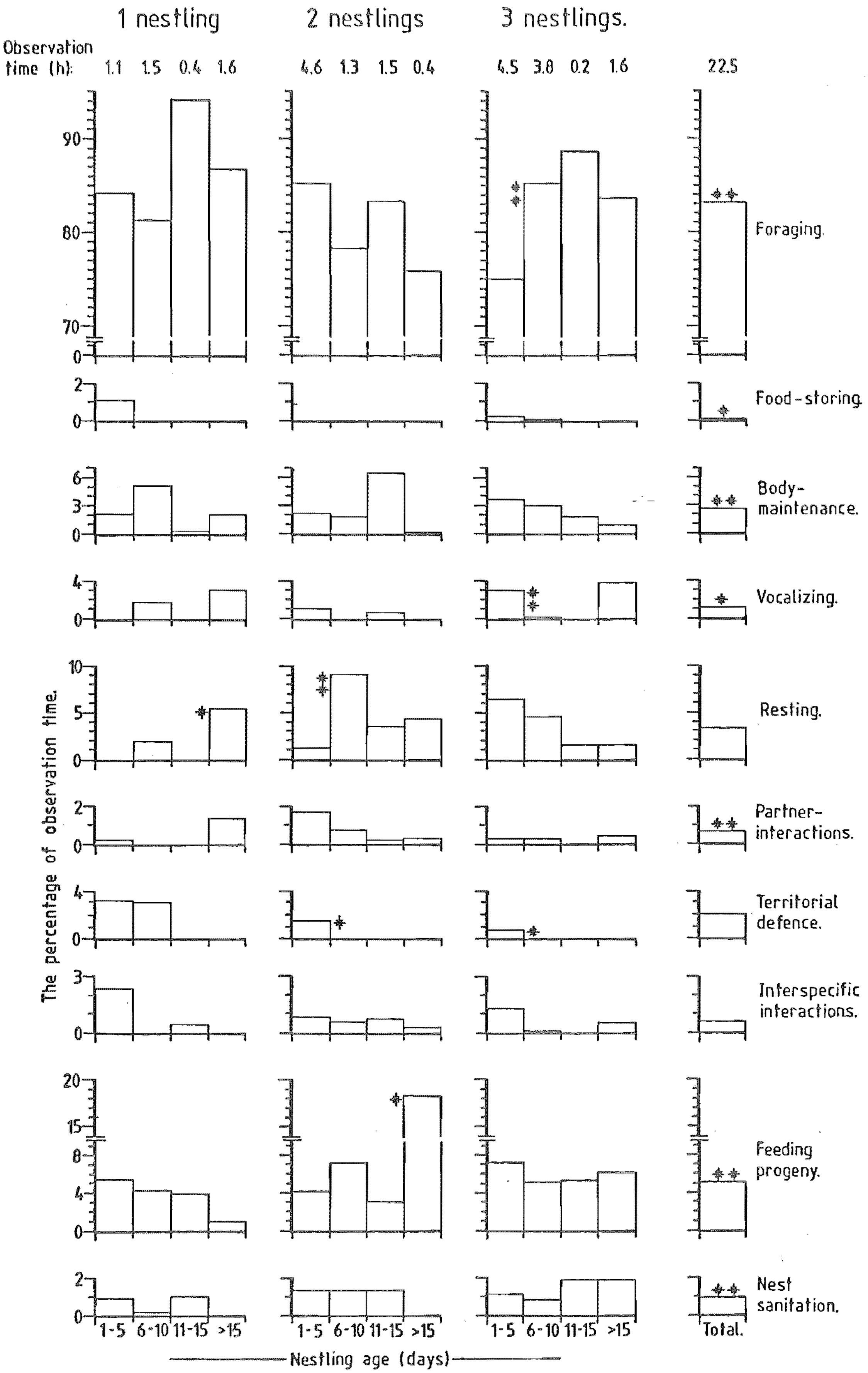
(c) Body-maintenance

For a particular brood size, males spent a similar time in body-maintenance as the nestlings aged. From the combined data, males spent nearly three percent of their time maintaining their body surfaces, significantly less than the 7.4% of time they spent on this behaviour during the incubation stage ($P < 0.01$).

Figure 17.1. The time-budgets for male Robins rearing nestlings of various brood sizes and age-classes, and in total (data for each brood size combined).

Appendix 29 gives the plotted values.

[a]The asterisks indicate significance levels: * = $P < 0.05$, ** = $P < 0.01$. Those placed next to the sides of columns denote significant differences between the adjacent age-class samples. Asterisks above the total time-budget columns show those behaviours on which males involved in the incubation stage (Fig. 16.1, p. 317) and those rearing nestlings spent significantly different proportions of time.


1 nestling
2 nestlings
3 nestlings.
Observation time (h):
1.1 1.5 0.4 1.6
4.6 1.3 1.5 0.4
4.5 3.8 0.2 1.6
22.5
90
80
70
0
Foraging.
2
Food-storing.
6
3
Body-maintenance.
4
Vocalizing.
10
5
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
20
15
8
Feeding progeny.
Nest sanitation.
The percentage of observation time.
1-5 6-10 11-15 >15
Total.
Nestling age (days)
*
**

(d) Vocalizing

In general, males spent a similar time vocalizing as the brood they were rearing became older. Males sang less when rearing nestlings (1.4%) than when attending an incubating partner (2.2%) ($P < 0.05$).

(e) Resting

The percentage of time males rested varied according to the brood-size and age of the nestlings they were rearing. When one nestling was present, males rested significantly more once the former was older than fifteen days. When the brood comprised two nestlings, males rested most while the young were six to 10 days old. However, males feeding three nestlings spent gradually less time resting as the nestlings aged. Overall, males tending nestlings or involved in the incubation stage rested for a similar time (about 4.0%).

(f) Partner-interactions and interspecific interactions

The proportion of time males interacted with their partners did not alter significantly as the nestlings of a particular brood size aged. A similar trend is apparent for the time males spent in interspecific interactions. From the total time-budget results, it is evident that males interacted with other species for a similar proportion of time whether rearing nestlings or involved in the incubation stage, but males interacted with their partners significantly less once the nestlings hatched ($P < 0.01$).

(g) Territorial defence

Territorial disputes involving males raising nestlings took place only while the nestlings were less than 11 days old. The larger the brood size, the less time males spent in interactions with neighbouring and intruding Robins. Males rearing nestlings or attending incubating partners spent a similar proportion of time in territorial defence.

(h) Feeding progeny

The proportion of time males fed nestlings varied with the brood size and nestling age. Less time was spent feeding a one-nestling brood as the nestling got older. However, males spent a significantly larger proportion of time feeding two nestlings greater than 15 days old than when the latter were younger. Males with three-nestling broods spent a similar proportion of time feeding them whatever the nestlings' age. In total, males fed nestlings for 5.2% of time.

(i) Nest sanitation

Adults ate most of the faecal sacs voided by nestlings up to five days old. Those from older nestlings nearly always involved the parents spending about thirty seconds carrying them several metres from the nest. Generally, nestlings voided a faecal sac immediately after being fed, but when they were about 18 days old they began defecating other than just after being fed. Faecal sacs deposited on the nest rim or that fell on vegetation close to the nest were removed by the adults, but those that fell to the ground and on to ground-storey vegetation remained there.

For a particular brood size, males spent a similar proportion of time accepting and removing faecal sacs from the four age-classes of nestlings. It seems that males spent more time in nest sanitation the larger the brood size. From the combined data, nest sanitation occupied one percent of a male's time.

17.3.2. The time-budgets for females

Figure 17.2 and Appendix 30 give the time-budgets of females rearing nestlings for each of four age-classes per brood size,there being three brood sizes. The total time-budget is from the combined data for all brood sizes and nestling age-classes.

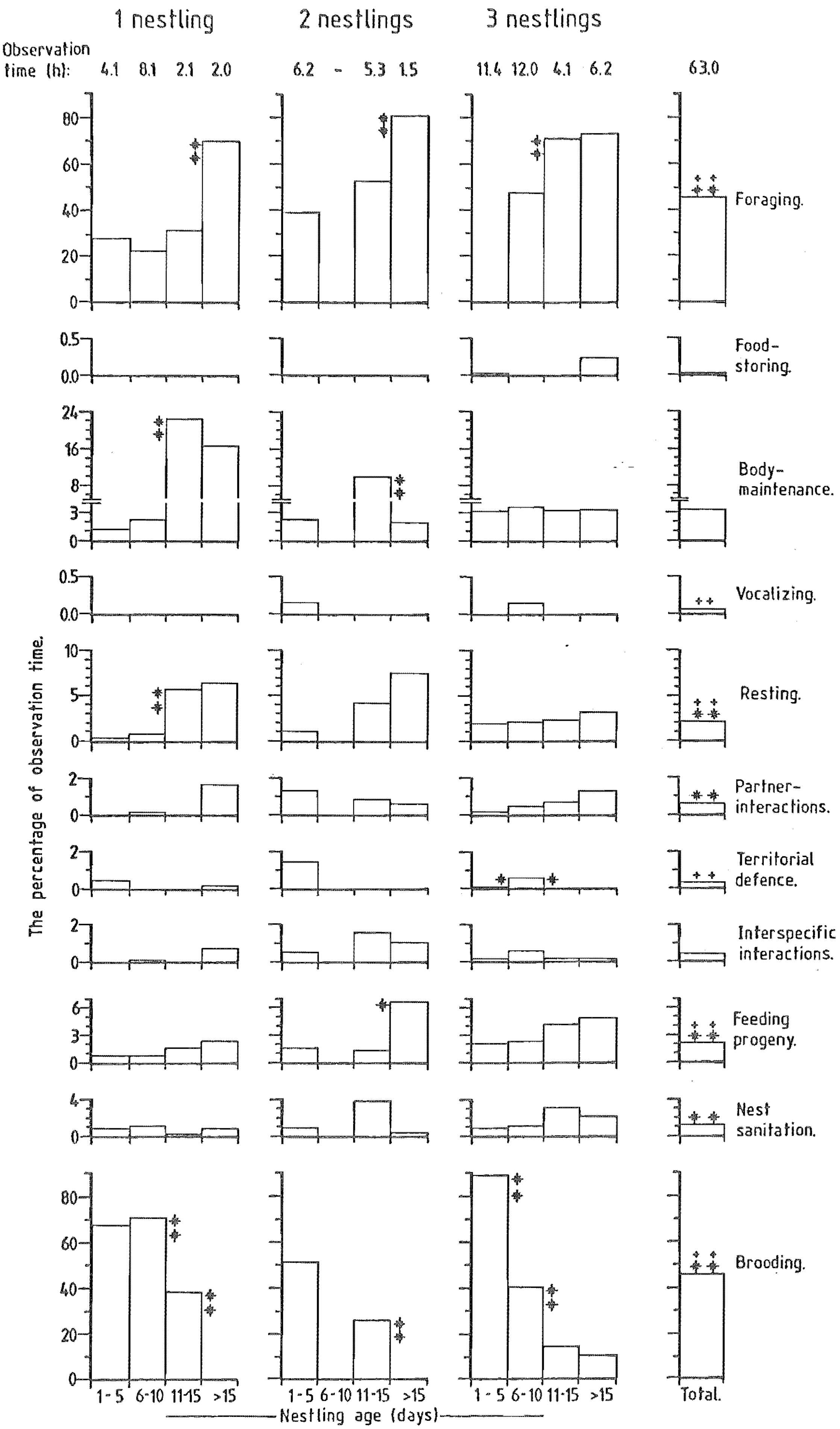
(a) Foraging

For each brood size, the proportion of time females foraged tended to increase as the nestlings aged, significantly so from the third (11-15 days) to the fourth (> 15 days) age-classes for broods of one and two nestlings. When rearing three-nestling broods, females significantly

Figure 17.2. The time-budgets for female Robins rearing nestlings of various brood sizes and age-classes, and in total (data for each brood size combined).

The plotted values are given in Appendix 30.

[a]The asterisks indicate significance levels: * = $P < 0.05$, ** = $P < 0.01$. Those placed next to the sides of columns indicate significant differences between the adjacent age-class samples. Asterisks above the total time-budget columns show in which behaviours incubating (Fig. 16.1, p. 317) and nestling-rearing females spent significantly different proportions of time. The crosses above the total columns indicate those behaviours in which females and males (Fig. 17.1) rearing nestlings spent significantly different proportions of time.


1 nestling
2 nestlings
3 nestlings
Observation time (h):
4.1 8.1 2.1 2.0
6.2 - 5.3 1.5
11.4 12.0 4.1 6.2
63.0
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
Feeding progeny.
Nest sanitation.
Brooding.
The percentage of observation time.
0
20
40
60
80
0.0
0.5
3
8
16
24
5
10
2
6
4
1-5
6-10
11-15
>15
Total.
Nestling age (days)

increased their foraging from the first to the second, and the second to the third age-classes. Overall, females foraged for 42.6% of time when raising nestlings, less than did their partners ($P < 0.01$), but more than did incubating females ($P < 0.01$).

(b) Food-storing

Females rarely stored food when caring for nestlings. Overall, they spent 0.03% of time in this behaviour, which was similar to the time males rearing nestlings spent storing food.

(c) Body-maintenance

The proportion of time females spent in body-maintenance varied with the brood size and age of the nestlings they tended. When one nestling was present, a female spent significantly more time in this behaviour once the nestling was greater than ten days old than previously. An increase in time devoted to body-maintenance by females with two nestlings was restricted to the period when the latter were 11 to 15 days old. Females tending three nestlings spent a similar proportion of time in body-maintenance whatever the nestlings' age. Comparing the budgets for females with the various brood sizes, it seems that females devoted less time to caring for their body surfaces the larger their brood. Overall, females spent 3.4% of time in body-maintenance when rearing nestlings, which was a similar proportion of time to that they spent in the behaviour when incubating, and as did males with nestlings.

(d) Vocalizing

Females feeding nestlings vocalized for less than 0.1% of time, as they had when incubating. This proportion of time was significantly less than that spent vocalizing by males rearing nestlings.

(e) Resting

Females rested mainly after their nestlings were older than 11 days of age for broods of one and two nestlings, but the data for females with three nestlings do not show this marked increase. Compared with those

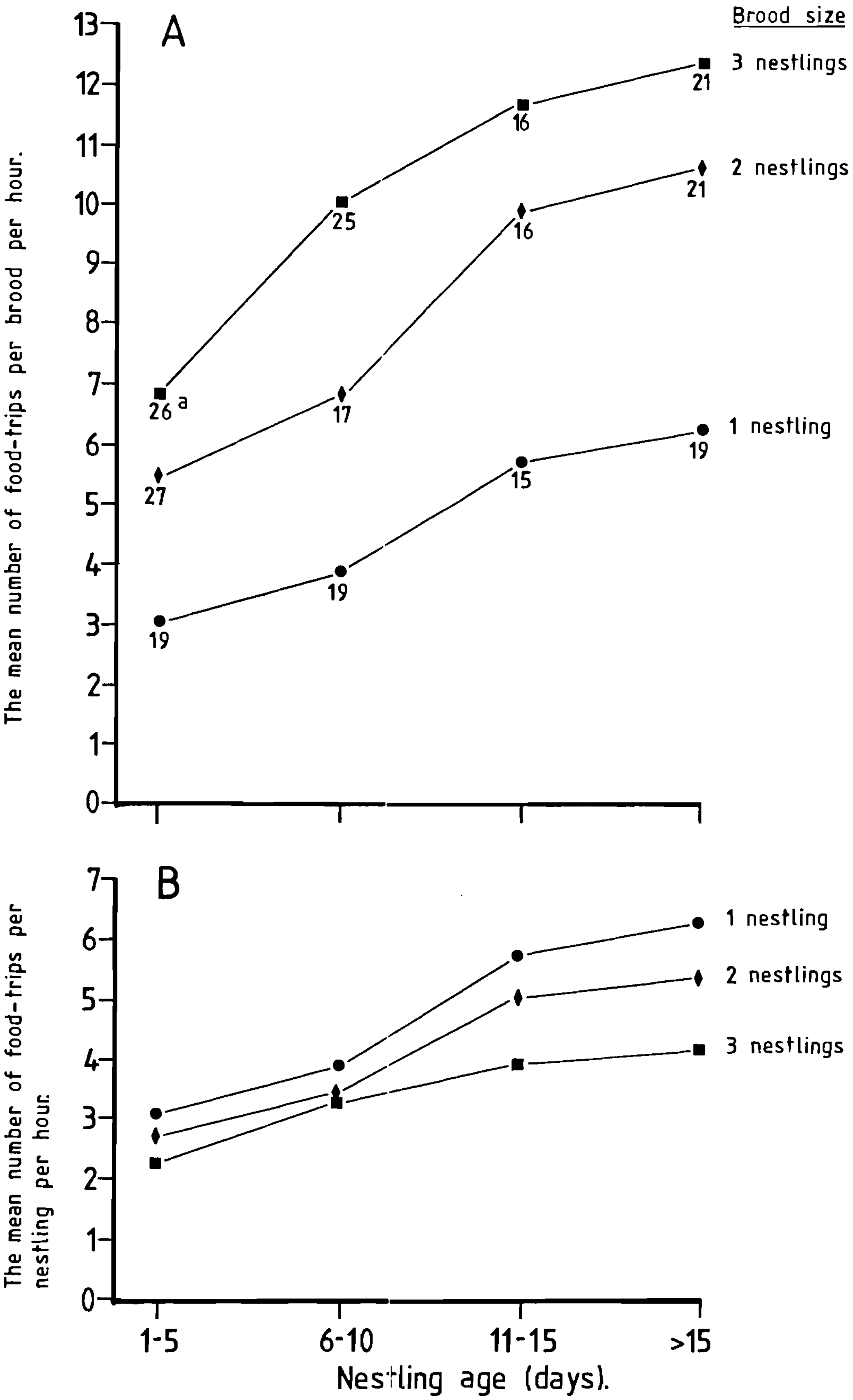


Figure 17.3 The rate of food-trips per brood (A) and per nestling (B) by parent Robins to nestlings of four age-classes.

[a] The number of hours during which nests containing the particular brood size and age-class of nestlings were observed - the same for both graphs.

incubating, females feeding nestlings rested more ($P < 0.01$), but less than did males caring for nestlings ($P < 0.01$).

(f) Partner-interactions

As for males, whatever the age of their nestlings, a similar proportion of time was spent in partner-interactions by females rearing nestlings. Overall, males and females spent a similar time interacting with each other, but females with nestlings devoted less time to such interactions compared with when incubating ($P < 0.01$).

(g) Territorial defence

Females, like males, were mainly involved in interactions with other Robins when their nestlings were less than 11 days old. In total, females spent less time in territorial disputes than did their partners.

(h) Interspecific interactions

The proportion of time females interacted with other species did not alter significantly as their nestlings aged. When rearing nestlings, females interacted with other species as much as males with nestlings and incubating females did.

(i) Feeding progeny

For a particular brood size, as the nestlings got older, females spent more time feeding them. Overall, females spent about half the time feeding nestlings compared with that for males ($P < 0.01$).

For each brood size, as the nestlings aged their parents increased the rate of food-trips *per brood* (Fig. 17.3A) and *per nestling* (Fig. 17.3B). For each age-class of nestlings, the larger the brood size the greater the rate of food-trips Robins made *per brood* (Fig. 17.3A). However, the rate of food-trips *per nestling* gradually decreased the larger the brood size (Fig. 17.3B).

The percentage of the total food-trips to the nest that involved males feeding their partners decreased as the nestlings aged and stopped

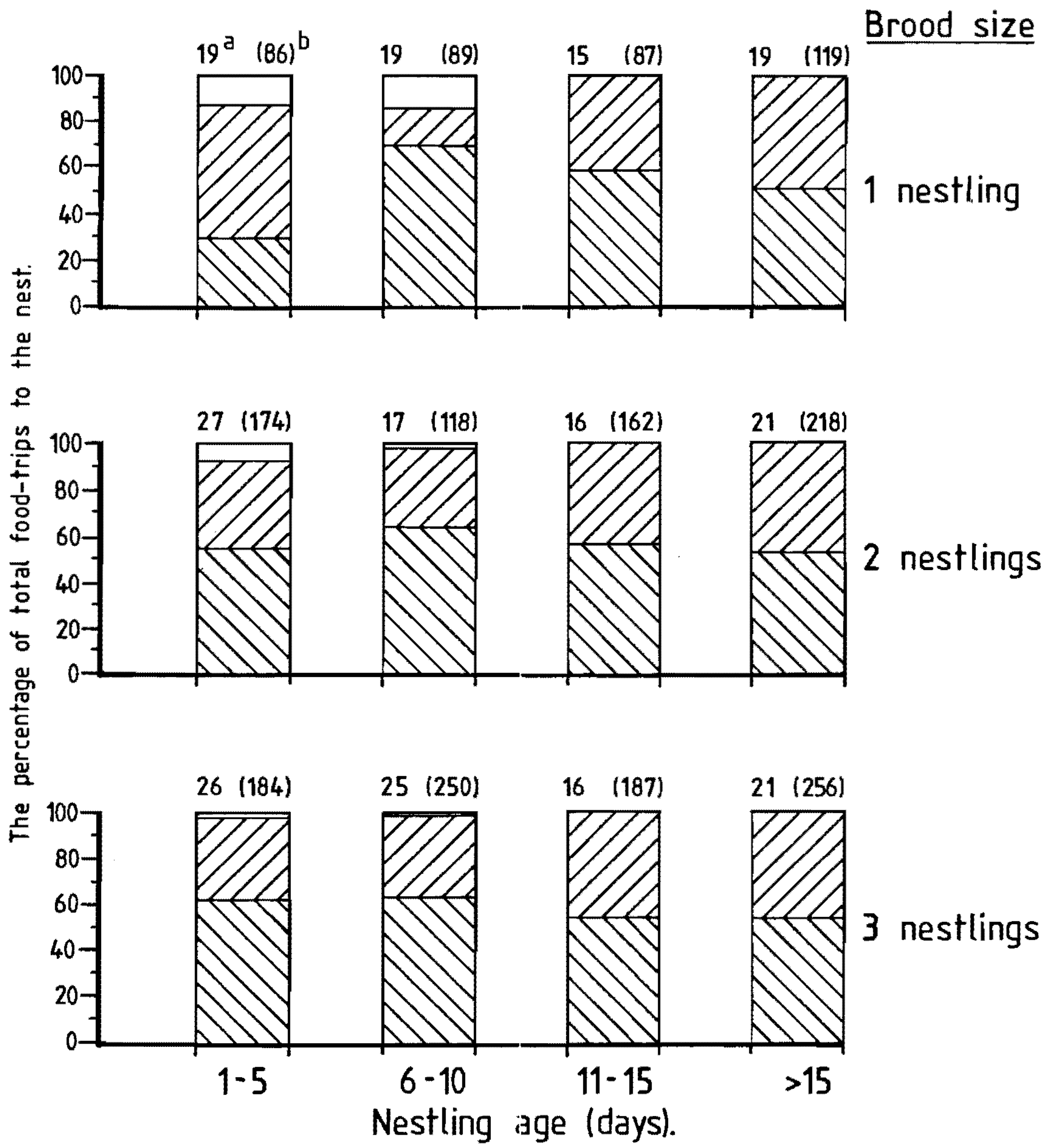


Figure 17.4 The percentage of the total food-trips to the nest by male and female Robins to nestlings, and by males to their partners with regard to brood size and nestling age.

☐ - % of food-trips by males to their partners.
▨ - % of food-trips by females to nestlings.
▧ - % of food-trips by males to nestlings.

[a] The number of hours of observation, [b] the total number of food-trips.

once the latter were more than 10 days old (Fig. 17.4). Furthermore, the smaller the brood size, the greater the percentage of food-trips to females. Whatever the size of the brood, the proportion of food-trips made by males to nestlings increased until they were 10 days old and then decreased slightly. To one- and two-nestling broods up to 15 days of age, males made significantly more food-trips than did females ($P < 0.01$), but to nestlings older than 15 days the difference was not significant. To three-nestling broods when the nestlings were less than 11 days old and greater than 15 days old, males made more food-trips than did females ($P < 0.01$). When the nestlings were 11-15 days old, male and female parent Robins made a similar proportion of the food-trips (Fig. 17.4). Of 1851 food-trips that resulted in nestlings being fed, males made 59.4% of them ($P < 0.01$).

(j) Nest sanitation

In general, the proportion of time females were engaged in nest sanitation increased slightly as their nestlings grew older. Likewise, the number of faecal sacs removed per hour by parent Robins per nestling increased with nestling age (Table 17.1).

Table 17.1. The rate of faecal sac removal (number/nestling/hour) by parent Robins from nestlings of four age-classes.

Nestling age-classes (days)	Faecal-sac removal rate	Hours of observation
1st (1-5)	0.1	40
2nd (6-10)	0.9	38
3rd (11-15)	1.2	28
4th (> 15)	1.5	36

Of note is the marked increase in faecal sac removal from the second age-class of nestlings over that from the first age-class.

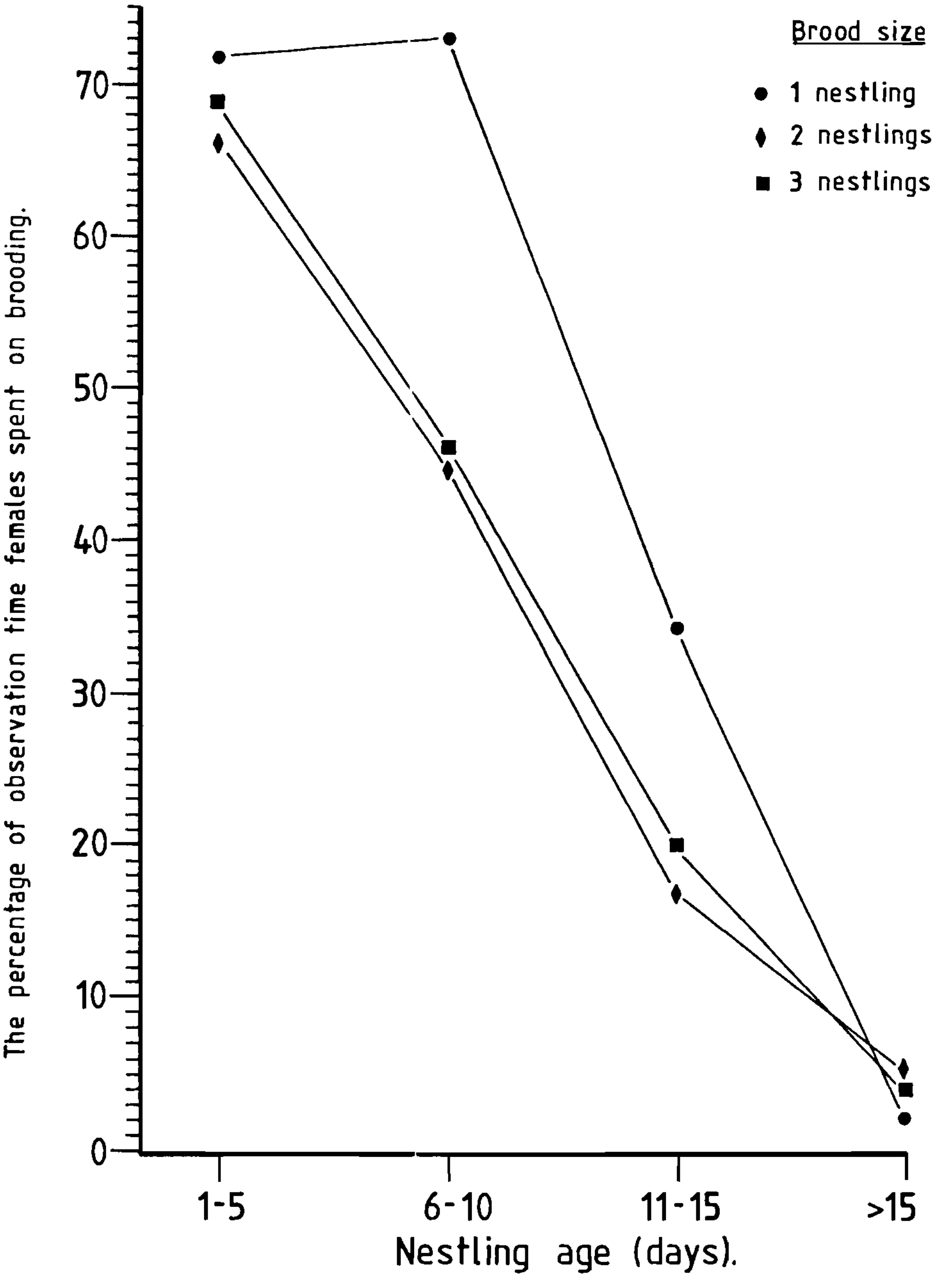


Figure 17.5 The percentage of observation time females spent on brooding with regard to their brood size and nestlings' age.

The number of hours females were observed caring for nestlings of each age-class and brood size are shown on Figure 17.3A.

(k) Brooding

Brooding by females declined as their nestlings got older. In total, females spent 46.6% of time in this behaviour (Fig. 17.2). Females spent significantly more time brooding a single nestling up to the age of 15 days than a brood of two nestlings ($P < 0.01$) (Fig. 17.5). When older than 15 days, a one-nestling brood was brooded less than a two- or three-nestling brood ($P < 0.01$). Broods of two and three nestlings of the same age-class were brooded for a similar proportion of time.

17.3.2. The diurnal patterns

(a) Foraging

Males foraged for a similar time during the course of the day, except for a significant increase in the early afternoon (Fig. 17.6 and Appendix 31). In contrast, females spent less time foraging as the day progressed.

(b) Food-storing

Males spent a similar time storing food from one day-period to the next, as did females. However, males carried out most storing in the afternoon while females stored food only in the morning.

(c) Body-maintenance

Both sexes spent a fairly constant time in body-maintenance during the morning and early afternoon. During the mid- and late afternoon, males significantly increased their involvement in this behaviour compared with previously. By comparison, females significantly decreased their time devoted to body-maintenance in the mid-afternoon, and then significantly increased it in the late afternoon.

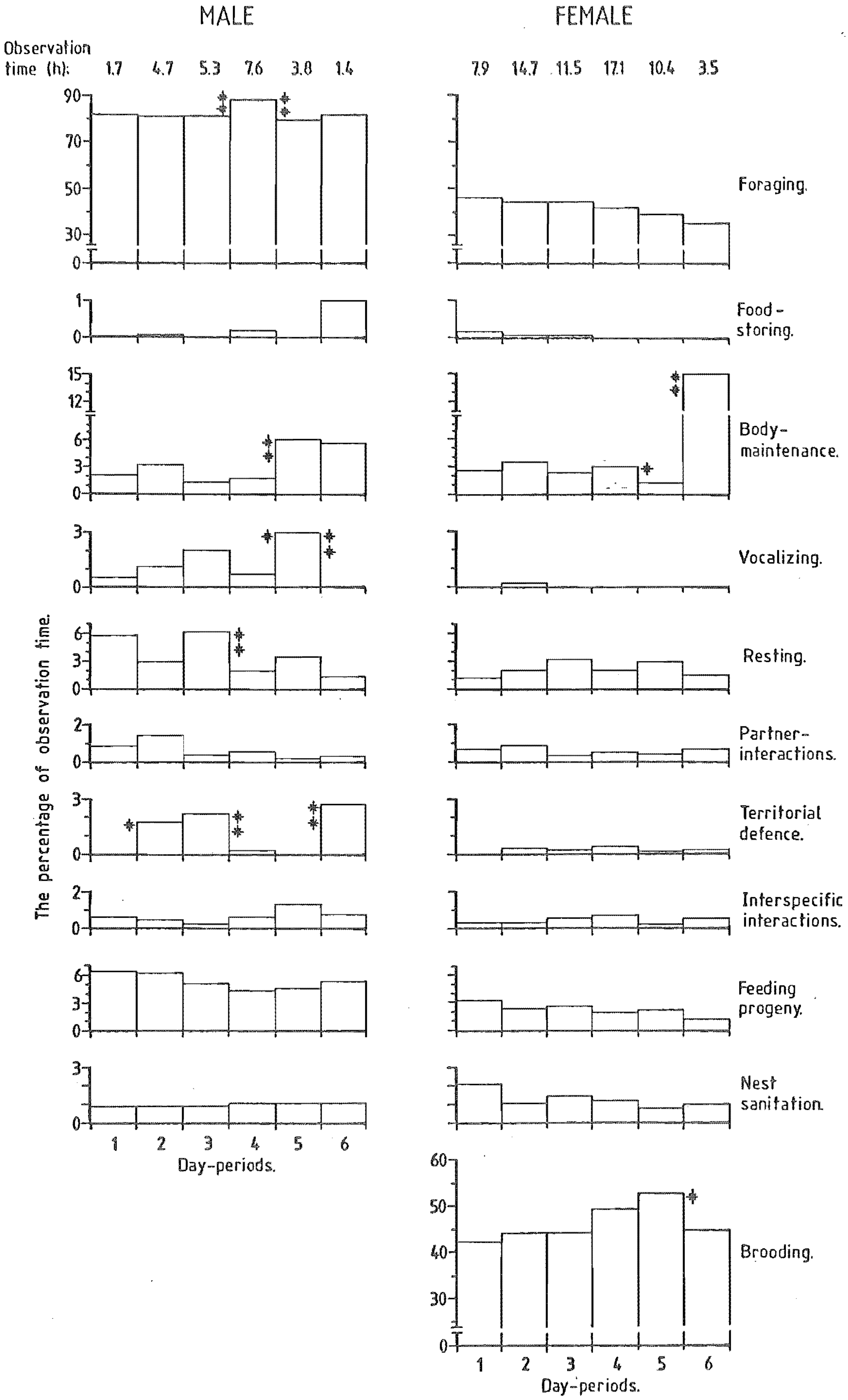
(d) Vocalizing

Males vocalized during each day-period from the early morning to the mid-afternoon. They sang more each day-period until the mid-afternoon, but for a slight decrease in the early afternoon. Females vocalized only during the mid- and late morning. Because they vocalized so little

Figure 17.6. The diurnal patterns of behaviours for male and female Robins rearing nestlings.

The plotted values are given in Appendix 31.

[a] The asterisks indicate significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the percentage of time Robins spent in a behaviour between two adjacent day-periods.


MALE
FEMALE
Observation time (h): 1.7 4.7 5.3 7.6 3.8 1.4
7.9 14.7 11.5 17.1 10.4 3.5
90
70
50
30
0
1
15
12
6
3
2
60
40
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
Feeding progeny.
Nest sanitation.
Brooding.
The percentage of observation time.
1 2 3 4 5 6
Day-periods.

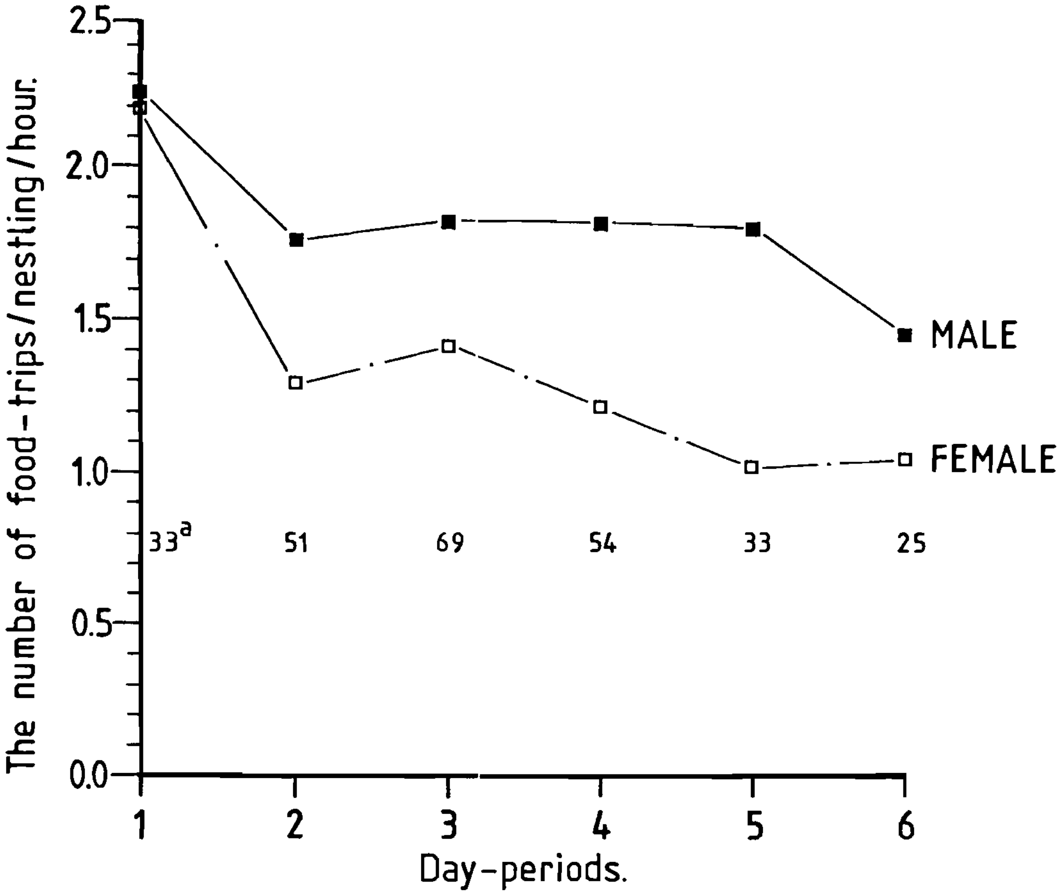


Figure 17.7 The diurnal patterns of food-trips (number/nestling/hour) by male and female Robins to nestlings.

[a]The number of hours of observation time per day-period, which were the same for both sexes.

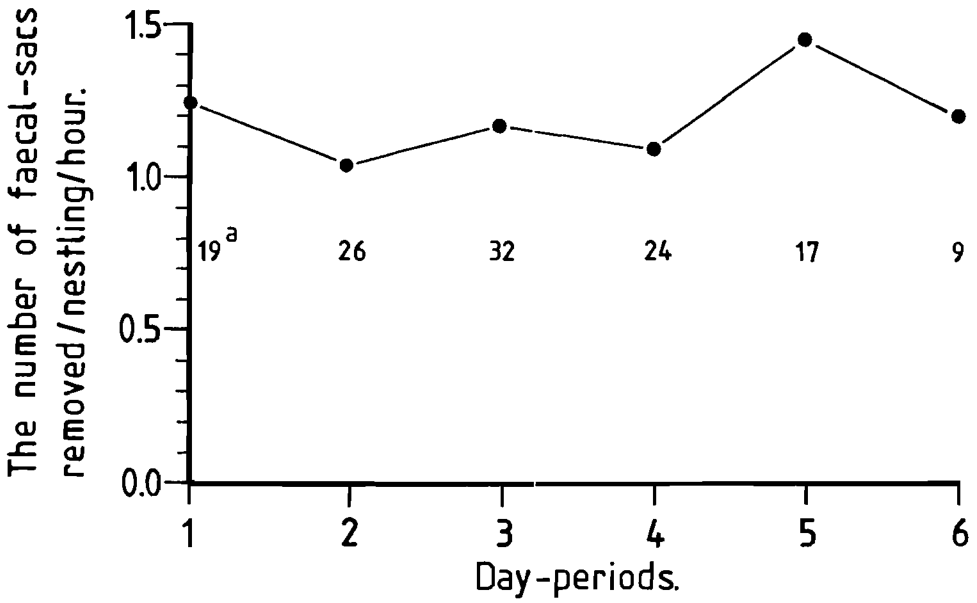


Figure 17.8 The diurnal pattern of faecal-sac removal by parent Robins from nestlings five or more days old.

[a]The number of hours observation time per day-period.

during these day-periods there was no significant change in the proportion of time females spent vocalizing during the course of the day.

(e) Resting

Males rested more in the morning than in the afternoon. In contrast, females rested most about midday.

(f) Partner-interactions and interspecific interactions

The data show that both males and females interacted with each other and with other species for a similar time during the course of the day. It is noteworthy that they spent slightly more time in partner-interactions during the early and mid-morning than afterwards.

(g) Territorial defence

The diurnal pattern of territorial defence for males involved two marked peaks of activity arising in the mid- to late morning and the late afternoon. Females spent a similar time in such disputes throughout the day.

(h) Feeding progeny

Per day-period, males spent the highest proportion of time feeding their nestlings in the early morning and then gradually decreased their involvement in this behaviour until the mid-afternoon, when it increased again. As the day progressed, females spent a decreasing time feeding their nestlings. The diurnal pattern of the rate of food-trips per nestling made by females (Fig. 17.7) shows a similar routine to the time they spent feeding nestlings (Fig. 17.6). However, instead of the rate of food-trips per nestling by males increasing after the early afternoon, as did the time they spent feeding nestlings (Fig. 17.6), the rate decreased (Fig. 17.7).

(i) Nest sanitation

Males spent a similar time each day-period in nest sanitation. So did females (Fig. 17.6). However, while males spent more time in this behaviour in the afternoon, the female's peak of nest-cleaning activity took place in the early morning. During the course of the day, the rate of faecal sac removal per nestling by parent Robins remained fairly constant, except for a slight increase in the mid-afternoon (Fig. 17.8).

(j) Brooding

The diurnal pattern of brooding for females shows a gradual increase to a peak in the mid-afternoon, followed by a decrease in the late afternoon ($P < 0.05$) (Fig. 17.6).

17.4. Discussion

17.4.1. The time-budgets for males

In passerines the rate at which parents bring food to the nest has been found to vary with the time of breeding (i.e. between early and late broods) (Kluyver 1950, Gibb 1955, Royama 1966b), between pairs (Balen 1973, Kluyver 1961), and with different brood sizes (Gibb 1955, Moreau 1947, Pinkowski 1978). Several investigators have shown that differences in the rates of food-trips per brood and per nestling were related to the weight of food brought each visit, so that the frequency of food-trips did not reflect the amount of food eaten by nestlings (Balen 1973, Gibb 1955, Kluyver 1950, 1961, Royama 1966b). However, because my concern is not to quantify the food consumption of nestlings, but to compare the apparent parental effort in bringing food to broods of various age-classes and sizes, I believe a comparison of the rates of food-trips is justified.

(a) Foraging

Although the rate of food-trips per brood made by parent Robins increased as the nestlings aged (Fig. 17.3A), males tended to spend a similar proportion of time foraging whatever their nestlings' ages (Fig. 17.1). There are several possible reasons why these apparently contradictory results arose. First, when broods were less than 11 days old, males made more of the total food-trips than to older broods (Fig. 17.4).

Therefore, the higher rate of food-trips per brood and per nestling as the nestlings aged probably arose because females increased their rate of food-trips to the nest. Similarly, the increased rate of fish given to fledging Ospreys *Pandion haliaetus* over that they received when nestlings was the result of the female, and not the male, increasing her rate of fish delivery (Levenson 1979). Second, some of the foraging of male Robins with nestlings less than 11 days old resulted in males providing food to their partners. This behaviour stopped once the nestlings were older than ten days of age, probably because the food was required by the nestlings. In support of this suggestion, I noted that the amount of food brought by males to the nest per food-trip increased as the nestlings got older. Lastly, perhaps males had to spend longer searching for suitably sized and textured prey per food-trip for young nestlings (1-5 days old) than for older ones. Pinkowski (1979) found that male Eastern Bluebirds spent slightly more time foraging for prey to feed to young nestlings than older ones. In agreement with this finding it seemed that as Robin nestlings aged the range of prey types both in size and texture that they accepted was greater.

Males foraged more when tending nestlings than when providing food to nest-building or incubating mates, probably because males had to find more food to sustain the mean rate of 4.9 food-trips per hour to nestlings compared with 3.2 and 2.9 food-trips per hour to nest-building and incubating partners respectively. Similarly, male Eastern Bluebirds, Yellow-billed Magpies and Long-billed Marsh Wrens foraged more when caring for nestlings than during the other stages of the breeding cycle (Pinkowski 1979, Verbeek 1972, Verner 1965). Biddy (1979) found that when a pair of Dartford Warblers *Sylvia undata* were provided with food they foraged less and spent long periods sunning and preening, but continued to supply the same amount of food to their nestlings as they had before the provision of food. I conclude from this that male Robins spent so much time foraging in order to maintain the supply of food to themselves and their progeny, and that a brood was more demanding than a partner.

(b) Food-storing

When rearing nestlings, males spent less time storing food than they had during the incubation stage. Also, the males with nestlings that stored food were mainly those whose chicks were less than six days old and could be readily satiated. This supports the above suggestion that the high proportion of time males rearing nestlings spent foraging was close to the maximum they were capable of, and that most of the prey they found was required to sustain themselves and their young.

(c) Body-maintenance

Although birds have to spend a certain minimum time cleaning and arranging their plumage to maintain it as an effective insulating layer (Thomson 1964), in general, the time Robins spent in body-maintenance was partly related to the time available after sufficient food had been found. The proportion of time males cared for their body surfaces did not change significantly as their nestlings aged because the time males foraged did not alter significantly. The reduction in body-maintenance by males raising nestlings compared with those attending an incubating partner ($P < 0.01$) was related to the low priority of such a behaviour, and the greater foraging during the nestling-rearing stage over that in the incubation stage ($P < 0.01$). Likewise, when rearing nestlings, male Eastern Bluebirds (Pinkowski 1979) and Yellow-billed Magpies (Verbeek 1972) spent less time in body-maintenance than during the incubation stage. In contrast, Gibb (1954) found that a marked increase in feeding by several species of tits (Paridae) rearing nestlings was not accompanied by a decrease in the preening frequency.

(d) Vocalizing

The reduction in singing by males with nestlings compared with the time they sang during the incubation stage may have been because singing was of lower priority than foraging. This is borne out by the finding that whereas immature males in Kowhai Bush and adult males on Outer Chetwode Island foraged more than did adult males in Kowhai Bush, the former categories of birds sang less than the latter. Furthermore, males of several other passerine species sang less once their nestlings hatched (Nice 1943, Pinkowski 1979, Post 1974, Verner 1965).

(e) Resting

Like tits (Gibb 1954), male Robins rearing nestlings did not reduce their resting compared with that during the incubation stage, even though time-budgets for Robins in the non-breeding season showed that resting time decreased when foraging time increased. As suggested by Gibb (1954), maybe resting was important when the days were long and the birds spent much of their time foraging and flying to and from the nest with food.

Did males spend less time in resting and body-maintenance when more time was used to forage and care for progeny? Males did not significantly increase the time devoted to foraging, feeding progeny and nest sanitation as the nestlings grew older. However, for males with two- and three-nestling broods, in general, an increase in foraging was correlated with a slight decrease in resting and body-maintenance. Therefore, from day to day, if males with nestlings had to forage more it seems that resting and body-maintenance were the behaviours that they devoted less time to.

(f) Partner-interactions

Except for those rearing a single nestling, males tended to interact less with their partners the older their nestlings and the larger the brood size. This was mainly a consequence of a change in the frequency of the "attraction" display and food-trips by the male to his partner as the nestlings aged, and between adults attending different brood sizes. The "attraction" display apparently served to direct the attention of the male to recently hatched nestlings. However, both sexes were also seen giving this display when their nestlings were older than 15 days of age. The display then seemed to signal to the partner that the nestlings were hungry and needed more food. As noted for other passerines (Pinkowski 1979, Skutch 1976), male Robins fed their partners mainly when their broods were less than six days old and contained one or two nestlings, because such broods were readily satiated.

The results in Figure 17.4 suggest that males with a single nestling should have interacted more with their partners than did males rearing two nestlings. That this is not obvious from Figure 17.1 may be a consequence of the few hours over which males with one-nestling broods were observed. Overall, males spent less time in partner-interactions during the nestling stage than when their mates were incubating. Males with nestlings infrequently interacted with their mates and the interactions usually lasted less than 30 seconds, compared with the more frequent and longer lasting food-trips that males made to incubating partners.

(g) Territorial defence

I cannot explain why males were not involved in territorial disputes when they had nestlings older than 10 days of age and why less time was spent in such interactions when they were rearing a larger brood size. Since resident males with nestlings were seen to evict all intruders, it seems that by chance intruders did not come into the territory of a male with nestlings older than 10 days of age when I was timing the resident's behaviour. There was no obvious behaviour on the part of resident males rearing nestlings that prevented intrusions by other Robins. Post (1974) found that the time male Seaside Sparrows spent in aggressive acts with conspecifics decreased markedly during the nestling stage. He considered that this resulted from the male's preoccupation with finding food and feeding the young. This does not explain the marked decrease in time male Robins with one- and two-nestling broods spent in territorial defence, because they spent a similar time foraging and feeding their progeny as the nestlings aged.

(h) Interspecific interactions

Male Robins spent a similar time in interspecific interactions whatever the brood size and age of the nestlings, presumably since these two factors did not influence the chance of such an interaction happening. Were males more protective of nestlings than eggs when other species came near Robin nests? No, male Robins spent just as much time in interspecific interactions whether their nests contained eggs or nestlings.

(i) Feeding progeny

Did an increase in nestling age result in males spending more time feeding their broods? The answer depends on the brood size involved. Generally, the younger the nestling, the longer per food-trip it took a male to feed it, because a young nestling did not always respond quickly by gaping to the male's arrival at the nest. This resulted in the male hopping about on the nest rim and giving low-volume phrases of song, as Skutch (1976) noted for adults of several passerine species which tried to coax their nestlings to gape. Another factor that lengthened visits to nestlings one to five days old than to older chicks was the frequency with which the prey presented were too large for chicks to swallow. Such prey items were retrieved and either presented to the same or another nestling, broken up and again offered to a nestling or eaten by the parent. By comparison, less time was spent feeding older nestlings per food-trip, because they were less often satiated and could swallow most prey offered. With broods of more than one, the time males spent feeding nestlings per food-trip decreased since usually one nestling begged for food when the male arrived at the nest.

For these reasons, males spent less time feeding one-nestling broods as the nestlings aged, even though a male made more food-trips per hour as the nestling got older. By comparison, males feeding a three-nestling brood spent a similar time feeding their nestlings whatever their age. While the nestlings were young (1-5 days old), a male took about the same time to feed three nestlings as he took to feed one, even though males made over twice as many food-trips per hour to the larger brood. This arose because usually at least one nestling of a brood of three begged when food was offered to them and the male often fed more than one young nestling per visit. Males did not spend less time feeding three-nestling broods as the nestlings aged. The reduction in time per food-trip by males feeding older nestlings was negated by the very high rate of food-trips to such broods. The significant increase in time males spent feeding two-nestling broods over 15 days old than previously was probably a consequence of the few hours I observed such males, rather than being a normal occurrence.

(j) Nest sanitation

Did an increase in nestling age result in males spending more time in nest sanitation? For a particular brood size, the time males spent in this behaviour remained fairly constant as the nestlings aged. Males often waited for up to a minute for nestlings less than six days old to defecate. Although older nestlings voided faecal sacs more promptly after being fed, the time males spent in nest sanitation did not decrease because such nestlings defecated more frequently than did younger nestlings, and each faecal sac voided by the former had to be carried some distance from the nest instead of being eaten. Overall, male Robins spent about one percent of time in nest sanitation, which was similar to the two percent of time male Eastern Bluebirds spent in this behaviour (Pinkowski 1979).

Did the time-budgets for males with an incubating partner and those rearing nestlings differ substantially? Yes, males feeding nestlings spent significantly less time in storing food, body-maintenance, vocalizing and partner-interactions than did those involved in the incubation stage. The decreased time males with nestlings spent in the above behaviours was devoted to foraging and engaged in behaviours directly associated with rearing nestlings (feeding progeny and nest sanitation).

17.4.2. The time-budgets for females

(a) Foraging and brooding

A bird cannot forage and brood at the same time so how a female allots her time between these two behaviours must depend on the relative efficiencies of foraging and brooding in maintaining the nestlings' growth and body temperature (Royama 1966b). Early in the breeding season cold, wet, stormy weather for more than a day sometimes led to broods being abandoned, probably because females spent so much time foraging to meet their maintenance needs that their nestlings died of exposure. The females simply forsook their broods, their own survival being of greater importance than that of their young. However, since all observations of Robin behaviour were made when it was not raining, generally females had sufficient time to forage and brood their nestlings adequately. During mild weather, and because males had no brood patch nor sheltered nestlings, a female's main priority was probably to brood for long enough to ensure the nestlings were kept at the optimum temperature for their development. The time females spent brooding presumably depended on several factors, such as ambient temperature, food availability, the ability of the nestlings to maintain their temperature, and how readily the male was able to satiate the young.

To determine whether a female's main concern was to brood or to feed her young, the mean weight of nestlings for each brood size at the same age would be required, which I did not investigate. A study of another passerine in Kowhai Bush having brood sizes similar to those of the Robin provides some insight to this problem. Gill (1980) found that individual nestling Grey Warblers from broods of two to four decreased in weight the larger the brood size. If this were also true for Robin nestlings it would suggest that even though females brooded two- and three-nestling broods less than one-nestling broods, they did not lower their brooding time sufficiently to increase the amount of food fed to members of larger broods to maintain the nestlings' growth rates at a level of that for nestlings of one-nestling broods. It seems unlikely that the small brood sizes of Robins, one to four nestlings, in cupular nests would have suffered from the heat stress that large broods of Great Tits (9-12 nestlings) did in nest boxes (Mertens 1969). Great Tit nestlings suffering from hyperthermia used energy to evaporate water to cool themselves. Thus, a lower weight for Robin nestlings from large broods would be a consequence of them receiving less food than individuals of smaller broods. This result is suggested by the lower rate of food-trips per nestling the larger the brood size (Fig. 17.3B).

Was the time females spent brooding related to (1) their nestlings' age and (2) the brood size? The answer is yes to both questions. For each brood size, female Robin's brooding declined with the maturation of the young, a result conforming with that of many similar studies of passerines (Welty 1975: 346). Brooding time also depended on the size of the brood. For nestlings one to 15 days of age, one-nestling broods received significantly more brooding than did broods of two or three nestlings, the latter two sizes being brooded for a similar time. From 16 days old until the nestlings fledged, females brooded a single nestling less than two- and three-nestling broods.

The reduction in brooding as the nestlings matured can be related mainly to their development of homoiothermy. The nestlings' increased ability to maintain their body temperature arises through the growth of insulating plumage. In addition, with the increase in body size, the rate of heat loss from an individual nestling declines - a smaller surface area to volume is exposed to the air. By fitting tightly into the nest and decreasing the area per nestling exposed to cooling each nestling of a large brood looses less heat per unit time than does one of the same age in a smaller brood (Mertens 1969). Dunn (1979) showed that large broods of House Wrens and Tree Swallows *Iridoprocne bicolor* in nest boxes thermoregulated effectively at half the age that a single nestling could. Therefore, larger broods required less brooding than small ones. This was true of Robin broods up until the age of about 16 days. It was not until the nestlings were older than 15 days of age that this trend reversed, which was probably the age at which Robin nestlings became homoiothermic.

Since only females brooded nestlings and much of the formers' time was devoted to this, until the nestlings became homoiothermic the outcome of this separation in the roles of the sexes resulted in females foraging less and making fewer food-trips than males ($P < 0.01$). Other than brooding and foraging, the time females devoted to the other behaviours changed little as the nestlings aged. Therefore, females foraged more as they spent less time brooding, and as a consequence made a larger proportion of the food-trips to their broods.

(b) Food-storing

Like males, females rarely had surplus food to store after meeting their own and their broods' food requirements. Probably, there was little opportunity for females to find extra food, because the time available after brooding seemed barely sufficient to carry out more important behaviours, such as body-maintenance and nest sanitation.

(c) Body-maintenance and resting

Did females spend more time in body-maintenance and resting when less time was devoted to foraging and care of their progeny? Yes, which supports the hypothesis that throughout the annual cycle these two behaviours were of low priority to Robins. This was why on mild days females rearing one- and two-nestling broods, that required little brooding and could be readily satiated, spent so much time preening, sunning and resting. Females with three-nestling broods did not spend more time in resting and body-maintenance as their broods matured because such females had to forage most of the time when not brooding to find enough food for the frequent food-trips needed to satisfy the larger number of nestlings. Ryan and Dinsmore (1979) suggested that in an effort to care more for their young, American Coots *Fulica americana* first rested less. When this increase in time for brood care was insufficient then body-maintenance activities were reduced. For Robins, the order of priority of the two behaviours differed between the sexes. When rearing nestlings, males spent less time in body-maintenance and rested as much as in the incubation stage, but for females the result was reversed.

It is possible that the approximately three percent of time females with three nestlings spent in body-maintenance was the minimum time they could devote to this behaviour and still keep their plumage clean and ordered. In winter, when adult females had fairly new plumage that probably required less maintenance than did older plumage, they also spent about three percent of time in body-maintenance (Appendix 11). Considering that days were much longer in the breeding season than in winter, and females with nestlings made frequent flights to and from their nests, were often exposed to such plumage contaminants as nest material and faeces, and the dishevelling of their plumage by brooding, I expected females to spend more time in body-maintenance when rearing nestlings than in winter. This did not occur, but because body-maintenance, and similarly resting, by brooding females was not timed separately this result is not apparent from the time-budgets.

I am unable to explain why males rearing one- and two-nestling broods more than 15 days old devoted less time to resting and body-maintenance than did females. Both sexes made a similar number of food-trips to such broods, and females were still spending some time brooding then.

Although females rested less than did males ($P < 0.01$), if some of the time females brooded involved them having a metabolic rate similar to that of resting males, as seems to have been the case in the incubation stage (Walsberg and King 1978), probably females rested as much as did males. Females rearing one or two nestlings rested more than did males once the chicks were older than 10 days of age, presumably because such nestlings required little brooding and their food demands were readily met. Gibb (1955) suggested that Great Tits feeding nestlings slackened their food-trip rate slightly in the afternoon because they were tired. This does not seem to explain the increased resting by female Robins because the larger their brood size, the faster their rate of food-trips and the less time females rested.

(d) Vocalizing

As happened in the incubation stage, females rearing nestlings seldom vocalized other than to make calls associated with feeding chicks and with interactions with partners, intruders and other species. That they vocalized only in situations of apparent necessity may have been to reduce the likelihood of a predator using the calls to locate Robin nests.

(e) Partner-interactions

Like males, females interacted with their partners for a similar proportion of time whatever the age of their nestlings and the brood size, because these two factors presumably had no influence on the frequency with which the adults interacted with one another. Although females were fed by their mates mainly when the nestlings were less than 11 days old, this had little influence on the females' time-budgets since the transfer of food took only a few seconds. Overall, females with nestlings spent less time interacting with their partners than did incubating females ($P < 0.01$), because the latter were fed regularly by their partners (about 3 times/h) and usually flew several metres from the nest to accept the food.

(f) Territorial defence

There were no obvious reasons why females interacted with other Robins mainly when their nestlings were less than 11 days old. The "chuck" calls given by a female when she sighted an intruder attracted her mate. The male drove the intruder from the territory while the female often remained near the nest. Thus, females spent less time in territorial defence than did males ($P < 0.01$). Likewise, male American Coots spent significantly more time in territorial defence than did females (Ryan and Dinsmore 1979). The authors suggested that male coots were more aggressive than were females because the former had invested more time and energy in establishing territories. This may also explain why female Robins interacted with intruders less than did male Robins. Bachelor males were able to establish and defend territories against neighbouring Robins, but lone females were usually ousted from theirs.

(g) Interspecific interactions

Male and female Robins rearing nestlings spent a similar time interacting with other species. Both sexes chased most other avian species from the immediate nest area, and together "chucked" at and followed predators in their territory. Were females more protective of eggs than they were of nestlings when other species came near Robin nests? Like males, females were just as protective of their nests whether they contained eggs or nestlings, females spent a similar time in interspecific interactions during the incubation and nestling-rearing stages.

(h) Feeding progeny

Did the rate of food-trips made by females vary according to their brood size and nestlings' age? The percentage of the total number of food-trips made by females increased as their nestlings aged, especially once the nestlings were more than 10 days old (Fig. 17.4). In addition, since females spent slightly more time feeding nestlings as they got older (Fig. 17.2), I conclude that the rate of food-trips made by females increased both with nestling age and with brood size. From the total time-budgets, females spent only half the time that males did feeding nestlings. This was a consequence of males making a greater proportion of the total food-trips to nestlings less than 11 days old than did females, and then each food-trip took longer than it did to older nestlings.

That females with a one-nestling brood less than six days old made more trips with food than did their partners seems to be related to two factors. Such nestlings were fed small prey items (< 5 mm) offered several at a time which kept them satiated for some time. Therefore, during the short spells that a female was off the nest she was able to find enough food to satisfy her own and the nestling's food requirements. However, once these nestlings were more than five days old, because of the increased frequency and larger sized prey they were fed, a female seemed to be unable to find enough food for herself and the nestling in the time available after the nestling's brooding requirements had been met. Thus, the male increased the rate of his food-trips to meet the nestling's increased food demands. The other reason why females made more food-trips to nests containing young single nestlings was because some males seemed unaware that the nestlings had hatched. In these cases, males continued to feed their partners away from the nest, as happened in the incubation stage, with the females alone feeding the nestlings.

Did the effort made by parent Robins to feed nestlings vary both with brood size and with nestling age? The food-trip rate or effort of parent Robins increased *per brood* as the nestlings aged and with an increase in brood size, but on the basis of effort *per nestling* it decreased the larger the brood size. Many other studies of passerines have also shown such a trend (Gibb 1950, 1955, Moreau 1947, Royama 1966b). It is possible that the greater rate of food-trips to single-nestling broods may have been to counteract the greater energy expenditure on heat production of such broods (Mertens 1969). A comparison of the mean weight of nestlings of each brood size would determine whether the lower parental effort per nestling in feeding three-nestling broods resulted in such nestlings being lighter than nestlings of the same age in one- and two-nestling broods.

(i) Nest sanitation

Did females spend more time in nest sanitation as their nestlings got older? Yes, although not a significant increase, females devoted more time to keeping their nests clean as the nestlings aged. This was because older nestlings produced faecal sacs more frequently than did younger nestlings, and sacs voided by nestlings older than five days of age were carried away from the nest rather than swallowed as they were when produced by younger nestlings. Also, females seemed to probe into their nests more frequently as the nestlings aged. This activity could be readily quantified during future studies at Robin nests.

Did the time-budgets for females differ much between the incubating and nestling-rearing stages? Comparing the total time-budgets, the time females devoted to their repertoire of behaviours changed markedly from the incubating to the nestling-rearing stage. When rearing nestlings, females foraged more and spent less time in resting, partner-interactions and "on the nest" (brooding and incubating) than during the previous stage. Furthermore, those rearing nestlings spent time in two behaviours not seen in the incubation stage, feeding progeny and nest sanitation. However, it was not such a drastic change as the comparison infers, females gradually foraged and fed their nestlings more as the nestlings required less brooding.

17.4.3. The diurnal patterns

Compared with the fairly distinct patterns of behaviours in most stages of the breeding cycle, Robins rearing nestlings tended to spend a similar time during the course of the day doing each behaviour. This seemed to be caused by the parent Robins devoting almost all their time to behaviours related to their own and their nestlings' maintenance. Foraging, brooding, feeding nestlings and nest sanitation took up 90 to 95%

of their time, with little left for the other behaviours.

(a) Foraging and brooding

The increased foraging of males in the early afternoon compared with the fairly constant proportion of time they devoted to this during the rest of the day may have been related to an increase in foraging efficiency in the early afternoon. At that time of day, ambient temperatures were highest and probably promoted increased invertebrate activity and hence their conspicuousness to Robins, making it a more efficient time to search for prey.

That females decreased the time they foraged as the day progressed seems to reflect the diurnal pattern of their own and their nestlings' food requirements, except in the late afternoon. In the late afternoon females were expected to spend more time foraging than earlier to stock up with food to last them during the night, as they did in previous stages (Figs 14.5, p. 258, 15.3, p. 290, 15.4, p. 293, and 16.6, p. 328).

The diurnal pattern of brooding was the reverse of that expected. Females brooded least of all in the early morning when ambient temperatures were lowest and nestlings would have required most brooding. This diurnal pattern of brooding can be understood when the birds food requirements during the course of the day are considered. I conclude that females brooded least in the early morning because they and their nestlings were hungriest then after the night fast. In support of this suggestion, females foraged most and fed their nestlings more frequently in the early morning than later in the day.

(b) Food storing

Generally, males spent a similar time during the course of the day foraging, storing food and feeding progeny. This suggests that they rarely had time to find surplus food and spent most time after meeting their own and their nestlings' food requirements on other behaviours. In contrast, female's diurnal pattern of storing food was the opposite of that expected. Although not significant, they spent most time storing food in the early morning, a time of day when they and their nestlings probably were hungriest and the nestlings required most brooding. Figure 17.2 shows that females stored food mainly when feeding three-nestling broods over 15 days old, a situation in which because of the high rate of food-trips to such broods, females were least likely to have excess food to store. For these reasons I cannot explain this diurnal pattern of storing food by females.

(c) Body-maintenance

The data for both sexes show a marked increase in body-maintenance in the mid- to late afternoon, possibly because it was then that less time was required for other behaviours compared with earlier. Although fewer food-trips per nestling per hour were made in the late afternoon than before, males continued to spend as much time foraging and feeding their young as previously. Therefore, it seems that males vocalized and rested less in the mid- to late afternoon compared with earlier in order to preen more.

By comparison, females spent much more time in body-maintenance in the late afternoon than earlier, presumably because they required less time to forage, rest, feed progeny and brood then. Parent Robins preened mainly in the late afternoon, perhaps because earlier in the day they postponed plumage-care activities to devote most of their time to more important behaviours. However, by the late afternoon possibly they had to spend more time in body-maintenance in order to clean and order their plumage to minimise heat loss at night.

(d) Vocalizing

Environmental conditions prevalent in the morning are less likely to attenuate vocalizations than they are in the afternoon (Wiley and Richards 1978). Thus, singing by Robins would be most effective if carried out in the morning. In general, males outside the breeding season and in some stages of the breeding cycle did sing mainly in the early morning. That males rearing nestlings sang more after the early morning seems to indicate that it was more important for them to carry out other behaviours then, such as foraging for themselves and their nestlings.

(e) Resting

Since males were probably hungriest in the morning after the night fast and they fed their nestlings more frequently then than later, it is surprising that males rested mainly in the morning. This result can be explained by remembering that, in general, males spent more time resting the younger their nestlings (Fig. 17.1). Thus, this diurnal pattern of resting can be attributed mainly to males feeding small nestlings. These nestlings were readily satiated, allowing males feeding them to rest even in the morning.

Likewise, females that rested most were those that foraged and brooded least, those that had one- or two-nestling broods old enough to require little brooding. Such females probably rested slightly more at midday than at other times because ambient temperatures would have been highest at midday decreasing the time they had to spend brooding. Also, since nestlings were fed less frequently after the early morning, presumably there was no need for females to spend most of their time foraging when not brooding and so were able to rest more then.

(f) Partner-interactions

Members of a pair spent slightly more time interacting with each other in the early and mid-morning than afterwards because of the diurnal pattern of "attraction" displays, and not from males feeding their partners. Except when feeding two nestlings, both partners interacted with each other more when their nestlings were over 15 days old (Figs 17.1 and 17.2), a time when males did not feed their mates (Fig. 17.4). Thus, I conclude that parent Robins spent more time displaying to each other in the early morning than afterwards because their nestlings were hungriest in the morning. The nestlings' vociferous begging in the early morning presumably prompted the parents to give "attraction" displays more often than later in the day when the nestlings seemed to beg less intensely. This hypothesised relationship between the intensity of nestling begging and the frequency of their parents "attraction" displays could be readily tested by observing parent- and nestling-Robin behaviour while seated near nests.

(g) Territorial defence

I am unable to explain why males rearing nestlings had two diurnal peaks of territorial-defence behaviour. The behaviour most likely to result in males interacting with intruding Robins was foraging, because it involved resident birds moving about their territories and therefore most likely to sight intruders. However, during the course of the day males rearing nestlings foraged for a similar time, except for an increase in the early afternoon when the time spent in territorial defence decreased! From the results in previous chapters there was some indication that during the day males spent less time in territorial defence when they vocalized most, but such a correlation is not apparent from the data for males rearing chicks.

Like females involved in most stages of the breeding cycle, those rearing nestlings spent a similar time through the day in territorial disputes. As previously explained, this seems to have been a consequence of females spending little time in such disputes.

(h) Interspecific interactions

The data show that neither males nor females had a diurnal pattern of interspecific interactions. These interactions seemed to take place at a similar frequency during each day-period.

(i) Feeding progeny

Like Robins, several other passerines feed their nestlings most frequently in the early morning: for example, Great Tits (Kluyver 1950), House Wrens (Kendeigh 1952) and Eastern Bluebirds (Pinkowski 1978). Probably, nestling Robins were hungry after the night fast and through the intensity of their begging stimulated their parents to deliver food more frequently in the early morning than later in the day. In general, the diurnal pattern of time parent Robins fed their progeny reflects the rate with which they brought food to nestlings as the day progressed (Fig. 17.7). Males spent slightly more time feeding nestlings in the late afternoon than at midday, even though the rate of food-trips per nestling decreased slightly during the afternoon. Perhaps nestlings were more often satiated towards the end of the day than earlier so that males took longer to feed a nestling per food-trip in the late afternoon.

During the course of the day, females spent fewer minutes feeding nestlings as a consequence of the diurnal pattern of their rate of food-trips per nestling.

The diurnal pattern of the rate of trips with food to nestlings by males differed from their pattern of foraging, but this was not true for females. When nestlings were fed less frequently (mid-morning and late afternoon), perhaps males continued to forage as much as earlier in order to find more food for themselves. The rate at which food is brought to the nest is determined partly by the intensity of begging calls and the speed and strength of the nestlings' gaping reaction (Kendeigh 1952, Haartman *in* Skutch 1976). The rate of food-trips and size of prey fed to nestlings was inversely related for the Great Tit (Balen 1973, Gibbs and Betts 1963). Therefore, another explanation is that when nestling Robins were fed less frequently, the parents spent longer searching for larger and less numerous prey.

(j) Nest sanitation

Males rearing nestlings spent a similar time each day-period in nest sanitation, the rate at which they removed faecal sacs during the day being fairly constant. The habit of females in probing the nest probably resulted in them spending slightly more time in the early morning in nest sanitation than at other times. This greater involvement in nest sanitation in the early morning was probably to find any faecal sacs voided by the nestlings at night and to air the nest (*British Birds* 38: 205-210, 300, 360 and 39: 159, 160, 255).

17.5. Summary

When rearing nestlings, males foraged significantly more (83.3% of observed time) than at any other stage of the breeding cycle: they had to find sufficient food to make 4.9 food-trips per hour when feeding nestlings, which was greater than the rate of trips with food during the other stages. Males spent a similar proportion of their time foraging whatever their nestlings' age, even though the rate of food-trips per brood made by both parents increased as the nestlings aged.

During the nestling-rearing stage, males spent less time storing food than they did when their partners were incubating ($P < 0.05$). I conclude that the large proportion of time males foraged when caring for nestlings was close to the maximum they were capable of, and that almost all prey they found was needed to sustain themselves and their nestlings. In support of this suggestion, males with nestlings devoted less time to body-maintenance, a low priority behaviour, than they had during the incubating stage.

The proportion of time females foraged seemed to be related to the brooding requirements of their young. Since males did not brood nestlings and the nestlings were poikilothermic until about 16 days old, much of a female's time had to be spent brooding. In mild weather, females were able to brood their nestlings adequately, and find sufficient food for themselves and some for the nestlings in the time they were off the nest. Thus, females foraged less and made fewer food-trips to broods than did males when the nestlings needed brooding. For nestlings one to 15 days old, females brooded one-nestling broods more than broods of two or three nestlings ($P < 0.01$), the latter two brood sizes being brooded for a similar proportion of time. Other than brooding and foraging, females spent a similar time in each of the other behaviours as their nestlings matured. Thus, it seems that as the nestlings required less brooding, females foraged more and as a consequence made a greater proportion of food-trips to their broods.

The proportion of time males devoted to feeding nestlings depended on the brood size and the nestlings' age. For a one-nestling brood, a male spent less time feeding the chick as it aged. However, when caring for a three-nestling brood males spent a similar proportion of time feeding them whatever their age. The food-trip rate or effort of parent Robins increased *per brood* as the nestlings aged and with increasing brood size, but on the basis of effort *per nestling* it decreased the larger the brood size.

For a particular brood size, males spent a similar proportion of time in nest sanitation whatever the nestlings' age. In contrast, females devoted more time to this as their nestlings got older. This difference arose because although both sexes removed faecal sacs, only females probed into the nest. The frequency of such probings seemed to increase as the nestlings matured.

Males foraged for a similar time each day-period, except for a significant increase in the early afternoon. By comparison, the females' foraging gradually declined as the day progressed. Females' diurnal pattern of brooding showed an increase from one day-period to the next until the mid-afternoon, followed by a decrease ($P < 0.05$). This routine of brooding was the opposite of that expected, considering that the brooding requirements of nestlings would have been greatest in the early morning when ambient temperatures were generally lowest. Females foraged most and fed their nestlings more frequently in the early morning compared with later in the day. Thus, the time females spent brooding was modified by their hunger and that of their young after the night fast.

In general, both sexes fed their nestlings most frequently in the early morning and gradually decreased the rate during the course of the day. However, for males, but not females, the diurnal pattern of food-trips per hour to nestlings differed from the time males foraged through the day.

During the course of the day, males spent a similar time in nest sanitation because the rate at which they removed faecal sacs remained fairly constant. Females spent slightly more time in nest sanitation in the early morning than afterwards, presumably because they probed more frequently into the nest then than at other times of the day to find faecal sacs voided at night.

CHAPTER EIGHTEEN

THE TIME-BUDGETS FOR ROBINS REARING JUVENILES

18.1. Introduction

The final stage of the breeding cycle was the rearing of juveniles. On leaving the nest, juveniles had short tails and a few down feathers adhering to their crowns. Initially, such birds were poor fliers and, if not disturbed, remained perched in the same place for several hours. However, by a fortnight after leaving the nest they flew quite proficiently, following an adult about and quickly flying to accept food. At about the same age they began foraging for themselves, mainly by hopping about on the ground and pecking at objects (pers. obs., Flack 1979).

The length of the stage that parents fed their juveniles varied. It depended on the number of fledglings present, how many the female cared for, and how soon the next clutch hatched (Flack 1973). Male and female Robins usually fed particular juveniles. I did not determine how soon after fledging this division of the brood took place, but it seemed to happen within the first week. If the brood was composed of an odd number of juveniles the male usually took care of the extra one. Once the female began nest-building, and certainly by the time she started incubating, all juveniles were then tended by the male. When only one juvenile fledged, the male took sole charge of it (number of occasions = 12), with the female occasionally starting to build the next nest within three days of the juvenile having fledged. In such a case, the juvenile was often fed for a few days after the subsequent clutch had hatched, but was then driven from the territory having received only about 24 days of parental care since fledging. At the other extreme, a female that cared for two juveniles sometimes delayed re-nesting for up to 35 days, or if her subsequent clutch was preyed upon, the juveniles were sometimes known to be fed for up to 50 days before being ousted from the territory (pers. obs., Flack 1973).

The budgets for male Long-billed Marsh Wrens (Verner 1965) and male Eastern Bluebirds (Pinkowski 1979) rearing juveniles were the only passerine time-budgets at this stage of the breeding cycle that I had for comparison. The monthly and total time-budgets for male and female Robins rearing juveniles are described and compared in this chapter. Also, the diurnal rhythms of each behaviour for both sexes are described. The main question I hoped to answer was whether or not Robins rearing juveniles spent as much time foraging and feeding their progeny as did Robins rearing nestlings, the point being that the findings of some investigators suggest that parent birds spend more time foraging and tending nestlings than juveniles (Pinkowski 1979, Verner 1965), while others have found the reverse to be true (Levenson 1979, Royama 1966b, Smith 1978).

18.2. Methods

For the first week after juveniles had left the nest, adults were usually wary of my presence near their juveniles and often refused to feed them or called them to another area of the territory. For these reasons most observations of adults rearing juveniles were made once the latter had been out of the nest for at least a week and flew proficiently. This is an important feature in understanding the time-budgets. No data are given for Robins rearing juveniles in August because September was the earliest month during which juveniles were present.

18.3. Results

18.3.1. The monthly and total time-budgets

(a) Foraging

While rearing juveniles, males foraged for a slightly lower proportion of time (though not significant) from one month to the next as the breeding season progressed (Fig. 18.1), and foraged for more hours per day during the course of the season as the daylength increased (Appendix 32). Likewise, females foraged for a similar proportion of time from September to November, but in December they foraged significantly more than previously ($P < 0.01$). Overall, males foraged for 79.4% of time, significantly less than the 83.3% they spent foraging while rearing nestlings ($P < 0.01$). Females foraged for 82.0% of time, significantly more than the 79.4% for males ($P < 0.05$). Females rearing juveniles spent twice as much time foraging as did those rearing nestlings ($P < 0.01$).

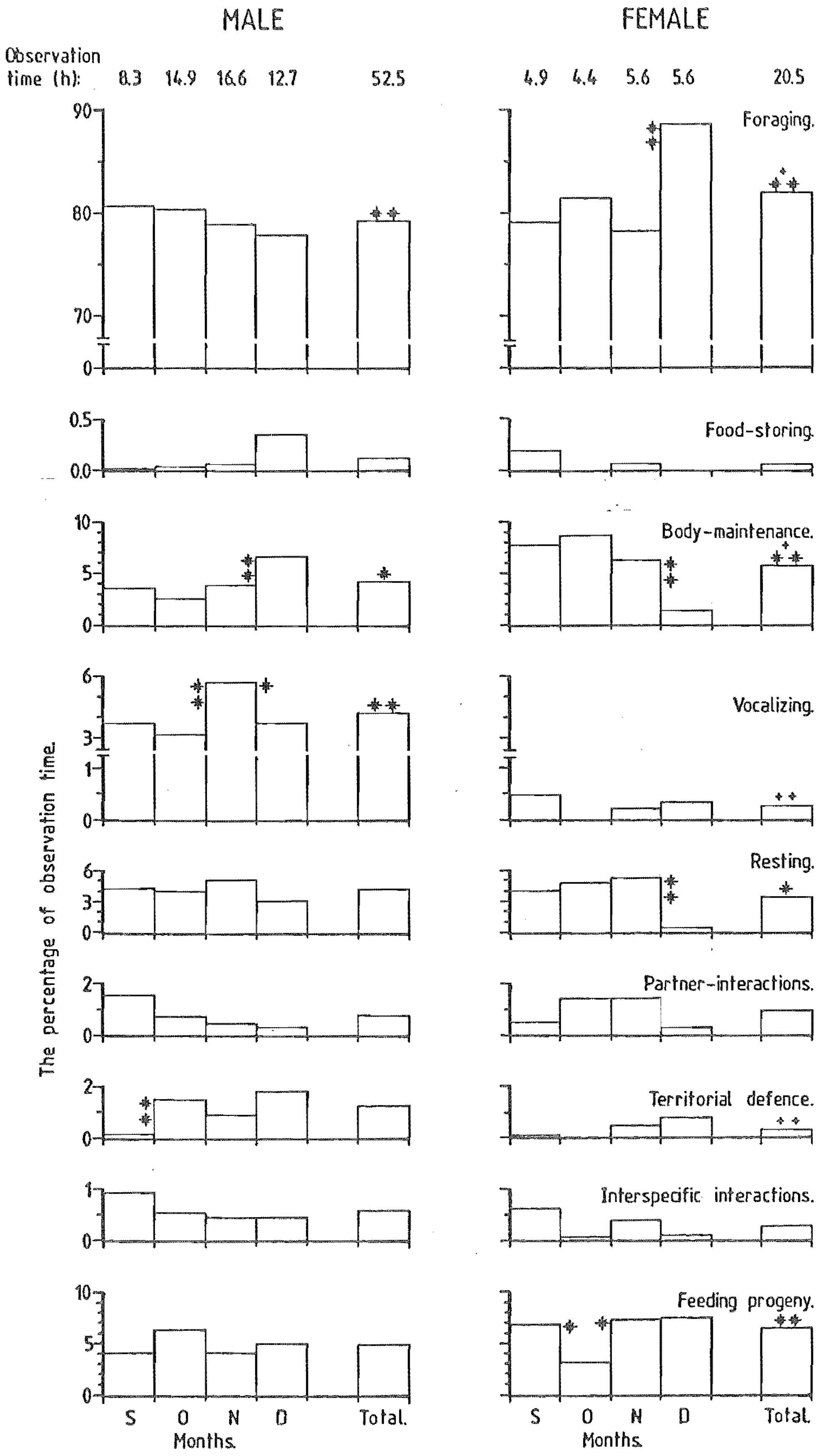
(b) Food-storing

While rearing juveniles, males spent a similar proportion of time each month storing food, as the females did. Furthermore, for the entire breeding season males and females spent the same proportion of time storing

Figure 18.1. The monthly and total time-budgets for male and female Robins rearing juveniles.

See Appendix 31 for the plotted values.

[a]The asterisks and crosses indicate significance levels: * or + = $P < 0.05$, ** or ++ = $P < 0.01$. The asterisks next to the sides of columns indicate significant differences between monthly samples. Those above the male "total" columns show the behaviours to which males rearing nestlings (Fig. 17.1, p. 348) and those rearing juveniles devoted significantly different proportions of time. The same procedure is used for comparing the female total time-budgets. Figure 17.2 (p. 352) shows the total time-budget for those rearing nestlings. The crosses indicate those behaviours on which males and females rearing juveniles spent significantly different percentages of their total time.


MALE
FEMALE
Observation time (h): 8.3 14.9 16.6 12.7 52.5
4.9 4.4 5.6 5.6 20.5
Foraging.
90
80
70
0
Food-storing.
0.5
0.0
Body-maintenance.
10
5
0
Vocalizing.
6
3
1
0
Resting.
6
3
0
Partner-interactions.
2
0
Territorial defence.
2
0
Interspecific interactions.
1
0
Feeding progeny.
10
5
0
The percentage of observation time.
S O N D Total.
Months.
S O N D Total.
Months.

food, and this was similar to that spent storing food when they were rearing nestlings.

(c) Body-maintenance

The proportion of time males spent in body-maintenance remained fairly constant from September to November, then increased in December ($P < 0.01$). Likewise, females spent a similar proportion of time maintaining their body surfaces during the first three months, but in contrast to males, markedly reduced their involvement in this behaviour during December ($P < 0.01$). In total, males spent 4.2% of time in body-maintenance, more than they had while rearing nestlings ($P < 0.05$). The 5.9% of time females rearing juveniles spent on body-maintenance was significantly more than that for males rearing juveniles ($P < 0.05$) or that for females rearing nestlings ($P < 0.01$).

(d) Vocalizing

Males vocalized for a similar proportion of time each month, except in November when they sang significantly more than during October and December. In total, they sang more than they did while rearing nestlings ($P < 0.01$). Females vocalized for a similar proportion of time each month, but vocalized much less than did males ($P < 0.01$).

(e) Resting

Males rested for a similar proportion of time each month. Overall, they rested for 4.3% of time, which was similar to that spent resting by males rearing nestlings. Except for a significant reduction in December ($P < 0.01$), females rested for a similar proportion of time each month, and overall they rested as much as did males. Females rearing juveniles rested more than those with nestlings ($P < 0.05$).

(f) Partner-interactions

As the season progressed, males rearing juveniles spent a lower proportion of time ($P > 0.05$) (Fig. 18.1) and less hours per day (Appendix 32) from month to month interacting with their mates, even though the daylength increased. By comparison, females feeding juveniles interacted with their partners for a similar proportion of time each month. In total, whether rearing nestlings or juveniles, males interacted with their mates for a similar proportion of time, and the same was true of females.

(g) Territorial defence

During September, males with juveniles spent less time defending their territories against conspecifics than during later months ($P < 0.01$). In total, males were involved in territorial defence for 1.2% of time, only slightly more than that while rearing nestlings. Females rearing juveniles spent a similar proportion of time in territorial defence each month, and spent as much time in this behaviour as did those rearing nestlings. However, while rearing juveniles, females spent much less time defending their territories than did males ($P < 0.01$).

(h) Interspecific interactions

Males spent a similar proportion of time each month in interspecific interactions, as the females did. In total, they each devoted as much time to this behaviour. It was no different from that spent in interspecific interactions when rearing nestlings.

(i) Feeding progeny

In each month, males spent about 5% of their time feeding juveniles, which was similar to that they had spent in feeding nestlings. Except for the low October result ($P < 0.05$), females fed juveniles for about 7% of time, which was not significantly different from that for males. However, females spent more time feeding their young as juveniles than they had spent feeding them as nestlings ($P < 0.01$).

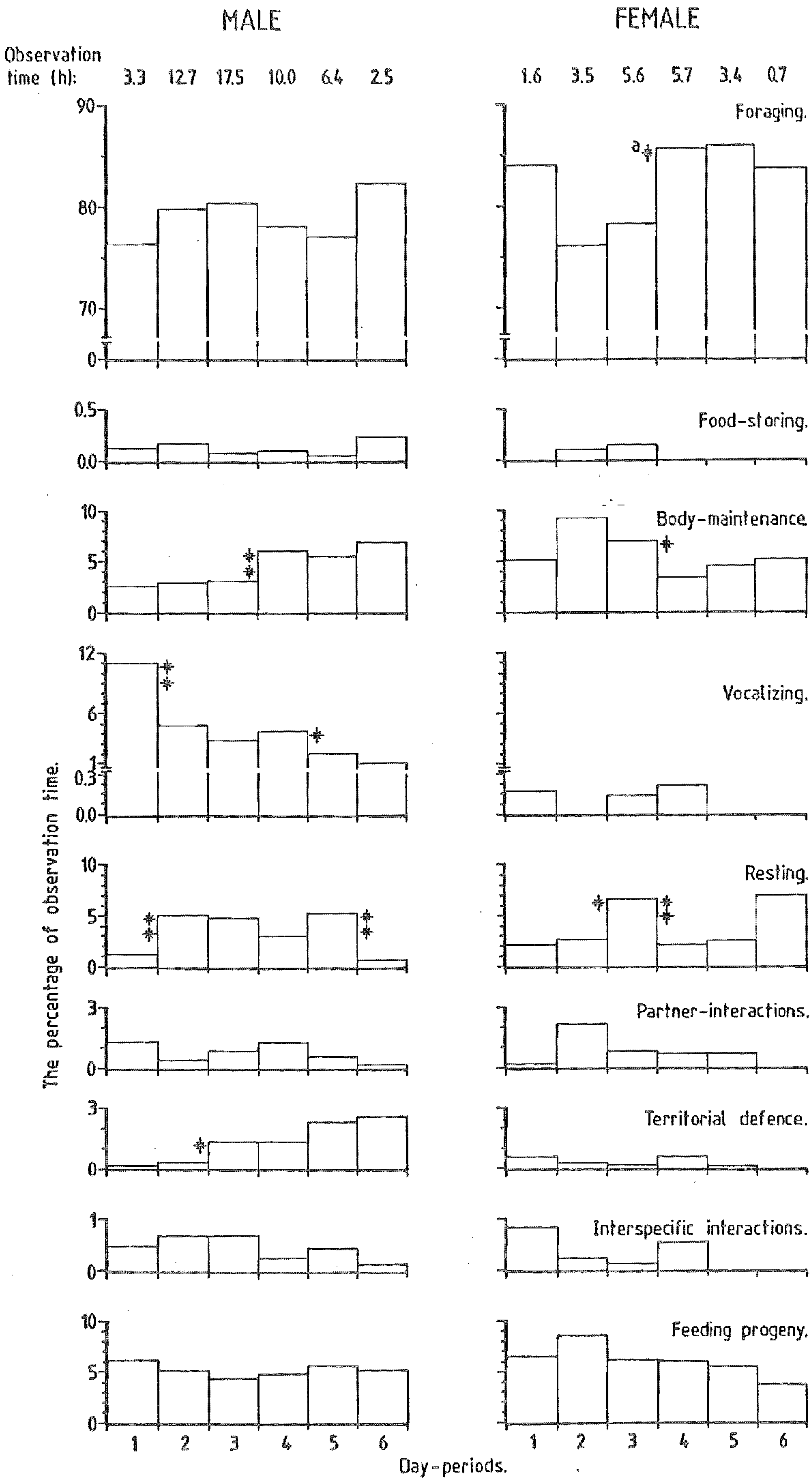
18.3.2. The diurnal patterns

Although the proportion of time males foraged did not change significantly from one period to the next as the day progressed, increases in foraging arose during the mid- to late morning and in the late afternoon (Fig. 18.2 and Appendix 33). Likewise, the foraging of females

Figure 18.2. The diurnal patterns of behaviours during the breeding season for males and females rearing juveniles.

See Appendix 32 for the plotted values.

[a] The asterisks indicate significant differences (* = $P < 0.05$, ** = $P < 0.01$) in the percentage of time males spent in a behaviour between two adjacent day-periods, likewise for female behaviours.


MALE
FEMALE
Observation time (h):
3.3 12.7 17.5 10.0 6.4 2.5
1.6 3.5 5.6 5.7 3.4 0.7
Foraging.
Food-storing.
Body-maintenance.
Vocalizing.
Resting.
Partner-interactions.
Territorial defence.
Interspecific interactions.
Feeding progeny.
90
80
70
0
0.5
0.0
10
5
0
12
6
1
0.3
0.0
10
5
0
3
0
3
0
1
0
10
5
0
a
The percentage of observation time.
1 2 3 4 5 6
1 2 3 4 5 6
Day-periods.

showed two increases, but in contrast to males, these occurred in the early morning and early to mid-afternoon.

There was no obvious diurnal pattern for food-storing by males raising juveniles; they spent a similar time in this behaviour each day-period. Females only stored food during the mid- and late morning, but because they devoted such a small proportion of time to this behaviour there was no significant difference from period to period.

Males spent more time in body-maintenance in the afternoon than in the morning ($P < 0.01$). In contrast, females were more involved in body-maintenance during the mid- and late morning than in the afternoon.

Males sang more in the early morning than during the other day-periods ($P < 0.01$), with a gradual decrease in singing during the course of the day. There was no diurnal pattern of vocalizing for females.

Most resting by males was carried out after the early morning and before the late afternoon ($P < 0.01$). In contrast, females rested for a similar proportion of time each day-period, except in the late morning when they rested more ($P < 0.05$) than during the mid-morning and early afternoon.

While rearing juveniles, males interacted with their partners and with other species for a similar percentage of time from one day-period to the next, as did females. There was no diurnal pattern of territorial defence among females. However, as the day progressed, males spent increasingly more time in disputes with conspecifics.

Males spent a fairly constant proportion of time per day-period feeding juveniles, whereas the feeding by females decreased after the mid-morning.

18.4. Discussion

18.4.1. The monthly and total time-budgets

(a) Foraging

As I found for male Robins, male Long-billed Marsh Wrens (Verner 1965) and Eastern Bluebirds (Pinkowski 1979) foraged less while feeding juveniles than when rearing nestlings. However, Smith (1978) stated that the number of food-trips per hour made by Song Sparrows to juveniles about two days out of the nest was significantly higher than the rate to nestlings about two days before fledging. His observations suggested that the size of food loads brought was the same for both age-groups of young. Similarly, the percentage of daylight time a pair of Ospreys with fledglings spent fishing and the total weight of fish the parents delivered per hour was greater than when they were raising nestlings (Levenson 1979). Experiments by Royama (1966b) with Great Tits suggested that juveniles require a higher daily food intake than a nestling. He found that the daily food intake relative to body weight for a nestling was far below that for an adult as a consequence of the former's lower rate of external activity, the brooding received, the efficiency of nest materials in heat insulation, and the clumping effect of the young so that a small proportion of the body surface-area was exposed to cooling. Therefore, by analogy, a recently fledged juvenile Robin would be expected to have a greater food requirement than a nestling about to fledge.

There are several possible explanations why adult males foraged less when rearing juveniles than they did when rearing nestlings. Most observations of males with juveniles were made once their chicks had been out of the nest for over a week. By about 14 days of age, many fledglings were finding some food for themselves and, therefore presumably required less from the male. This would have had the effect of decreasing the foraging carried out by males, compared with that for males feeding newly fledged juveniles. In addition, juveniles that had been out of the nest for 10 days or more responded to short bursts of full song from the male by flying to him to be fed or followed him about as he foraged. This would have reduced the maintenance requirements of such males, compared with those of males feeding nestlings and recently fledged chicks: for such parents this involved long food flights to their progeny as well as flights to dispose of faecal sacs. This topic could be readily investigated by sitting near recently fledged juveniles, instead of trying to follow the adults as I did, and comparing the feeding rate with that to chicks that have been out of the nest for about 14 days.

When rearing juveniles, females foraged significantly more than did males partly because of the high December figure for females. The greater proportion of time females foraged in December than previously arose because 4.5 of the 5.6 hours of observations made then were of female B-36296 feeding two juveniles, rather than one juvenile as most did. Overall, B-36296 foraged for 87.7% of observed time. However, this greater time spent by females in foraging and feeding juveniles, may reflect a differing investment in time and energy by the members of a pair in breeding and territorial dominance (Trivers 1972). Female Robins invested much more time and energy in nest-building, egg formation and incubation than did males, whereas males spent more time securing a territory, ousting intruders and establishing the location of their territories' boundaries with their neighbours than did females because, in general, females were dominated by male intruders. Therefore, as predicted by the Trivers's energy-investment hypothesis, males spent significantly more time in territorial defence and vocalizing (full song may help to ward off intruders), than did females. Similarly, Ryan and Dinsmore (1979) found that female American Coots spent more time foraging and feeding young than did males, but that males defended their territories from intruding conspecifics more than did females.

While rearing juveniles, females were able to forage much more than when rearing nestlings, because during the latter stage they spent about 40% of their time brooding.

(b) Food-storing

When rearing juveniles, males and females each spent a similar time storing food, which was about the same as they had while rearing nestlings, presumably because during each stage they caught a similar amount of prey surplus to their own and their progenys' immediate requirements. They stored food for about 0.1% of their time so that such behaviour was infrequent. Storing usually took place when a parent cared for a single juvenile and both birds presumably became satiated. Such an event was rare because if a parent had time to find more than enough food for itself and its young, it usually switched to another behaviour.

(c) Body-maintenance

For males rearing juveniles, a greater proportion of time was spent in body-maintenance in December than in November ($P < 0.01$). This difference arose because sunning began in December. The mean length of a sunning exposure and its associated-preening session was four minutes (Section 7.4.3, p. 102), which was much longer than for most other body-maintenance activities. In addition, some males began moulting in December, even though they were feeding juveniles, and seemed to preen more than did non-moulting males.

The proportion of time non-moulting Robins spent in body-maintenance was inversely related to that they spent foraging (Chapters 9-11). Thus, the increased involvement in this behaviour by males rearing juveniles, compared with those raising nestlings, was probably because the former category of Robins had more time "free" from foraging. Similarly, the marked reduction in body-maintenance by females in December, compared with earlier months ($P < 0.01$), can mainly be attributed to their increased foraging in December ($P < 0.01$).

While rearing juveniles, females spent more time in body-maintenance than did males, probably because females had more time to do so having spent less on vocalizing and territorial defence than did males. Also, perhaps females' brood-patches, which may have been changing from the condition required for brooding, were preened more than the same areas on the male. The apparently greater time females rearing juveniles spent maintaining their plumage (5.9%) compared with those with nestlings (3.4%) may be misleading since females brooding nestlings often preened, but the time was included in brooding.

(d) Vocalizing

I am unable to explain why in November males vocalized more than during October and December. However, the increased singing by males rearing juveniles, compared with when rearing nestlings, probably occurred because males in the former category foraged less and so had more time to sing. Furthermore, this increased singing may have been related to courtship behaviour - pairs were now at the prelaying stage. The female often began another breeding cycle while the male fed the first batch of juveniles. During prelaying, males sang more than at other times (Fig. 6.2A, p. 60), and so it seems likely that the increased singing by males rearing juveniles was related to the fact that some had partners about to lay.

Since females were not heard to sing and spent less time giving the other vocalizations (sub-song and "chucks") than did males during the juvenile-rearing stage (Fig. 6.2, p. 60), females vocalized less than did males. Full song made up 90% of the male's vocalization time during this stage.

(e) Resting

Although Robins tended to rest more when they spent less time foraging, this was not always the case, as is apparent when the total time-budget for males rearing juveniles is compared with that for males rearing nestlings (Figs 18.1 and 17.1, p. 348). Instead of resting more, males with juveniles sang more and were more involved in body-maintenance. Presumably, the need to carry out these two behaviours was greater than that to rest.

For females, the reduced resting and body-maintenance in December, compared with time spent in these behaviours in November, arose because of their increased foraging. Since the proportion of time females spent doing all other behaviours did not change significantly from November to December, this result supports the belief that even while breeding, resting and body-maintenance were low priority behaviours.

(f) Partner-interactions

Even though the partners of males rearing juveniles were sometimes involved in a breeding stage other than rearing juveniles, and the types and frequency of partner-interactions were dependent on the stage of the cycle in which the female was involved, males spent a similar time interacting with their partners as they had when rearing nestlings. Instead of the "attraction" displays used by both partners when rearing nestlings, when tending juveniles the main type of interaction involved males feeding their partners when another breeding cycle had begun, as well as occasional sexual chases, "butterfly-flights", and "attraction" displays (Section 8.3.1, p. 115). Therefore, even though the time spent in partner-interactions was similar for males rearing nestlings or juveniles, and likewise for females, the types of such interactions differed between the two stages.

(g) Territorial defence

The increased time males defended their territories against conspecifics after September was the result of more frequent disputes: these were mainly with juveniles and immatures which strayed into breeding males' territories. Not only did an adult chase out intruding juveniles, but he defended his juveniles from the attacks of a neighbour when the former's progeny moved into a neighbouring territory. During September, few, if any, juveniles were old enough to be independent: many had only recently fledged, had not started to hunt and consequently rarely strayed from their territory. Therefore, they did not get their parents involved in territorial disputes as did older juveniles.

When rearing juveniles, a female spent less time in territorial defence than did the male, because once the male arrived at a dispute that had initially involved his partner and another Robin, the female often returned to foraging or preening, leaving the male to evict the intruder or to display along the boundary if a neighbour was the culprit. Perhaps this reflects the difference in the ability of males and females to secure and retain a territory. Unpaired females were not seen successfully to defend territories against neighbouring males for more than a few days, whereas males usually retained their territories for life. Also, females often began nest-building and stopped feeding their juveniles once the latter had been fledged for 10 to 14 days. Therefore, compared to males, females less often cared for juveniles that were proficient fliers and consequently more likely to stray into a neighbouring territory.

(h) Interspecific interactions

When rearing juveniles, males spent a similar proportion of time each month in interspecific interactions during the course of the breeding season, as did females, and overall each spent as much time in this behaviour as the other. This arose probably because no matter what the month they both responded just as readily to predators and chased other species of birds from near their juveniles. Furthermore, Robins with nestlings or juveniles spent as much time in interspecific interactions, because whether they possessed nestlings or juveniles did not seem to influence the frequency or duration of such interactions.

(i) Feeding progeny

Males spent as much time feeding juveniles as nestlings, but since I did not record the food-trip rates to juveniles it is not known whether males made more trips and spent less time per trip when feeding these than when they fed nestlings. The time that a male took to feed a juvenile was quite variable. If the young bird was near the male when a prey item was found the transfer took only a couple of seconds. However, if the juvenile was some distance away, responded slowly to the male's song, or dropped the food so that the male had to retrieve and return it, the time involved might be more than a minute.

During this study, because the mean date for Robins laying the first egg of their first clutches was about mid-August, by early October the resultant juveniles had been out of the nest for 10 days or more. Therefore, perhaps females spent less time feeding juveniles in October than in September and November, because in the former month most juveniles could fly well, flew to their parent to be fed, and found some food for themselves. During September and November, a greater proportion of the juveniles was newly fledged that females delivered food to. It is of interest that while females foraged more in December than in November ($P < 0.01$), during these two months they spent a similar proportion of time feeding juveniles. This arose because, in December most observations of females raising juveniles were of female B-36296. She foraged more than most females, but did not spend more time feeding her juveniles. Her progeny were more than a fortnight old when I began observations of her and they accompanied her closely so that feedings took place quickly. From the total time-budgets, in contrast to males, females spent more time feeding juveniles than nestlings ($P < 0.01$), because females with juveniles foraged twice as much as did those with nestlings. Presumably, females had more food to feed to juveniles than they had for nestlings.

When rearing juveniles, did male and female Robins spend as much time foraging and caring for their progeny as they did when rearing nestlings? Males raising juveniles spent less time in these behaviours than when rearing nestlings, 84.4 and 88.5% respectively ($P < 0.01$). However, because most juveniles that the observed males were feeding had left the nest for more than a week it is possible that males caring for newly fledged juveniles may have foraged and fed such progeny as much as did males tending nestlings. Since females rearing nestlings spent 46.6% of their time brooding, a behaviour incompatible with foraging and that was crucial to the survival of nestlings, brooding time is incorporated into this calculation. Thus, females rearing juveniles spent 88.5% of time foraging and feeding their young, less than the 91.6% spent foraging, brooding and feeding their young by those rearing nestlings ($P < 0.01$). As for males, this difference may have been because I observed mainly females with juveniles that had been out of the nest for over 10 days and not often were those watched that were caring for newly fledged broods.

As found for Robins, members of a pair of other passerines have been noted to feed particular individuals of their fledged broods: for example, Snares Fernbirds (Best 1973), Grey Warblers (Gill 1980) and Song Sparrows (Smith 1978). Juvenile Robins of a brood were often widely separated from each other and flew weakly when newly fledged. Thus, a likely advantage to parents in caring for specific individuals was to aid the former in locating juveniles and therefore reducing the travel time and energy expenditure when carrying food (Smith 1978). Perhaps the food intake of each juvenile could be more easily regulated. Also, compared with caring for several widely separated young, parents feeding fewer juveniles remaining nearer the latter would be more effectively able to give warnings of the presence of predators.

18.4.2. The diurnal patterns

(a) Foraging

As with males engaged in the prelaying and laying stages (Figs 15.3, p. 290 and 15.4, p. 293), those rearing juveniles tended to forage more in the mid- to late morning than earlier, presumably to make up for their night-time fast and the reduced foraging in the early morning when they sang a lot. Furthermore, because males spent a similar time feeding juveniles during each day-period, but foraged slightly less in the early morning than later, perhaps males ate little of the food they found early on, giving most of it to their juveniles. If this is correct, the increased foraging later in the morning was probably necessary to restore the male's energy reserves.

Since males spent a similar time feeding juveniles as they did nestlings, and both were fed for a similar time each day-period, probably the male's diurnal pattern of food-trips to juveniles was the same as to nestlings (Fig. 17.7, p. 362). Therefore, because the rate of food-trips to nestlings decreased during the course of the afternoon, the increased foraging in the late afternoon may have enabled males to continue feeding their juveniles then and to find extra food to sustain themselves throughout the night.

Females rearing juveniles had the same diurnal pattern of foraging as those involved in the prelaying stage (Fig. 15.3, p. 290), these being the only stages in the breeding cycle when the female's diurnal pattern of foraging was not influenced by nest-building, incubating or brooding. In the afternoon, females foraged more and spent less time feeding their young than in the morning, presumably to allow them to increase their bodily reserves for the night. This second and major diurnal peak in foraging coincided with high ambient temperatures, and perhaps therefore greater invertebrate activity and conspicuousness than at lower temperatures. As a consequence, females would have been able to hunt more efficiently in the afternoon than in the morning and probably foraged in the afternoon to build up their bodily reserves in preparation to start another breeding cycle.

(b) Food-storing

Since males foraged and fed juveniles for a similar time as the day progressed, it was expected that they would also spend a similar time storing food throughout the day. Food stored by Robins rearing juveniles seemed to be surplus to their immediate requirements, so probably by chance males found and stored a similar amount of food each day-period. Females stored food only in the mid- and late morning when they foraged less ($P < 0.05$) than previously. Presumably, they then required less food. At this time of day they also spent more time resting and in body-maintenance, both low priority behaviours compared to foraging. This correlation supports the belief that the stored food was surplus to their needs.

(c) Body-maintenance

Body-maintenance behaviour has been shown to be a low priority behaviour for Robins throughout the year. Males rearing juveniles engaged in body-maintenance mainly in the afternoon. Unfavourable weather conditions for sound propagation are more likely to occur in the afternoon than in the early morning (Section 6.5.1, p. 76). Therefore, having found sufficient food to meet their own and their juveniles' maintenance requirements, it was probably more efficient for males to spend any "spare" time during the morning singing, and that in the afternoon in body-maintenance. By comparison, because females did not sing, but foraged for most of the early morning, presumably by the mid- to late morning they had time to spare for body-maintenance.

(d) Vocalizing

As discussed above and in previous chapters, males spent most time singing in the early morning and reduced it during the course of the day because the early morning was the better time for sound propagation and the least efficient time to forage. Females had no diurnal pattern of vocalizing since their calls, unlike male singing, were of a few seconds duration and were given just as often each day-period.

(e) Resting

Being a low priority behaviour, Robins tended to rest when they had time available after satisfying more important requirements. Therefore, males rearing juveniles rested little in the early morning because almost all time was spent foraging, feeding juveniles and singing. In the late afternoon, foraging, feeding juveniles, body-maintenance and territorial defence took up 97% of males' time, leaving little for resting. Presumably, females rested mainly in the late morning and late afternoon because they found enough food to satisfy themselves and their juveniles in less time then than during the other day-periods.

(f) Partner-interactions

Sexual chasing was the only type of interaction between members of a pair that was found to occur in a distinct diurnal pattern, such chases took place mainly in the early and mid-morning (Fig. 8.2, p. 117). Since members of a pair rearing juveniles were rarely seen in sexual chases, and the other types of partner-interactions occurred at a similar frequency throughout the day, there was no diurnal pattern of involvement in such behaviour for these Robins.

(g) Territorial defence

For songbirds, full song seems to serve to advertise that the territory is occupied and will be defended, and probably helps to warn neighbouring conspecifics against entering the singing birds territory (Krebs

1977, Nice 1943, Welty 1975). Therefore, as would be expected from the above suggestion, when males rearing juveniles sang most during the day, they spent least time defending their territories against conspecifics and *vice versa*. Even though the diurnal pattern of singing for males varied during the various stages of the breeding cycle, males tended to spend less time in territorial defence when they sang most (Figs 14.4, p. 256, 14.5, p. 258 and 15.3, p. 290).

Like those raising nestlings (Fig. 17.6, p. 361), females rearing juveniles exhibited no diurnal pattern of territorial defence, perhaps because they were less often involved in territorial disputes than were males and their involvement was usually for only a short duration.

(h) Interspecific interactions

Almost all cases of Robins interacting with other species involved Robins interacting with birds, rather than mammals. Each species of bird seemed to be just as likely to encounter a Robin during one day-period as another, and this is a possible reason why Robins with juveniles spent a similar time each day-period in interspecific interactions.

(i) Feeding progeny

Unfortunately no record was kept of the rate that Robins fed juveniles each day-period and so it is not known whether the change in time spent feeding juveniles as the day progressed reflects a change in the rate of food-trips to juveniles. However, because the rate of food-trips to nestlings by parent Robins (Fig. 17.7, p. 362) was fairly similar to the parent's diurnal time-pattern when feeding nestlings (Fig. 17.6, p. 361), possibly the same relationship held for Robins feeding juveniles. Adults spent slightly more time feeding juveniles in the early to mid-morning probably because the latter were hungriest then after the night fast.

18.5. Summary

When rearing juveniles, male and female Robins spent 85 to 90% of time in foraging and feeding juveniles, leaving them little time for other behaviours. Such males spent less time foraging than did males rearing nestlings ($P < 0.01$). However, the findings of Royama (1966b) and Smith (1978) were the reverse of mine. The likely reason for my results is that most of my observations were of males whose juveniles were ten or more days old. These juveniles flew to their parents for food, found some food for themselves, and their feather growth was nearly complete. In contrast, males feeding newly fledged juveniles may have had to forage as much as or more than did males when rearing nestlings. Males took food to newly fledged juveniles that remained perched at one place, and these juveniles probably had higher maintenance costs than did nestlings or older juveniles, because newly fledged chicks had incomplete plumage, did not clump and would need further energy to complete feather growth.

Females rearing juveniles foraged much more than did those with nestlings, because the former did not brood their young and so had more time to forage. Overall, females brooded nestlings for about 40% of their time. When rearing juveniles, females foraged more than did males ($P < 0.01$), partly because time spent watching a female rearing two juveniles, instead of the usual one, biased the results. However, it is possible that this represented the true situation and reflected the differing investment in time and energy by the members of a pair in reproduction and territorial defence (Trivers 1972).

In total, males spent 5% of time feeding juveniles, which was similar to the proportion of time spent feeding nestlings. By comparison, females spent more time feeding juveniles than nestlings ($P < 0.01$), because those with juveniles foraged for twice as long as those rearing nestlings and so probably found more food to feed their mobile chicks.

For both males and females rearing juveniles foraging tended to fit a bimodal diurnal pattern, but with the peak times of activity differing between the sexes. Males' peak times were about a day-period later than those of females, because males spent much time singing in the early morning which females spent foraging.

Males spent more time in resting and body-maintenance during the afternoon, but females carried out these behaviours more in the morning. The later peak times of involvement during the day by males compared to females, resulted because males spent most of their "spare" time in the morning singing.

Females devoted gradually less time as the day progressed to feeding juveniles after the mid-morning. Males showed no diurnal pattern in the time they spent feeding juveniles.

GENERAL SUMMARY AND CONCLUSION

Between August 1976 and December 1978, over two non-breeding seasons and three breeding seasons, I studied the South Island Robin's use of time at Kowhai Bush and Outer Chetwode Island (South Island, New Zealand). This species is an insectivorous passerine weighing about 35 g and measuring about 185 mm in length. Robins at the two study areas were colour-banded and of known-age. Five categories of Robins were defined in the non-breeding season (January to July); adult male, adult female, bachelor (unpaired adult male), immature male and immature female. For each month of the non-breeding season, the proportion of observation time spent in each behaviour (a time-budget) and the diurnal patterns of behaviours were determined for each Robin category. During the breeding season (August to December), three categories were evident; male, female and bachelor. Monthly time-budgets and diurnal patterns of behaviours for bachelors were determined. Seven stages to the breeding cycle were distinguishable. For each of these stages monthly time-budgets and diurnal patterns of behaviours were determined for both males and females.

1. The order of priority of behaviours

What was the order of priority in which Robins engaged in the various behaviours? The comparisons between the time-budgets for adult male Robins at Kowhai Bush and on Outer Chetwode Island, and between the monthly time-budgets for the various Robin categories during the non-breeding season at Kowhai Bush showed that a Robin's main priority was to find sufficient food to meet its maintenance needs, with body-maintenance to keep its body surface clean and the plumage ordered being of slightly lesser importance. It seemed that the birds had little control over some of the time spent in a few behaviours; for example, in territorial defence and interspecific interactions. Females, which were usually dominated by their mates, had little control over the time spent in partner-interactions (interactions between members of a pair). When the minimum time necessary for foraging and body-maintenance had been spent, any "spare" time was devoted to resting and more body-maintenance. If still more time was available this was devoted to behaviours associated with reproduction, such as vocalizing and interactions between members of a pair.

The priority of the behaviours did not differ between the various Robin categories, except in the case of vocalizing. In the non-breeding season, males vocalized significantly more than females. Females were not heard to give full song and spent less time giving the other types of vocalizations compared with males. It seemed that males foraged less in order to sing more, since they foraged less than females. However, foraging remained the main priority of males because a significant increase in foraging was sometimes correlated with reduced singing.

On a diurnal basis, it seemed that Robins foraged mainly when they could do so with the greatest efficiency (late morning to mid-afternoon), and to "stock-up" with food before the night fast. The foraging success of Robins was probably lowest in the early morning when low light intensities may have impeded their sighting prey, while low temperatures reduced invertebrate activity. Generally, resting and body-maintenance increased about midday and in the late afternoon. Reproductive behaviours took place more in the early and mid-morning than at other times of the day, particularly in the non-breeding season. Thus, reproductive behaviours seem to be scheduled for that part of the day when they have least effect on time needed for foraging.

In addition, this comparison of the behaviour of the two South Island Robin populations illustrates the plasticity of behaviour possible in passerines. Not only did the adult males of the two populations have very different time-budgets for the same months, but some activities were not exhibited by both populations. Thus, it shows that the findings from the study of a species made in one habitat to deduce the behaviour of other members of the same species elsewhere must be done with great caution. Furthermore, the formulation of theories and models of bird behaviour should not be attempted on the basis of the study of just one population.

2. The non-breeding season

Two important events took place in the non-breeding season, the moult (January to March) followed by a resurgence in territorial and sexual behaviour. Adult birds underwent a complete post-nuptial moult, while immatures seemed to replace all plumage, except their rectrices and remiges. These events have to be borne in mind when considering in what ways the monthly time-budgets differed for the various categories of Robins outside the breeding season.

(a) Foraging

Adults foraged most at the start of their moult, with the proportion of time devoted to this behaviour declining gradually as the moult proceeded, followed by an increase after the completion of the moult during the course of autumn (April-May) and winter (June-July). While moulting, they foraged for more hours per day than at any other time in the non-breeding season. However, in July, just before breeding began, they spent a greater proportion of daylight hours foraging than they did earlier. In contrast, immatures spent a fairly similar proportion of time on foraging throughout the non-breeding season. From January to May they foraged significantly more than adults, but after this birds in the two age classes spent a similar time foraging. Some observations suggested that immatures were less efficient foragers than adults, and therefore the former may have had to forage longer in order to meet their maintenance needs. From May to July, bachelors foraged much less than did paired Robins, while the reverse was true for the time spent singing. Bachelors were not subject to restraints in singing by a mate as were paired males. Mortality data suggest that the low proportion of time bachelors foraged was only just sufficient to meet their immediate food needs, thus having low bodily reserves for use when sudden changes in weather conditions reduced their hunting success.

(b) Food storing

In general, Robins of both age classes spent the most time per day storing food in May and June, even though they spent least hours per day foraging in these months. This was either a consequence of prey availability, especially earthworms being more available in winter than previously, or it could be that Robins stored some food to eat when food found by hunting did not meet their maintenance needs. I consider that the latter hypothesis is the more likely because Robins spent a lower proportion of time foraging and storing food in summer, when food was apparently readily available, than in winter.

(c) Body-maintenance

Adult birds gradually reduced the time spent on body-maintenance as the non-breeding season progressed. In contrast, within the two periods from January to April and from May to July immatures tended to spend similar amounts of time per month in this behaviour, with a significant decrease from April to May. Adults devoted significantly more time per month to body-maintenance than did immatures. With all categories of Robins, a significant increase in foraging from one month to the next was usually correlated with a significant decrease in body-maintenance. Therefore, because adults tended to devote more time to foraging from month to month during the course of the non-breeding season, probably time spent in body-maintenance had to be curtailed. Thus, body-maintenance seems to have been of lower priority than foraging.

(d) Vocalizing

Females vocalized for about 0.3% of the daylight time throughout the non-breeding season. Following the moult, adult males increased the time spent on singing until April (9.5%), after which they drastically reduced singing to 1.5% of their time. This level of vocalizing was maintained throughout winter. This reduction in singing was brought about by females "chucking" at their singing mates, thereby stopping males singing. Likewise, immature males sang more after the moult, but instead of singing less in the late autumn and winter, as adults did, immatures devoted more time to this behaviour then. This was a consequence of immature females not intervening as readily as adult females did when their mates began singing. Thus, from January to April, adult males sang significantly more than did immatures, but in June and July the reverse was true. Bachelors sang much more than did paired males from May to July. As stated earlier, the singing of bachelors was not reduced by the interactions of a mate. The function of bachelor singing seems to be to attract a mate: as soon as a bachelor became paired he abruptly ceased giving almost all full song.

(e) Resting

Adult Robins rested most in February and March, and least during the winter months. Like adults, immatures had a similar pattern of involvement in resting during the course of the non-breeding season, but the latter rested significantly less than did adults from January to May. Generally, a significant increase in foraging was often correlated with a decline in resting. Therefore, because the proportion of time devoted to foraging gradually increased from January to July, that spent on resting had to decline. In addition, after the moult the birds spent much of their "spare" time once they fulfilled their food needs on vocalizing and partner-interactions rather than on resting, as they seemed to do before.

(f) Partner-interactions

All categories of Robins interacted least with their partners during the moult. The proportion of time they spent in this behaviour peaked in autumn and tended to remain at about 2% of their budgets in autumn and winter. Presumably, following the moult an increased secretion of sex hormones from enlarging gonads stimulated the birds to reinforce their pair-bonds, and for unpaired individuals to seek a mate. In general, immatures spent as much time or less in partner interactions than did adults. This may have been a result of immature birds receiving less hormonal stimulation than adults, and/or the immatures having less time to devote to such interactions after finding enough food to meet their maintenance requirements since they foraged more than adults. Because many of the activities involving interactions between members of a pair were related to courtship when the survival of the individual was at stake, such activities were excluded or reduced from their time-budgets.

(g) Territorial defence

Males tended to spend more time in territorial defence (i.e. in interactions with Robins other than their partners) than females, this difference being statistically significant in some months. Male Robins dominated females so that a lone female was unable to defend a territory against neighbouring males, and it seemed that males required a territory before they could establish a pair-bond with a female. Thus, it is not surprising that a male spent more time defending the pair's territory than his partner did. Females spent a rather constant proportion of time in such behaviour (about 1%) throughout the non-breeding season.

Likewise, immature males spent 1.5 to 2.0% of time each month in this behaviour, except in winter when they spent much less time in territorial disputes. There are two possible reasons why immatures defended their territories less in winter than earlier. First, by then each Robin probably recognised his neighbours and the positions of their common boundaries. Consequently, movements beyond their boundaries took place less frequently and therefore less time was spent in boundary disputes. Second, immatures foraged most during the non-breeding season in June and July (winter). Thus, perhaps they had less time available to spend in disputes after meeting their maintenance needs then than previously.

In contrast to immatures, adult males spent significantly more time in territorial defence in March and April (2.5-3.0%) than during other months of the non-breeding season (1.5%). This arose because adult males that had completed their moult began evicting any immatures that had established sub-territories impinging on their territories. Furthermore, the former spent more time in boundary disputes with neighbouring adults, presumably to re-establish the location of their common boundaries. The time immatures spent in interactions with other Robins in March and April is not reflected in their time-budgets. I was unable to follow immature males that were being displaced from a sub-territory, or that had no territory because when I did the resident bird was often attracted as well and this inevitably led to the birds interacting.

(h) Interspecific interactions

In general, all categories of Robins interacted with mammals and with other species of birds for a similar proportion of time each month during the course of the non-breeding season. Almost all such interactions were of Robins chasing or being chased by other birds; interactions with mammals were seldom seen.

Was a diurnal pattern of involvement in each behaviour detectable in the non-breeding season? If so, did the patterns vary from category to category of Robin and from one part of the non-breeding season to another?

Yes, diurnal patterns were evident for all behaviours, except food-storing and interspecific interactions, and these patterns often varied between the sexes and between other categories of Robins. In addition, for a particular category of Robin, the diurnal patterns of some behaviours differed between summer, autumn and winter. The findings are summarised below:-

(a) Foraging

The diurnal pattern of foraging was similar in summer and autumn, but changed in winter. In general, during summer and autumn all categories of Robins had a bimodal pattern of foraging with peaks of activity in the mid- to late morning and mid- to late afternoon, and a significant decline about midday. The morning peak of activity presumably arose to make up for at least some of the energy loss at night and to provide for the morning's activity. The afternoon feeding peak was probably to ensure that an adequate amount of food was eaten to sustain the bird during the night. For males, the major peak of foraging usually arose in the afternoon, but for females it was in the morning. This result was mainly related to the male's diurnal pattern of singing; they spent much of the early and mid-morning singing. In contrast, females devoted little time to vocalizing in the morning and foraged instead.

In winter, none of the data for the various categories of Robins revealed any lull in foraging at midday: the reverse happened, a single diurnal peak of foraging arose in the early to mid-afternoon.

(b) Food-storing

Generally, all categories of Robins spent a similar time during the course of the day storing food throughout the non-breeding season. I am uncertain why the birds had no distinct diurnal pattern of food storing because they did for foraging. Perhaps it was advantageous to have at least some stored food available at all times of the day in case the weather conditions deteriorated and prevented them from finding sufficient food.

(c) Body-maintenance

In summer and autumn, the diurnal pattern of body-maintenance behaviour for adult males and adult females was that of a gradual increase as the morning progressed to a peak about midday, followed by a decline during the afternoon. Although not a significant increase, birds in some categories increased the time spent in body-maintenance in the late afternoon compared with earlier in the day. The midday peak of body-maintenance behaviour was largely a consequence of the decline in time devoted to foraging then, so that more time was available for a low priority behaviour such as this. However, it was also the best time of day for the birds to be able to dry themselves quickly after bathing and for sunning.

Adults in winter and immatures throughout the non-breeding season tended to devote a similar time to this behaviour whatever the time of day. These categories of Robins at the above mentioned times of the year foraged for a similar time each day-period. Thus, there was no increase in time available to devote to body-maintenance activities at midday as there had been earlier for adults.

(d) Vocalizing

In summer, both age classes of females vocalized significantly more early in the morning compared with the rest of the day. This was a result of them giving more sub-song in the early morning than later. For neither category of female was a diurnal pattern of vocalizing evident in autumn and winter. By comparison, male Robins sang much more in the morning than in the afternoon, usually with most singing in the early morning. Sometimes they had a second smaller increase in singing activity about midday. Males sang much more in the early morning than afterwards, probably because it was the time of day when foraging was least profitable and when weather conditions were best for sound propagation.

(e) Resting

When moulting (summer), adults rested most about midday with another slight increase in resting during the late afternoon. Overall, adults in autumn and winter, and immatures throughout the non-breeding season rested for a similar time as the day progressed. It seems that instead of resting more when less time was needed for foraging, the birds devoted their "spare" time to other behaviours, primarily body-maintenance.

(f) Partner-interactions

In summer, paired Robins did not have a distinct diurnal pattern of partner-interaction behaviour. The birds were moulting then and throughout the day interactions between members of a pair were mainly brief skirmishes involving dominant-submissive interactions. However, in autumn and winter they interacted with their partners significantly more in the early and mid-morning compared with later in the day. This resulted because males initiated sexual chases (an interaction involving the male chasing his mate about their territory for an average duration of two minutes) more often in the early and mid-morning than later in the day.

(g) Territorial defence

During summer and autumn all categories of Robins gradually spent more time in territorial defence in the afternoon than in the morning. This seems to be related to the bird's diurnal pattern of vocalizing and foraging. Neighbouring birds were most often near their territorial boundaries when foraging and therefore were more likely to see each other or intrude into an adjacent territory in the afternoon. In the morning males foraged less and vocalized much more than in the afternoon. Therefore, not only were they less likely to notice a trespasser from their song-perches in the canopy, but their singing probably helped to ward off intruders. In winter, when Robins devoted a similar time to foraging each day-period they tended to spend similar amounts of time from one day-period to the next in territorial defence.

(h) Interspecific interactions

Throughout the non-breeding season, all Robins spent similar amounts of time in interspecific interactions as the day progressed. Presumably, this took place because such interactions arose at random during the day.

Why did the Robins stop breeding and begin to moult in summer?

The reason why Robins stopped breeding in early summer and began to moult at such a favourable time of year (long days, high ambient temperatures and, seemingly, abundant food supplies) can largely be attributed to their high food requirements during the moult. A major cause of the increased energy costs of moulting is the loss of heat from highly vascularized feather papillae and the increased surface area exposed to cool temperatures (Lustick 1970, Payne 1972). In summer moulting adult Robins foraged for more hours per day compared with in autumn and winter, when they had completed their moult. Also, it was apparent that January, February and March (summer) were the only months when days were long enough for them to spend sufficient time foraging. By April, not only was daylength too short to enable foraging for the number of hours per day required, but lower ambient temperatures would have increased their maintenance costs. Furthermore, the Robin's prey species seemed less abundant in autumn than in summer. Therefore, it seems that Robins have to moult in summer because later in the non-breeding season they would be unable to find enough food within the day to satisfy their maintenance needs and those associated with moulting.

Do the time-budgets help to explain the Robin's annual pattern of mortality?

Because only two dead adult Robins were found during this study (2.5 years), the birds were sedentary, and very few that had lived in the study area were subsequently found outside it, it was inferred from the disappearance of an adult that it had died. However, because some immatures dispersed considerable distances, such an assumption cannot be applied to them with the same confidence.

In the non-breeding season, the highest mortality of immatures was in summer. It seemed that more immatures died then than later because most had just become independent of their parents and so had to find all their food. Thus, many probably starved because their foraging techniques were poor. By autumn and winter, mortality declined presumably because only the more proficient foragers remained.

In summer, autumn and winter, more immatures than adults died each month. Since in summer and autumn, immature Robins foraged significantly more than adults, it seems highly probable that immatures were less efficient foragers than were adults. Perhaps this inefficient foraging was responsible for the higher mortality of immatures than of adults until autumn, but by winter both age classes spent a similar time foraging.

In the non-breeding season, adult mortality was highest in autumn, even though adults foraged for a greater proportion of time in winter than in summer and autumn. This regular increase in adult mortality could not be explained from the time-budget data.

3. The breeding season

(a) Bachelors

How did the monthly time-budgets for bachelors differ from those for breeding males?

Bachelors foraged less ($P < 0.05$) and sang more ($P < 0.01$) than did breeding males. From the negative correlations between the changes in time bachelors foraged and sang from month to month as the breeding season progressed, it seems that the only time free for singing was that available after maintenance requirements had been met. Therefore, for bachelors, vocalizing was of a lower priority compared with foraging. Their diurnal patterns of involvement in these behaviours support this hypothesis.

For each stage of the breeding cycle, what were the total breeding season time-budgets (time-budgets determined from the combined monthly data recorded over the entire breeding season) for male and female Robins?

(b) Nest-site selection

When selecting a nest-site, both sexes foraged for a similar time (56.0%). Females devoted more time to body-maintenance and resting than did males, the reverse being true for vocalizing, territorial defence and partner-interactions. Males spent 12% of their time enticing their partners to nest-sites. By comparison, females devoted 14% of time to visiting these sites, collecting material and placing it in them. Robins selecting nest-sites did so mainly in the morning. As was evident for other behaviours associated with reproduction, Robins devoted more time to selecting a nest-site in the morning than in the afternoon, possibly because they foraged less efficiently in the early morning. At that time of day prey would be harder to see in the dull light and also they would be less active, hence less conspicuous, at low temperatures. Furthermore, the birds had to spend much of the afternoon stocking up with food to sustain themselves at night and so non-maintenance activities had to be curtailed so that foraging could take place.

(c) Nest-building

During this stage, males foraged (75%) more than their partners (37%). Males made an average of 3.2 food-trips per hour and devoted over four times more time to partner-interactions than did their mates. Nest-building was done solely by the female. She devoted 51% of her time to building, making an average of 22.4 trips per hour with material to the nest. For several reasons it seems that for females to be able to continue building at such an intense rate for up to four days it was necessary for the food females found for themselves to be supplemented by food supplied by their partners.

In the course of the day, females spent gradually less time building and made fewer trips per hour to their nests with building materials. In the afternoon, these birds replaced building as their predominant behaviour with foraging. Males foraged more in the early to mid-morning and had a higher rate of food-trips to their partners then than later in the day.

(d) Prelaying

Males foraged 68% of their time and made 1.5 food-trips per hour to their partners during the prelaying stage. Prelaying females foraged (71%) more than did their mates, probably because they had to meet the high energy requirements of egg formation (King 1972).

When involved in the prelaying stage, males foraged least in the early morning, singing much more then than later, probably because early morning was a less favourable time to forage (Kacelnik 1979) but a good time for sound propagation (Wiley and Richards 1978). In contrast, females foraged most in the early morning, presumably because they had little energy reserves left after the night as a consequence of the drain of self-maintenance and egg formation.

(e) Laying

Males foraged 74% of their time, compared with 62% for their mates. This increased foraging by males over that when involved in the prelaying stage was probably related to the need to find sufficient food to make more frequent food-trips to laying partners (2.5/h) than to prelaying ones (1.5/h). Laying females foraged less than previously for one or any combination of the following possible reasons: they had less time to do so, the food supplied by their partners met more of their requirements than formerly, and/or because the energy required for egg formation was lower in the laying stage when fewer yolks were being formed.

Robins spent a similar time in interspecific interactions during the prelaying and laying stages: they were just as protective of their nests whether they contained eggs or not. Laying females incubated their incomplete clutches 14% of time.

(f) Incubating

In the incubating stage, males foraged 78% of the time. This was significantly more than during the laying stage, probably because they made slightly more trips with food each hour to incubating partners (2.9/h) than to laying ones (2.5/h). It seems reasonable to conclude that incubating females foraged for only 13% of time because their energy requirements were lower than those of non-incubating Robins (Mertens 1977, Walsberg and King 1978), they received much food from their partners, spent little time in energetically-expensive activities and, towards the end of the stage, some of the heat required to keep the eggs warm would have been supplied by the embryos. Females incubated for about 80% of the time. The proportion of time females incubated was influenced by the rate that they received food from their partners. Those females receiving 1.1 food-trips per hour (females whose mates were tending juveniles from the previous nesting) incubated less ($P < 0.01$) than did those that received them 2.9 times per hour (females whose mates were not feeding juveniles). A 10°C rise in ambient temperature in the range of 1.0 to 20.9°C significantly decreased female attentiveness (the proportion of total observation time devoted to incubating). Females were most attentive at the start of the incubation stage and least towards the end.

The diurnal pattern of incubating by females was inversely related to that for foraging; thus a significant increase in foraging was correlated with a significant decline in incubating. In addition, when females received fewer food-trips per hour from their mates from one day-period to the next, females subsequently incubated less and foraged more.

(g) Rearing nestlings

When rearing nestlings, males foraged more (83%) than at any other stage of the breeding cycle: they had to find sufficient food to make about five food-trips per hour when feeding nestlings, a rate greater than the rate of visits with food in the other stages. The proportion of time females foraged (43% overall) seemed to be related to the brooding requirements of their young (47% overall). Thus, when their nestlings were poikilothermic, females foraged less and made fewer food-trips to their broods than did males. When nestlings were one to 15 days old, females brooded one-nestling broods more than broods of two or three ($P < 0.01$), the latter two brood sizes being brooded for a similar proportion of time. The percentage of time males devoted to feeding nestlings depended on the brood size and the nestling's age. The food-trip rate or effort of parent Robins increased *per brood* as the nestlings aged and for a larger brood size, but on the basis of effort *per nestling* it decreased the larger the brood size.

The female's diurnal pattern of brooding showed an increase as the day progressed until mid-afternoon. This routine of brooding was the opposite of that expected, considering that the brooding requirements of nestlings would have been greatest in the early morning when temperatures were generally lowest. It seemed that the female's time spent brooding was modified by her hunger and that of her young after the night fast. In general, both sexes fed their nestlings most frequently in the early morning and the rate gradually slackened during the course of the day.

(h) Rearing juveniles

When caring for juveniles, male and female Robins spent 85 to 90% of their time on foraging and feeding juveniles. Such males foraged less than males raising nestlings ($P < 0.01$). However, the findings of

Royama (1966b) and Smith (1978) for two other species of passerines were the reverse of mine. The likely reason is that most of my observations were of males whose juveniles were ten or more days old. It seems probable that these young would have had lower maintenance costs than would have newly fledged juveniles because the former found some food for themselves and their feather growth was nearly complete. Females with juveniles foraged much more than did those with nestlings, because the former did not brood and so had more time to devote to foraging. Overall, males spent 5% of time on feeding juveniles, which was similar to the proportion of time they spent feeding nestlings. In contrast, females spent more time feeding juveniles than nestlings ($P < 0.01$), because those caring for juveniles foraged for twice as long as those rearing nestlings and so probably had more food to feed their mobile chicks.

For both males and females tending juveniles, foraging tended to fit a bimodal diurnal pattern, but with the peak times of activity differing between the sexes. The male's peak times were slightly later in the day than those of the females, because males spent some time singing in the early morning whereas females foraged. Females devoted gradually less time during the course of the day to feeding juveniles after mid-morning. In contrast, males spent a similar time feeding juveniles throughout the day.

Conclusion

Is "time" a limiting resource for the Robin?

The daily and seasonal allotment of time by birds to their various activities needed for self-maintenance is of vital importance to their survival. The amount of time they devote to a particular activity depends, among other things, on their life style (Pearson 1954, Orians 1961) and body size (Gibb 1954), and the food availability (Gibb 1954) and temperature (Verbeek 1964). Certainly, the most important behaviour of any animal is foraging for food to accumulate sufficient energy to exist. Since foraging is synonymous with energy procurement, it can be considered the behaviour of greatest priority of birds. The time spent foraging is related to the ambient temperature (Verbeek 1964) and the abundance and availability of food (Gibson 1978, Pennycuick and Bartholomew 1973). Time as a limiting factor for birds during particular stages of their annual cycles has been shown by Schartz and Zimmerman (1971) for Dickcissels and Verbeek (1972) for Yellow-billed Magpies. Thus, time is as important a commodity for a species as, for instance, the presence of a suitable nest site.

Only when enough food is eaten to satisfy self-maintenance demands in less than the total available time (the daylight hours for Robins) can other activities and bodily processes requiring additional energy take place. Into the annual cycle birds must fit various bodily functions which require energy, and therefore time, surplus to that needed for self-maintenance; these include reproduction and the moult. Thus, a series of peaks in energy demand occur during the year and these must never exceed the maximum available environmental energy resources. Since environmental energy supplies are variable, the bird is faced with the need to partition conflicting demands for energy in as adaptive a manner as possible (Murton and Westwood 1977). That excessive demands are not made on the environment for food (energy) by the Robin is apparent from the time-budgets.

In winter, when invertebrate production is probably lowest for the year and the low temperatures result in high energy demands for self-maintenance, the birds spent almost all their time on foraging. During spring and summer, higher daytime temperatures lower the energy requirements for existence and food abundance reaches its highest level. It was during these seasons that the Robins bred and underwent their moult. These two processes, requiring extra energy above that needed for self-maintenance, did not occur at the same time, the moult following the completion of breeding. This is particularly evident from Figure 10.1 (p. 145), since late breeders began to moult up to six weeks after bachelors, the former postponing their moult until they had finished breeding.

The belief that winter is the time of year when medium- to small-sized passerines have most difficulty in meeting their self-maintenance requirements is partly supported by the time-budget results for the two Robin populations studied. During June and July (winter), all paired Robins at Kowhai Bush and adult males on Outer Chetwode Island spent 90% or more of their time foraging. This proportion of their time devoted to foraging was greater than for the other months of the non-breeding season and even compared with when the birds were rearing young; the stage of the breeding cycle considered to be most energetically demanding for birds (Murton and Westwood 1977, Verner 1965). With the birds spending most of their time foraging in winter, little, if any, time was devoted to behaviours associated with reproduction. Also, in winter less time was spent on low priority behaviours, such as body-maintenance and resting, compared with in summer and autumn. Thus, these results tend to support the belief that winter is a time when medium-sized passerines have to spend almost all their time foraging in order to meet their self-maintenance needs.

However, some evidence suggests that the large proportion of time the Robins devoted to foraging was not just for the above reason. First, most pairs began breeding in August, by which time daylengths and monthly mean temperatures had increased little compared with the previous two months. Second, while paired males foraged for about 90% of their time in winter, bachelors fed for only 60-80% of theirs. Lastly, the mortality of paired Robins was lower in winter than in autumn. Therefore, perhaps the paired birds spent so much time feeding and fed so intensely in winter not to meet their maintenance demands, but to build up bodily reserves in preparation for breeding. Therefore, it cannot be concluded that for the Robins in Kowhai Bush time was a limiting factor in winter that prevented them finding enough food to survive.

As mentioned above, reproduction requires energy above that needed for self-maintenance, and that the rearing of young is considered to be the most energetically demanding stage of the reproductive cycle. This is borne out by the time-budget results in that parent Robins foraged significantly more and spent less time in low priority behaviours when rearing nestlings than when involved in any of the other stages of the breeding cycle. That breeding Robins devoted as much time as possible to behaviours associated with reproduction is supported by the fact that as daylength, ambient temperature and, apparently, food availability increased during the course of the breeding season females laid larger clutches and the pairs raised more chicks per brood (Flack 1979, pers. obs.).

Studies estimating the energetic cost of egg production have suggested that it is a high energy demanding process for passerines (King 1973, Ricklefs 1974) and that most of the products required for egg formation must be drawn from the daily intake (Murton and Westwood 1977). Therefore, for females to meet this increased energy need, they would be expected to forage more than previously. Again, the time-budget data reflects these high energy costs for female Robins. An experiment suggested that the rapid phase of yolk formation began while the female was nest-building and that it continued as the prelaying and laying stages progressed. During these stages, females devoted most of their time to nest-building and/or foraging. It seems that for females to maintain their intense rate of building over several days and at the same time provide energy nutrients for yolk formation, it was necessary for males to supplement their partners' food intake. Males made an average of 3.2 food-trips per hour to their nest-building partners, a rate greater than at any other stage of the breeding cycle. Once a female had completed her nest and was able to devote more of her time to foraging, her mate's rate of food-trips declined to 1.5 times per hour. Similarly, in order for the female to maintain a high degree of attentiveness to the eggs during the incubation stage, she depended on the food supplied by her partner to supplement that she found herself.

Thus, the bodily processes and activities during the reproductive cycle previously shown by investigators to require high energy inputs to be sustained in other birds were reflected in the time-budget data for Robins. To meet these increased food requirements both parent Robins spent more time foraging. However, if the activities of the female prevented her from foraging for as long as was necessary to meet her requirements, the male increased the time he spent on foraging, supplying food to the female to supplement her own intake. Overall, it seems that early in the breeding season Robins at Kowhai Bush were limited by time from raising a bigger brood than they did. This is suggested by the fact that they spent little, if any, time on low priority behaviours while breeding and increased their clutch size as the breeding season progressed. Presumably, the energy needed to meet self-maintenance requirements declined during the course of the season, either because the days became longer and warmer, or because the birds were able to find the same amount of food (energy) in less time later in the season.

From the results of laboratory experiments, several investigators have found that the food needs and metabolic rates of moulting birds were greater than those of non-moulting individuals (Lustick 1970, Payne 1972, Thompson and Boag 1976). Kendeigh (1973) found that the maximum potential metabolism of the House Sparrow varied seasonally, while the actual total metabolism varied at a value which was approximately constantly lower. Thus, there was a fairly constant margin of safety to allow for conditions of extreme cold or food deprivation, except at the height of the moult when the birds functioned at almost their maximum metabolic rate possible. That free-living populations when moulting do function close to their maximum metabolic rate is shown by the findings of Newton (1966). He noted that in one season, adult Bullfinches *Pyrrhula pyrrhula* which moulted late were faced with diminished food supplies and these birds survived less well than those which had moulted earlier. Therefore, it is apparent from these investigations that the moult can place birds under physiological strain, so that it should not take place at the same time as another process requiring additional energy above that needed for self-maintenance.

That the moult is an energy demanding process for Robins is apparent from the time-budget data. First, few Robins bred and moulted at the same time. The exceptions were birds feeding juveniles at the end of the breeding season. In this case the moulting parents had only just started to moult and did not expend much energy feeding their juveniles, because by then the latter found a large proportion of the food needed to meet their energy requirements. Second, that the Robins stopped breeding in early summer and began to moult at such a favourable time of year (long days, high ambient temperatures and, apparently, abundant food supplies) seems to indicate high food requirements for moulting Robins. Therefore, the moult was undertaken when environmental conditions during the year were optimal for self-maintenance so that as much energy as possible could be devoted to the replacement of the feathers resulting in the process being completed quickly. Third, from the number of hours moulting Robins spent on foraging, it was obvious that January, February and March were the only months of sufficient daylength for the birds to forage for as long as they did. By April, not only was the daylength too short to allow foraging for the number of hours required, but the lower ambient temperatures would have increased self-maintenance costs. Thus, I conclude that the breeding of Robins was terminated before environmental conditions for reproduction became restrictive. They stopped breeding to moult, because there was insufficient time per day for the birds to forage in order to meet the energy requirements of breeding and moulting at the same time.

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Appendix 1. The proportion of total foraging time Robins spent in five foraging methods each month from August 1976 to July 1978. The time spent in hawking and flycatching was not determined from August to November 1976, this time was included as scanning.

Month	Total foraging time (h)	---------Percentage of foraging time spent---------				
		Ground gleaning	Scanning	Vegetation gleaning	Hawking	Fly-catching
1976						
A	13.8	71.48	22.79	5.73		
S	25.9	58.73	37.13	4.14		
O	28.3	58.02	37.85	4.13		
N	32.5	61.81	35.16	3.03		
D	12.4	53.72	39.17	6.78	0.03	0.30
1977						
J	29.0	57.92	38.58	3.28	0.27	0.00
F	40.8	43.08	50.55	5.99	0.19	0.19
M	43.2	43.18	45.81	8.93	1.82	0.26
A	43.6	61.89	32.38	5.47	0.23	0.03
M	46.7	64.65	27.88	7.31	0.14	0.02
J	47.7	68.13	24.57	7.23	0.06	0.01
J	46.5	70.86	22.30	6.77	0.06	0.01
A	33.2	70.06	26.76	3.07	0.10	0.01
S	33.8	75.54	22.00	2.33	0.12	0.01
O	34.4	67.55	29.23	3.05	0.15	0.02
N	33.9	62.69	34.68	2.07	0.50	0.06
D	32.4	50.88	45.90	1.79	1.26	0.17
1978						
J	47.2	55.16	42.35	1.79	0.55	0.15
F	51.4	58.93	39.62	1.14	0.26	0.05
M	52.4	60.01	37.71	1.91	0.30	0.07
A	43.9	61.83	30.10	7.78	0.25	0.04
M	57.2	65.63	29.48	4.76	0.11	0.01
J	43.0	62.24	32.93	4.75	0.08	0.00
J	49.5	67.27	28.25	4.41	0.07	0.00

Appendix 2. Large prey items in the Robin's diet.

A description is given of the large prey animals (>5 mm) and berries that were seen being eaten by Robins. Many smaller invertebrate species were eaten, but as I was usually several metres from the Robin being observed, such foods could not be identified.

The Robin's diet at Kowhai Bush consisted almost entirely of invertebrates with some berries. The large invertebrates which seemed to form the bulk of biomass eaten included earthworms (Oligochaeta), spiders (Arachnida), wetas (*Hemideina* and *Hemiandrus* spp.), stick-insects (*Acanthoxyla* and *Clitarchus* spp.), cicadas (*Amphipsalta zelandica* and *Kikihia subalpina*), snails and slugs (Mollusca), all stages of moths and butterflies (Lepidoptera), and beetles (Coleoptera). Also, many very small items were eaten, especially when Robins foraged amongst litter.

Most food species arose seasonally in the diet. In winter and spring when the soil was moist, earthworms, slugs, snails and larvae of the March Fly predominated. However, by late spring-early summer increasing numbers of larval and adult stages of Lepidoptera were eaten. During January, the cicada *Amphipsalta zelandica* emerged in profusion, and some adult Robins seemed to feed on it almost exclusively. Few cicadas remained by early April when the Robins began feeding on stick-insects, but as soon as autumn rains activated soil-inhabiting invertebrates the stick-insects were largely ignored. In addition, during autumn, mushrooms and toadstools (Agaricales) were broken up by Robins to get at the small invertebrates living in them.

Many instances of berry eating by Robins were seen. *Astelia fragrans, Coprosma rhamnoides, C. robusta, C. propinqua, Coriaria arborea* and *Cyathodes fasciculata* berries were most often eaten, but others included *Carpodetus serratus, Corokia cotoneaster, Melicytus ramiflorus, Muehlenbeckia australis, Pittosporum eugenioides, Pseudopanax arboreus* and *Rubus fruticosus*. Most berries were eaten in summer and autumn. Watson and Bull (1956) recorded a Robin feeding on the fleshy receptacle of *Dacrydium cupressinum* in Westland.

Vegetable matter frequently has a lower nutritive value and poorer digestibility than animal matter (Taitt 1973). Therefore, it might be argued that the proportion of vegetable food ingested is likely to increase only when insufficient animal food is available (Berthold 1976). Such an explanation seems to be the main reason for berry eating by Robins in the summer months. Invertebrate prey was sometimes scarce in summer when dry conditions inhibited the activity of soil-inhabiting organisms and prevented Robins from probing the ground. Moulting took place during summer, and this is known to be an energy demanding process (Lustick 1970). Also, immature Robins may have been forced to consume berries to make up for energy deficiencies caused by their inexperience at finding seasonally occurring prey. Analysis of cast pellets showed that seeds from berries were more numerous in pellets from immature Robins than those from adults ($t = 1.84$, $P < 0.1$) (Powlesland 1979).

Appendix 3. A comparison of monthly time-budgets for adult male Robins at Kowhai Bush and Outer Chetwode Island from April to June 1978.

	Observation time (h)	--Percentage of observation time spent in the various behaviours---							
		F[a]	Fst	Bm	V	R	P	Td	Ie
<u>Kowhai Bush</u>									
April	14.4	71.84	0.85	6.91	12.47	2.51	2.04	2.09	1.29
May	15.5	85.90	0.90	5.27	2.07	2.06	2.18	0.67	0.95
June	15.4	87.07	0.92	2.87	2.30	1.46	3.12	1.40	0.86
<u>Outer Chetwode Island</u>									
April	24.0	86.45	0.19	5.20	0.15	1.73	0.66	2.02	3.80
May	21.6	93.87	0.39	0.89	0.28	1.00	0.36	1.02	2.19
June	17.3	94.93	0.36	0.88	0.21	0.81	0.18	1.04	1.59

F[a] = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting,
P = partner-interactions, Td = territorial defence, Ie = interspecific interactions.

Appendix 4. A comparison of the diurnal patterns of behaviours for adult male Robins at Kowhai Bush and Outer Chetwode Island. The results were from the combined data collected during April to June 1978, see Appendix 3.

Behaviour	Day-periods[a] 1	2	3	4	5	6
Kowhai Bush						
Foraging	74.66	78.43	85.71	84.40	83.90	84.96
Food-storing	0.58	0.99	1.66	1.01	0.65	0.51
Body-maintenance	4.21	7.05	3.53	6.02	4.75	4.39
Vocalizing	13.10	3.22	4.47	1.28	4.75	4.89
Resting	1.73	2.77	1.73	1.57	2.67	1.34
Partner-interactions	3.90	5.80	0.86	1.48	1.08	1.38
Territorial defence	1.25	0.74	0.53	3.45	0.74	1.82
Interspecific interactions	0.57	1.02	1.51	0.81	1.48	0.73
Observation time (h)	8.2	7.6	7.4	6.9	8.5	6.6
Outer Chetwode Island						
Foraging	91.28	91.25	87.73	92.70	91.56	93.58
Food-storing	0.62	0.43	0.19	0.06	0.19	0.18
Body-maintenance	2.68	2.70	5.80	1.56	1.44	0.76
Vocalizing	0.08	0.12	0.31	0.12	0.29	0.39
Resting	0.71	1.33	0.93	1.63	1.52	1.18
Partner-interactions	0.53	0.41	0.12	0.10	0.33	1.18
Territorial defence	2.48	1.14	1.31	1.54	1.27	0.72
Interspecific interactions	1.62	2.62	3.61	2.29	3.40	2.01
Observation time (h)	9.8	11.3	10.9	10.2	11.6	9.1

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[a] The division of the daylight hours into six day-periods of equal length.

Appendix 5. The monthly time-budgets (percentage of observation time) for adult male Robins during the non-breeding season.

Month and Year	Observation time (h)	Hours/day spent foraging	Behaviours[a] F	Fst	Bm	V	R	P	Td	Ie	χ^2 [b]
Jan. 1977	25.2		72.23	0.12	10.30	5.12	10.05	1.01	0.95	0.22	
1978	14.8		80.15	0.22	11.50	1.51	4.31	1.22	0.36	0.73	
Combined	40.0	11.2	75.16	0.16	10.74	3.78	7.93	1.09	0.73	0.41	8 956.8
Feb. 1977	26.5		73.99	0.29	8.52	2.85	11.01	1.34	1.56	0.44	
1978	15.3		76.71	0.09	12.41	1.64	7.34	0.27	1.14	0.40	
Combined	41.8	10.4	74.98	0.22	9.94	2.41	9.67	0.95	1.40	0.43	1 656.8
Mar. 1977	34.6		68.24	0.06	7.39	6.82	12.50	1.18	3.06	0.75	
1978	19.0		82.62	0.21	6.71	2.85	3.27	0.91	2.59	0.84	
Combined	53.6	9.1	73.33	0.11	7.15	5.42	9.23	1.09	2.89	0.78	1 660.9
Apr. 1977	25.0		75.02	0.50	4.89	7.69	7.39	1.24	2.33	0.94	
1978	14.4		71.84	0.85	6.91	12.47	2.51	2.04	2.09	1.29	
Combined	39.4	8.0	73.86	0.63	5.63	9.44	5.61	1.53	2.24	1.06	1 197.9
May 1977	10.9		84.59	0.50	3.69	0.36	4.74	2.61	1.66	1.85	
1978	15.5		85.89	0.91	5.27	2.07	2.06	2.18	0.67	0.95	
Combined	26.4	8.2	85.36	0.74	4.62	1.36	3.16	2.36	1.08	1.32	1 793.4
June 1977	12.5		92.00	0.30	1.33	0.36	1.66	2.09	1.82	0.44	
1978	15.4		87.06	0.92	2.88	2.31	1.45	3.12	1.40	0.86	
Combined	27.9	8.1	89.28	0.64	2.18	1.43	1.55	2.66	1.59	0.67	1 288.0
July 1977	12.2		90.42	0.56	0.79	2.44	2.92	1.61	1.11	0.15	
1978	14.8		89.89	0.39	4.25	0.92	0.87	2.25	0.70	0.73	
Combined	27.0	8.3	90.13	0.47	2.69	1.60	1.80	1.95	0.89	0.47	

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions.

[b] χ^2 values from the variance test for homogeneity of the binomial distribution comparing "combined" time-budgets from month to month. At 7 d.f., $\chi^2 > 20.3$, $P < 0.005$.

Appendix 6. The monthly time-budgets (percentage of observation time) for immature male Robins during the non-breeding season.

Month and Year	Observation time (h)	Hours/day spent foraging	Behaviours[a] F	Fst	Bm	V	R	P	Td	Ie	χ^2 [b]
Jan. 1977	1.2		80.21	2.51	5.93	0.86	8.13	0.00	2.36	0.00	
1978	13.8		85.78	0.64	4.15	2.26	3.45	1.28	1.52	0.92	
Combined	15.0	12.7	85.33	0.79	4.29	2.15	3.83	1.18	1.59	0.84	73 558.0
Feb. 1977	3.3		80.40	0.24	6.50	2.47	8.37	1.42	0.54	0.06	
1978	14.3		91.18	0.00	4.09	0.84	2.10	0.42	1.02	0.35	
Combined	17.6	12.3	89.15	0.05	4.54	1.14	3.28	0.61	0.93	0.30	3 793.0
Mar. 1977	3.2		82.09	0.00	1.62	3.49	8.11	0.49	2.61	1.59	
1978	14.4		90.13	0.03	2.83	3.57	0.75	0.40	1.65	0.64	
Combined	17.6	11.0	88.69	0.03	2.61	3.56	2.07	0.41	1.82	0.81	4 516.6
Apr. 1977	5.5		82.48	0.69	4.90	0.38	7.60	1.41	1.24	1.30	
1978	11.7		86.04	0.56	3.32	3.95	1.61	2.61	1.33	0.58	
Combined	17.2	9.2	84.90	0.60	3.83	2.80	3.53	2.23	1.30	0.81	8 463.0
May 1977	7.6		90.15	0.00	1.18	1.96	2.77	1.04	1.59	1.31	
1978	14.5		89.48	0.55	2.33	2.00	0.96	2.84	1.19	0.65	
Combined	22.1	8.7	89.71	0.36	1.94	1.99	1.58	2.22	1.33	0.87	2 024.7
June 1977	9.8		91.83	1.03	1.05	3.11	1.73	0.87	0.08	0.30	
1978	5.9		88.79	0.70	0.73	2.98	1.70	0.71	0.13	4.26	
Combined	15.7	8.2	90.69	0.91	0.93	3.06	1.72	0.80	0.10	1.79	455.6
July 1977	7.2		86.86	0.20	1.24	8.76	1.36	1.04	0.00	0.54	
1978	7.8		91.02	1.13	1.28	2.50	0.74	1.94	1.04	0.35	
Combined	15.0	8.3	89.03	0.69	1.26	5.49	1.04	1.51	0.54	0.44	

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions.

[b] χ^2 values from the variance test for homogeneity of the binomial distribution comparing "combined" time-budgets from month to month. At 7 d.f., $\chi^2 > 20.3$, $P < 0.005$.

Appendix 7. The monthly time-budgets (percentage of observation time) for bachelor Robins during the non-breeding season.

Month and Year	Observation time (h)	Hours/day spent foraging	Behaviours[a]							χ^2[b]
			F	Fst	Bm	V	R	Td	Ie	
May 1977	10.5		81.94	0.30	3.84	6.42	4.99	1.22	1.29	
1978	4.8		68.13	0.81	2.97	18.61	1.53	6.81	1.14	
Combined	15.3	7.5	77.65	0.46	3.57	10.21	3.91	2.96	1.24	
June 1977	8.2		82.69	0.39	0.77	12.58	2.60	0.42	0.55	2 334.9
1978	4.2		69.01	0.35	2.43	25.19	1.01	1.24	0.77	
Combined	12.4	7.1	78.01	0.38	1.34	16.89	2.05	0.70	0.63	
July 1977	10.6		65.95	0.68	0.62	28.96	2.42	0.99	0.38	2 904.5
1978	5.4		59.53	1.79	1.49	34.78	1.54	0.00	0.87	
Combined	16.0	6.0	63.80	1.05	0.91	30.92	2.12	0.66	0.54	

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, Td = territorial defence, Ie = interspecific interactions.

[b] χ^2 values from the variance test for homogeneity of the binomial distribution comparing "combined" time-budgets from month to month. At 6 d.f., $\chi^2 > 20.3$, $P < 0.005$.

Appendix 8. The diurnal patterns of behaviours (percentage of observation time per day-period) for adult male Robins during parts[a] of the non-breeding season.

	Behaviours[b]								Observation
Day-periods	F	Fst	Bm	V	R	P	Td	Ie	time (h)
Summer									
1	73.43	0.64	8.01	6.98	6.64	1.54	2.50	0.26	21.2
2	75.01	0.08	8.48	4.20	8.48	1.25	2.01	0.49	30.1
3	68.54	0.09	11.81	6.13	11.35	0.88	0.67	0.53	27.2
4	76.30	0.05	9.47	1.51	9.55	0.75	1.47	0.90	23.0
5	77.83	0.02	6.98	2.22	7.80	0.87	3.44	0.84	17.6
6	78.26	0.08	8.74	1.13	9.47	0.91	1.07	0.34	16.2
Autumn									
1	65.69	1.01	3.30	21.88	3.97	2.36	0.53	1.26	12.3
2	80.51	0.95	6.33	3.01	4.11	3.53	0.56	1.00	9.6
3	82.33	0.67	5.35	2.82	5.31	1.10	0.20	2.22	10.0
4	78.34	0.78	7.52	1.03	4.29	2.01	5.24	0.79	12.2
5	82.49	0.45	5.65	2.96	4.58	1.07	1.84	0.98	13.0
6	84.06	0.05	2.76	3.35	5.92	1.13	1.72	1.01	9.0
Winter									
1	85.64	0.47	2.74	2.26	2.07	5.14	0.84	0.84	10.1
2	90.30	0.38	0.78	1.25	1.98	2.89	1.93	0.49	10.0
3	88.52	1.05	3.00	3.02	1.19	1.20	1.63	0.39	7.8
4	92.84	0.57	1.33	1.03	1.53	1.54	0.90	0.26	9.2
5	90.61	0.48	3.51	0.79	1.41	1.29	1.31	0.60	10.1
6	90.52	0.46	3.50	0.85	1.76	1.25	0.80	0.86	7.9

[a] Summer = January, February and March; Autumn = April and May; Winter = June and July.

[b] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions.

Appendix 9. The diurnal patterns of behaviours (percentage of observation time per day-period) for immature male Robins during three parts[a] of the non-breeding season.

	Behaviours[b]								
Day-periods	F	Fst	Bm	V	R	P	Td	Ie	Observation time (h)
Summer									
1	81.51	0.06	3.99	9.38	2.32	1.04	0.90	0.80	7.7
2	87.82	0.08	4.28	0.86	4.45	1.54	0.61	0.36	10.0
3	88.66	1.00	5.00	0.78	2.84	0.18	0.47	1.07	7.5
4	86.00	2.11	4.22	2.11	3.24	0.00	1.95	0.37	8.6
5	90.20	0.00	2.09	0.38	1.76	0.37	4.57	0.63	8.6
6	90.24	0.15	3.52	0.81	3.29	0.91	0.66	0.42	9.1
Autumn									
1	81.14	0.40	2.03	4.28	3.58	7.30	0.55	0.72	7.3
2	90.61	0.96	2.31	0.42	1.55	1.27	1.89	0.99	6.8
3	85.07	0.45	3.98	2.68	3.38	1.19	2.48	0.77	6.8
4	89.10	0.30	1.79	3.90	1.73	0.86	1.51	0.81	6.2
5	91.24	0.32	2.78	0.74	1.32	0.59	2.20	0.81	5.7
6	85.33	0.41	4.15	0.55	2.50	1.99	4.00	1.07	5.6
Winter									
1	88.34	0.49	0.41	3.95	2.03	2.28	1.95	0.55	2.9
2	92.88	0.06	0.85	2.78	1.58	1.19	0.32	0.34	5.1
3	90.08	0.74	2.75	2.56	1.26	1.46	0.24	0.91	3.6
4	91.66	0.37	0.76	2.26	1.22	1.63	0.12	1.98	6.4
5	93.53	1.10	0.60	1.54	1.12	1.18	0.00	0.93	6.3
6	93.36	0.94	0.45	1.25	0.95	0.88	0.14	2.03	5.1

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[a] Summer = January, February and March; Autumn = April and May; Winter = June and July.

[b] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions.

Appendix 10. The diurnal patterns of behaviours (percentage of observation time per day-period) for bachelor Robins (unpaired adult males) during parts[a] of the non-breeding season.

	Behaviours[b]							Observation
Day-periods	F	Fst	Bm	V	R	Td	Ie	time (h)
Autumn								
1	64.99	0.26	0.62	27.69	6.14	0.00	0.30	3.1
2	73.20	0.59	2.81	17.25	3.48	0.13	2.54	3.7
3	89.66	0.24	0.59	1.70	3.64	2.53	1.64	1.6
4	76.78	0.33	8.54	1.48	4.40	7.95	0.52	2.7
5	75.24	0.97	8.93	0.24	3.08	9.90	1.64	1.8
6	94.37	0.46	1.09	0.57	2.04	0.72	0.75	2.5
Winter								
1	43.47	0.37	0.85	52.34	2.73	0.14	0.10	7.3
2	66.84	0.72	1.03	28.48	2.19	0.34	0.40	6.3
3	67.61	0.12	1.20	26.32	3.08	0.38	1.29	3.1
4	85.91	1.74	1.36	7.66	1.56	0.49	1.28	7.1
5	90.28	0.42	1.28	2.30	0.71	4.95	0.06	2.3
6	96.86	0.25	0.89	0.49	1.51	0.00	0.00	2.3

[a] Autumn = May only; Winter = June and July.

[b] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, Td = territorial defence, Ie = interspecific interactions.

Appendix 11. The monthly time-budgets (percentage of observation time) for adult female Robins during the non-breeding season.

Month and Year	Observation time (h)	Hours/day spent foraging	Behaviours[a] F	Fst	Bm	V	R	P	Td	Ie	χ^2 [b]
Jan. 1977	8.3		60.12	0.06	27.53	0.27	9.83	1.67	0.43	0.09	
1978	15.7		75.54	0.05	16.43	0.56	4.01	1.10	1.49	0.82	
Combined	24.0	10.5	70.23	0.06	20.25	0.46	6.01	1.30	1.12	0.57	6 290
Feb. 1977	16.6		76.69	0.09	9.49	0.13	10.45	1.58	0.95	0.62	
1978	15.0		87.45	0.19	7.25	0.05	2.58	1.13	0.90	0.45	
Combined	31.6	11.3	81.78	0.14	8.43	0.09	6.72	1.37	0.93	0.54	378
Mar. 1977	12.6		77.21	0.00	7.72	0.17	12.26	1.81	0.15	0.68	
1978	12.3		83.26	0.04	8.32	0.32	4.06	1.54	1.90	0.56	
Combined	24.9	9.9	80.20	0.02	8.01	0.25	8.21	1.68	1.01	0.62	7 774
Apr. 1977	18.7		70.16	0.14	6.85	0.12	6.15	3.49	12.56	0.53	
1978	13.3		87.72	0.56	4.04	0.05	1.49	3.47	1.80	0.87	
Combined	32.0	8.4	77.44	0.31	5.69	0.09	4.22	3.48	8.10	0.67	10 229
May 1977	17.3		89.16	0.09	4.72	0.02	2.82	1.61	0.88	0.70	
1978	14.4		92.57	0.18	2.55	0.09	1.11	2.81	0.39	0.30	
Combined	31.7	8.8	90.71	0.13	3.73	0.05	2.04	2.16	0.66	0.52	794
June 1977	9.8		90.20	0.05	1.88	0.26	1.93	1.52	1.88	0.28	
1978	11.4		88.91	1.05	6.35	0.26	0.87	1.94	0.35	0.27	
Combined	21.2	8.2	90.42	0.59	4.29	0.26	1.36	1.75	1.06	0.27	1 598
July 1977	13.0		92.85	0.18	0.88	0.12	2.22	2.26	1.15	0.34	
1978	14.9		93.98	0.19	2.31	0.07	0.71	2.13	0.08	0.53	
Combined	27.9	8.7	93.45	0.19	1.65	0.09	1.41	2.19	0.58	0.44	

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions

[b] χ^2 values from the variance test for homogeneity of the binomial distribution comparing the combined time-budgets from month to month. At 7 d.f. $\chi^2 > 20.3$, $P < 0.005$.

Appendix 12. The monthly time-budgets (percentage of observation time) for immature female Robins during the non-breeding season.

Month and Year	Observation time (h)	Hours/day spent foraging	Behaviours[a] F	Fst	Bm	V	R	P	Td	Ie	χ^2 [b]
Jan. 1977	2.5		89.36	0.26	2.12	0.11	5.79	0.80	1.36	0.20	
1978	12.7		91.52	0.02	4.39	0.89	1.12	0.65	0.81	0.60	
Combined	15.2	13.6	91.16	0.06	4.01	0.77	1.89	0.68	0.90	0.53	
Feb. 1977	7.4		82.76	0.16	7.68	0.09	6.13	1.37	1.13	0.68	832
1978	14.9		90.84	0.18	5.22	0.41	2.03	0.74	0.52	0.06	
Combined	22.3	12.2	88.16	0.17	6.03	0.30	3.39	0.96	0.72	0.27	
Mar. 1977	7.3		87.32	0.06	3.54	0.04	4.47	3.67	0.70	0.20	908
1978	14.7		92.01	0.18	4.26	0.07	1.12	0.85	0.99	0.52	
Combined	22.0	11.2	90.45	0.13	4.02	0.06	2.24	1.79	0.90	0.41	
Apr. 1977	7.7		88.58	0.00	2.49	0.02	4.28	2.38	2.08	0.17	313
1978	13.2		89.59	0.25	4.13	0.19	1.70	1.81	1.01	1.32	
Combined	20.9	9.7	89.22	0.16	3.52	0.13	2.65	2.02	1.40	0.90	
May 1977	7.2		92.72	0.07	0.79	0.16	2.72	2.38	0.35	0.81	1 711
1978	15.3		94.24	0.42	1.67	0.17	0.42	2.09	0.69	0.30	
Combined	22.5	9.1	93.76	0.31	1.39	0.17	1.15	2.18	0.58	0.46	
June 1977	11.4		94.46	0.25	1.14	0.24	1.20	1.92	0.53	0.26	280
1978	12.1		93.57	0.82	1.34	0.26	0.97	1.39	1.42	0.23	
Combined	23.5	8.5	94.01	0.54	1.24	0.25	1.08	1.65	0.99	0.24	
July 1977	9.7		94.80	0.35	0.87	0.10	1.32	1.99	0.21	0.36	1 004
1978	14.1		93.28	0.52	3.16	0.12	0.52	2.31	0.02	0.07	
Combined	23.8	8.8	93.90	0.45	2.23	0.11	0.84	2.18	0.10	0.19	

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions.

[b] χ^2 values from the variance test for homogeneity of the binomial distribution comparing the "combined" time-budgets from month to month. At 7 d.f. $\chi^2 > 20.3$, $P < 0.005$.

Appendix 13. The diurnal patterns of behaviours (percentage of observation time per day-period) for adult female Robins during three parts[a] of the non-breeding season.

	Behaviours[b]								Observation
Day-periods	F	Fst	Bm	V	R	P	Td	Ie	time (h)
Summer									
1	83.84	0.14	6.65	0.88	4.67	2.45	0.71	0.66	10.8
2	80.13	0.17	11.63	0.16	4.68	2.17	0.56	0.50	11.4
3	71.79	0.00	16.73	0.17	8.89	1.59	0.38	0.45	17.8
4	77.07	0.11	12.27	0.12	8.24	0.84	0.79	0.56	17.6
5	77.28	0.06	13.42	0.07	6.06	1.16	1.57	0.38	12.3
6	81.40	0.00	6.47	0.23	7.55	0.71	2.62	1.02	10.5
Autumn									
1	85.91	0.20	2.67	0.10	2.73	7.14	0.35	0.90	6.8
2	86.06	0.31	5.53	0.04	2.74	3.90	0.85	0.57	12.0
3	88.12	0.22	4.97	0.13	3.20	2.54	0.29	0.53	15.2
4	76.15	0.16	7.04	0.07	3.71	1.25	11.35	0.27	11.3
5	83.30	0.13	3.25	0.03	2.66	1.75	8.37	0.51	12.0
6	87.60	0.29	2.55	0.03	3.33	1.39	4.12	0.69	8.4
Winter									
1	90.31	0.67	2.05	0.31	1.46	4.92	0.00	0.28	5.1
2	90.21	0.72	2.76	0.17	1.63	2.65	0.86	1.00	8.3
3	92.97	0.17	3.52	0.14	1.11	1.12	0.75	0.22	12.5
4	94.20	0.45	1.55	0.04	1.16	1.47	0.95	0.18	8.1
5	92.25	0.12	3.83	0.03	1.46	1.34	0.63	0.34	7.2
6	91.89	0.22	2.42	0.37	1.70	1.96	1.24	0.20	7.9

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[a] Summer = January, February and March; Autumn = April and May; Winter = June and July.

[b] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions.

Appendix 14. The diurnal patterns of behaviours (percentage of observation time per day-period) for immature female Robins during three parts[a] of the non-breeding season.

Day-periods	Behaviours[b] F	 Fst	 Bm	 V	 R	 P	 Td	 Ie	Observation time (h)
Summer									
1	89.88	0.46	3.89	1.12	3.17	0.52	0.77	0.19	8.4
2	90.57	0.05	3.39	0.04	2.75	1.43	1.48	0.29	9.9
3	92.10	0.25	3.75	0.28	2.01	0.82	0.29	0.50	9.1
4	85.11	0.00	7.75	0.59	5.27	0.60	0.31	0.37	11.2
5	89.91	0.08	3.92	0.05	2.46	2.23	0.83	0.52	11.4
6	89.67	0.02	5.09	0.01	2.16	1.31	1.47	0.27	9.3
Autumn									
1	88.82	0.06	3.31	0.03	1.46	4.48	0.31	1.53	7.6
2	91.15	0.73	2.40	0.13	2.03	2.89	0.00	0.67	7.4
3	93.05	0.70	2.62	0.06	0.53	1.57	0.56	0.91	5.4
4	87.24	0.06	1.99	0.23	1.50	0.96	7.78	0.24	9.1
5	90.97	0.00	1.68	0.18	3.00	1.33	2.26	0.58	7.2
6	91.89	0.00	2.57	0.19	2.42	1.28	1.43	0.22	6.9
Winter									
1	93.18	0.31	0.38	0.33	1.46	3.80	0.37	0.17	6.5
2	92.70	0.16	2.72	0.47	0.58	2.91	0.36	0.10	7.3
3	94.34	0.96	1.49	0.06	1.27	1.62	0.00	0.26	7.6
4	95.50	0.17	2.53	0.05	0.54	0.84	0.16	0.21	6.8
5	94.87	0.34	0.91	0.29	1.38	1.04	0.98	0.19	10.4
6	92.65	0.60	2.45	0.33	0.59	1.95	1.06	0.37	9.1

[a] Summer = January, February and March; Autumn = April and May; Winter = June and July.

[b] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions.

Appendix 15. The monthly and total time-budgets (percentage of observation time) for bachelor Robins during the breeding season.

Month and Year	Observation time (h)	Hours/day spent foraging	Behaviours[a]						
			F	Fst	Bm	V	R	Td	Ie
Aug. 1976	3.8		56.05	0.25	4.48	24.63	13.27	0.78	0.54
1977	6.9		57.23	0.15	2.35	36.51	3.11	0.02	0.63
Total	10.7	5.9	56.82	0.18	3.11	32.26	6.74	0.29	0.60
Sept.1976	5.8		49.69	0.02	0.79	38.09	11.33	0.00	0.08
1977	7.9		72.05	0.23	1.82	22.61	2.77	0.00	0.52
Total	13.7	7.4	62.61	0.14	1.39	29.13	6.40	0.00	0.33
Oct. 1976	4.8		48.49	0.06	2.68	34.74	11.08	2.52	0.43
1977	8.7		66.35	0.40	7.48	23.30	1.46	0.67	0.34
Total	13.5	8.0	59.99	0.28	5.77	27.37	4.89	1.33	0.37
Nov. 1976	5.7		50.16	0.29	3.13	39.79	6.30	0.02	0.31
1977	5.3		60.50	0.24	8.74	25.37	4.52	0.00	0.63
Total	11.0	8.1	55.13	0.26	5.83	32.87	5.44	0.01	0.46
Dec. 1976	2.9		48.82	0.00	11.39	23.53	14.36	1.75	0.15
1977	5.6		48.08	0.10	36.12	10.16	3.28	0.64	1.62
Total	8.5	7.4	48.33	0.07	27.63	14.75	7.08	1.02	1.12
Total 1976	23.0		50.50	0.13	3.73	33.72	10.74	0.88	0.30
1977	34.4		61.95	0.24	10.01	23.97	2.86	0.28	0.69
Total	57.4		57.35	0.20	7.49	27.88	6.03	0.52	0.53

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizations, R = resting, Td = territorial defence, Ie = interspecific interactions.

Appendix 16. The diurnal patterns of behaviours (percentage of observation time per day-period) for bachelor Robins during three portions[a] of the breeding season.

	Behaviours[b]							Observation time (h)
Day-periods	F	Fst	Bm	V	R	Td	Ie	
Early								
1	36.72	0.15	0.69	57.50	4.76	0.00	0.18	4.0
2	51.41	0.00	0.54	42.40	5.41	0.00	0.24	5.7
3	60.56	0.09	1.51	29.93	7.59	0.00	0.32	4.4
4	68.97	0.60	3.94	16.76	8.90	0.00	0.83	4.9
5	73.71	0.00	0.33	15.99	9.97	0.00	0.00	2.2
6	80.19	0.00	6.13	8.12	3.57	0.95	1.04	3.3
Middle								
1	33.40	0.75	1.38	60.93	3.10	0.00	0.44	3.3
2	52.01	0.23	5.91	36.67	4.82	0.02	0.34	7.0
3	63.63	0.07	5.25	25.01	3.81	1.81	0.42	5.3
4	65.94	0.17	5.89	18.12	8.17	1.25	0.46	4.6
5	66.82	0.40	10.43	15.32	6.23	0.67	0.13	3.7
6	92.22	0.00	3.69	0.16	1.34	0.00	2.59	0.5
Late								
1	8.23	0.00	4.83	78.77	6.20	1.57	0.40	0.5
2	51.82	0.00	26.56	14.76	5.06	0.75	1.05	2.1
3	35.74	0.00	37.69	16.06	8.48	0.00	2.03	2.4
4	66.61	0.00	16.57	5.24	9.77	1.73	0.08	2.1
5	51.81	0.38	35.54	4.62	4.33	1.90	1.42	1.6
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[a] Early = August and September, Middle = October and November, Late = December.

[b] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, Td = territorial defence, Ie = interspecific interactions.

Appendix 17. The monthly and total time-budgets (percentage of observation time) for male and female Robins during the nest-site selection stage of the breeding cycle. The data from observations made over the three breeding seasons have been combined.

Month	Observation time (h)	Hours/day spent foraging	Behaviours[a]										
			F	Fst	Bm	V	R	P	Td	Ie	Nss	Nb	Fp
Male													
Aug.	2.0	5.6	54.00	0.00	1.71	1.57	10.37	9.62	3.80	0.66	18.27		
Sept.	3.2	7.6	64.48	0.14	4.85	7.35	3.88	6.58		0.49	10.17		2.06
Oct.	1.7	8.9	67.11	0.66	5.09	7.72	6.60	4.60		1.20	7.02		
Nov.	2.2	8.4	57.42	0.70	2.68	11.50	7.02	3.91		0.25	16.12		0.40
Dec.	0.3	8.6	55.90		8.15	6.20	22.10	1.10		1.15	5.40		
Total	9.4		60.81	0.33	3.84	7.13	7.11	6.05	0.80	0.62	12.52		0.79
Female													
Aug.	2.8	6.5	62.26	1.50	7.29	0.06	12.40	1.98			1.33	13.18	
Sept.	3.4	5.7	48.17	1.11	17.47	0.04	18.13	2.73		0.20	1.60	7.69	2.86
Oct.	3.7	7.8	58.72	0.06	11.24	0.89	9.28	2.59		1.07	14.86	1.29	
Nov.	1.4	8.1	55.29	0.42	8.24	3.87	10.63	2.37			7.24	11.94	
Dec.	-												
Total	11.3		56.00	0.77	11.77	0.80	12.88	2.45		0.41	6.60	7.46	0.86

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Nss = nest-site selection, Nb = nest-building, Fp = feeding progeny.

Appendix 18. The monthly and total time-budgets (percentage of observation time) for male and female Robins during the nest-building stage of the breeding cycle. The data from observations made over the three breeding seasons were combined.

			Behaviours[a]								
Month	Observation time (h)	Hours/day spent foraging	F	Fst	Bm	V	R	P	Td	Ie	Nb
Male											
Aug.	5.4	8.7	84.11	0.31	2.58		6.71	3.55	0.16	2.58	
Sept.	4.6	9.1	77.01	0.99	4.56	6.03	2.63	6.15	1.00	1.63	
Oct.	3.2	9.7	73.25	0.12	3.43	11.45	3.37	7.52	0.51	0.35	
Nov.	4.6	10.3	70.47	0.41	5.64	7.24	3.62	10.72	0.43	1.47	
Dec.	1.7	8.9	57.92	0.22	3.90	14.57	8.12	13.96		1.31	
Total	19.5		75.20	0.45	4.02	6.25	4.59	7.40	0.47	1.62	
Female											
Aug.	5.8	5.5	52.64	0.25	3.68	0.04	6.17	1.67	0.58	0.43	34.54
Sept.	6.9	3.3	28.14		2.12	0.26	7.68	1.76	0.26	0.36	59.42
Oct.	4.0	1.8	13.74	0.07	0.53	0.01	4.18	2.57	0.21	0.46	78.23
Nov.	4.5	8.4	57.38		4.26		6.30	0.62	0.10	1.21	30.13
Dec.	1.0	3.1	20.11		7.45		6.77				65.67
Total	22.2		37.51	0.08	2.92	0.09	6.33	1.57	0.29	0.55	50.66

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Nb = nest-building.

Appendix 19. The diurnal patterns of behaviours (percentage of observation time) during the nest-site selection stage for male and female Robins.

Day-period	Observation time (h)	Behaviours[a]										
		F	Fst	Bm	V	R	P	Td	Ie	Nss	Nb	Fp
Male												
1	0.9	58.70	1.77	0.21	7.50	0.47	4.60		0.44	22.08		4.23
2	3.5	60.09		1.61	2.34	9.60	8.05	2.14	0.37	15.62		0.18
3	2.2	52.73	0.72	8.50	15.43	4.55	8.43		0.65	8.99		
4	1.5	64.94		5.44	6.49	6.70	2.94		1.65	9.94		1.90
5	1.3	73.03		2.58	6.46	9.64	1.22		0.17	6.71		0.19
6	-											
Female												
1	-											
2	3.3	62.78	0.12	4.42		7.93	1.65		0.46	15.12	7.52	
3	1.7	55.98		7.09	3.26	9.43	3.05			4.90	16.29	
4	4.8	59.65	0.94	14.54	0.72	15.08	1.70		0.50	1.32	5.55	
5	1.3	29.98	2.81	26.66		24.47	4.65		0.50	7.34	3.59	
6	-											

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Nss = nest-site selection, Nb = nest-building, Fp = feeding progeny.

Appendix 20. The diurnal patterns of behaviours (percentage of observation time) during the nest-building stage for male and female Robins.

Day-period	Observation time (h)	Behaviours[a] F	Fst	Bm	V	R	P	Td	Ie	Nb
Male										
1	2.2	83.46	1.44	1.92	3.36	1.35	6.29	0.40	1.78	
2	6.7	77.42	0.30	2.47	3.41	3.93	10.41	0.68	1.38	
3	2.8	64.51	0.75	7.15	15.93	4.76	5.95	0.59	0.36	
4	3.8	72.09	0.09	6.02	4.08	7.61	7.50	0.52	2.09	
5	3.5	78.68	0.61	3.38	6.72	4.87	3.29		2.45	
6	0.3	63.90		7.15	22.60	0.85	5.50			
Female										
1	2.3	14.09		0.06	0.01	8.18	1.39		0.34	75.93
2	7.5	27.60	0.04	1.41	0.13	4.49	2.23	0.56	0.52	63.02
3	4.1	30.41		5.15	0.13	5.69	1.74	0.43	0.94	55.51
4	3.7	55.04		2.21	0.07	6.19	0.83		0.53	35.13
5	3.3	53.27	0.42	5.72	0.06	11.89	1.87	0.05	0.12	26.60
6	1.2	69.50		4.48		1.38		0.25	1.09	23.30

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Nb = nest-building.

Appendix 21. The monthly and total time-budgets (percentage of observation time) for male and female Robins during the prelaying stage.

Month	Observation time (h)	Hours/day spent foraging	Behaviours[a] F	Fst	Bm	V	R	P	Td	Ie	Nb
Male											
Aug.	6.0	7.8	74.86	0.01	2.04	12.98	6.31	3.34	0.38	0.08	
Sept.	4.9	6.3	60.42	0.31	2.57	28.30	7.03	0.86	0.30	0.21	
Oct.	8.5	9.5	71.28	0.14	2.31	16.85	3.48	3.89	0.86	1.19	
Nov.	4.1	8.5	57.90		9.17	14.15	11.72	4.37	1.85	0.84	
Dec.	5.3	10.3	67.41	0.06	15.74	6.36	4.27	2.35	2.07	1.74	
Total	28.8		67.57	0.11	5.75	15.65	6.00	3.05	1.03	0.84	
Female											
Aug.	11.1	8.2	78.62	0.06	8.03	0.15	10.04	2.10	0.50	0.44	0.06
Sept.	9.9	8.2	69.73	0.25	13.43	0.17	13.53	1.89	0.19	0.56	0.25
Oct.	7.8	9.0	67.83	0.39	15.66	0.64	11.89	1.89	0.01	0.42	1.27
Nov.	13.3	10.4	71.46	0.23	18.23	0.04	6.33	1.90	1.04	0.76	0.01
Dec.	9.6	10.3	67.20	0.03	14.47	0.13	10.71	4.14	0.09	1.65	1.58
Total	51.7		71.33	0.18	14.04	0.20	10.15	2.36	0.43	0.76	0.55

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Nb = nest-building.

Appendix 22. The monthly and total time-budgets (percentage of observation time) for male and female Robins during the laying stage of the breeding cycle.

Month	Observation time (h)	Hours/day spent foraging	Behaviours[a]									
			F	Fst	Bm	V	R	P	Td	Ie	Nb	Inc
Male												
Aug.	2.3	9.1	87.37		2.21	1.12	6.37	1.22		1.71		
Sept.	5.4	7.9	67.02	0.79	13.28	8.34	2.08	7.69		0.80		
Oct.	4.0	10.9	82.14	0.20	5.87	4.36	1.66	4.38		1.39		
Nov.	4.9	11.5	78.78		6.90	2.66	3.79	4.98	1.29	1.60		
Dec.	5.1	9.8	64.02	0.03	21.79	3.79	2.82	4.70	2.69	0.16		
Total	21.7		73.95	0.24	11.26	4.49	3.02	5.08	0.92	1.04		
Female												
Aug.	4.5	7.5	72.34	0.04	8.27	0.29	4.22	1.36		0.53	0.53	12.42
Sept.	6.3	9.1	77.37	0.56	5.39	0.59	11.45	2.94		1.22	0.43	0.05
Oct.	11.6	7.5	56.16	0.04	11.61		9.95	1.47	0.94	0.82	0.43	18.58
Nov.	5.3	8.0	54.60	0.33	7.30		7.01	2.57		0.33		27.86
Dec.	3.9	8.4	54.93	0.25	15.03		19.70	2.01	0.75	2.45	0.74	4.14
Total	31.6		62.22	0.22	9.60	0.16	10.16	2.00	0.44	0.98	0.41	13.81

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Nb = nest-building, Inc = incubating.

Appendix 23. The diurnal patterns of behaviours (percentage of observation time) during the prelaying stage for male and female Robins.

Day-period	Observation time (h)	Behaviours[a]								
		F	Fst	Bm	V	R	P	Td	Ie	Nb
Male										
1	1.6	47.21	0.33	1.65	46.60	3.31	0.90			
2	7.3	68.52	0.28	4.30	15.91	5.66	3.47	0.87	0.99	
3	8.8	66.76	0.03	7.21	15.72	5.29	2.65	0.77	1.57	
4	5.4	63.05		7.69	11.65	11.07	5.06	0.94	0.54	
5	3.1	71.35	0.09	5.10	10.66	5.71	3.44	2.98	0.67	
6	2.6	85.16		4.21	4.49	4.30	1.61		0.23	
Female										
1	2.5	79.87		8.65		2.20	6.29		2.10	0.89
2	10.8	68.94	0.33	14.64	0.11	11.74	2.82		1.15	0.27
3	11.1	67.02	0.20	15.26	0.67	12.76	3.46	0.17	0.27	0.19
4	14.0	73.51	0.05	13.35	0.10	9.51	1.18	0.49	0.95	0.86
5	10.9	73.65	0.14	14.59	0.03	7.78	1.58	1.21	0.20	0.82
6	2.4	70.04	0.14	12.86		13.81	1.23	0.12	1.75	0.05

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Nb = nest-building.

Appendix 24. The diurnal rhythm of behaviours (percentage of observation time) for male and female Robins during the laying stage of the breeding cycle.

Day-period	Observation time (h)	Behaviours[a]									
		F	Fst	Bm	V	R	P	Td	Ie	Nb	Inc
Male											
1	0.6	65.91		17.52	2.73	5.46	8.38				
2	3.9	72.73	0.10	5.91	9.83	1.41	4.53	3.65	1.84		
3	4.2	79.86	0.34	7.76	3.88	4.97	3.03		0.16		
4	7.4	79.35	0.35	8.95	3.25	2.68	4.21	0.48	0.73		
5	6.1	71.15	0.13	17.52	2.04	2.09	5.60		1.47		
6	1.2	77.35		3.75	4.03	5.18	7.49		2.20		
Female											
1	2.5	50.65	0.39	4.75	0.05	11.15	0.72		0.40	0.48	31.41
2	8.3	56.45	0.39	13.25	0.09	12.15	2.53	1.24	1.29	0.39	12.22
3	7.4	60.82	0.23	10.20	0.39	7.65	3.14	0.09	0.37	0.28	16.83
4	8.5	64.49	0.11	5.61	0.15	10.45	1.38	0.35	1.43	0.47	15.56
5	3.9	77.32		9.56		10.37	1.19		0.94	0.62	
6	1.0	71.00		21.12		6.43	0.83		0.62		

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Nb = nest-building, Inc = incubating.

Appendix 25. The timing of yolk formation in the Robin.

Introduction

The rapid phase of yolk formation is an energy demanding process (King 1973), so that to understand the time-budgets for female Robins during the breeding cycle it is important to know precisely when and for how long this process occurs. By comparing the number and size of the oocytes of autopsied birds with the sizes of eggs and the intervals between them, estimates were made of the time required to form yolk in some non-captive birds (King 1973, Ricklefs 1974). However, recently a technique was developed for making such estimates without direct contact with the female (Grau 1976). It has been known for many years that yolk is formed by addition of material to the periphery of the oocyte (Thomson 1859), and by a method involving the fixing and staining of yolks, Grau (1976) showed that yolk varied in staining properties depending on the time of day it was deposited. Stained yolks contained alternating light and dark rings. From timed dye-feeding experiments with domestic fowl *Gallus gallus* and quail *Coturnix coturnix* it was found that lighter staining rings were deposited at night, so that each pair of light and dark rings represented one day's growth. By counting the number of these paired rings in yolks Grau (1976) and Roudybush *et al.* (1979) estimated the number of days for the rapid phase of yolk formation for several species.

Three yolks were examined during this study. One yolk was dye-marked and the other two were not.

By making a timed feeding of dye to a Robin, knowing when she laid, and using the yolk fixing and staining methods of Grau (1976), I was able to estimate the number of days for the rapid phase of yolk formation in Robins and to determine at what point in the breeding cycle it occurred.

Methods

On the morning of 20 December 1979, female B-36287 was found carrying nest material. By the following morning she was lining an almost completed nest. Ten milligrams of the red dye, Sudan IV, were placed inside a beetle pupa which she swallowed when it was placed near her at 0830 h NZST, 21 December. The first egg (Fig. 1, A) was

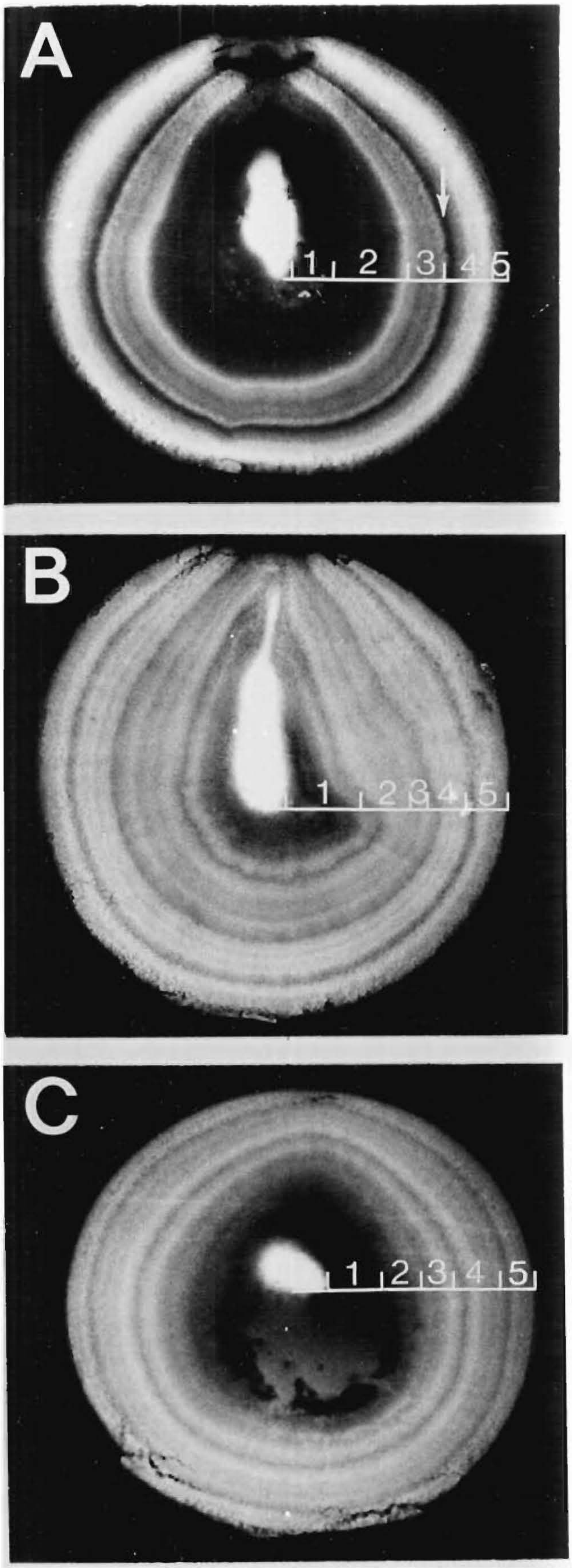

Figure 1. Cross-sections of the three Robin yolks stained with potassium dichromate. Each numbered section indicates an estimated day's growth during the rapid phase of yolk formation.

A - the yolk laid by female B-36287. The arrow indicates the dye-marker.

B & C - the yolks laid by female B-41088.

laid in the early morning of 24 December, it was removed and replaced by another Robin egg. Two more eggs were laid on subsequent mornings, but each was preyed upon within a few hours of being laid.

Two other Robin eggs (Fig. 1, B and C) were found in a nest in the territory of female B-41088. I did not know when these were laid. Since the bird never gave a distraction display (Section 8.3.3, p. 122) when I climbed to the nest and because the eggs did not contain embryos, it seemed that the clutch was abandoned during laying. All three eggs were stored at 5°C until the 4 January.

The following methods used to prepare the eggs to count the stained rings in the yolks were taken from Grau (1976) and Roudybush *et al.* (1979). The eggs were degassed in a vacuum chamber for seven hours, then frozen in air at -20°C overnight. The shells were removed, and the frozen contents placed in 4% formalin at 65°C for 16 hours to fix the yolks. After freeing them from the albumen and vitelline membrane, the yolks were cut in half. One half of each yolk was stained by leaving it in 6% potassium dichromate for 16 hours at 65°C. Each yolk was then rinsed in water and a 1 mm slice was cut for observation.

Results

In spring, female Robins weighed about 35 g (Flack in prep.) and their eggs averaged 4.5 g (n = 132) on the day of laying. The average size of 363 eggs was 24.9 × 18.6 mm (length × maximum breadth).

At the centre of each slice of yolk was an area of unstained yolk, the primordial yolk (Fig. 1). Next to this central area were one or two rings of very darkly staining yolk followed by alternating dark and light rings that are characteristic of yolk formation over a 24 hour period (Grau 1976). Each yolk had about five pairs of light and dark staining rings. However, towards the centre of eggs A and B the lighter staining rings were less well defined and so there may have been more present than estimated. Thus, the number of paired rings in three Robin eggs suggests that these birds took five or more days to deposit the yolk during the rapid phase of growth before ovulation.

Yolk A had a distinct red ring, the result of the ingested Sudan IV dye being incorporated into the yolk (Fig. 1). Dye fed in a capsule was estimated to take about three hours to be digested, absorbed and deposited in the yolk (Grau 1976). In accordance with Grau's findings (1976) that in domestic fowl lighter staining yolk was deposited at night, the dye fed to the Robin in the early morning was incorporated into the start of a dark staining ring. From the ring of dye to the circumference of the yolk two dark and one light staining rings were present suggesting that about 1.5 days of yolk formation occurred from the deposition of the dye to ovulation. The time from ovulation to oviposition, which involves albumen and shell secretion, takes about 24 hours for species that lay an egg each day (Gilbert 1971, Ricklefs 1974, Scott & Ankney 1979, Wood-Gush & Horne 1970). Therefore, an estimated 2.5 days passed from dye-feeding to laying of the egg, which agrees well with the 3.0 days it actually took.

Discussion

The estimated five or more days it took the Robins to form the yolk during the rapid phase of deposition is similar to estimates for other birds of much the same weight. From measured follicle sizes, King (1973) concluded that four medium to small passerines formed yolks in about four days. Ricklefs (1974) concluded from the progression of follicle weights, which he assumed represented the daily increment of growth, that Starlings took only two days to form a yolk. However, because the birds had already laid one or two eggs when collected (Ricklefs 1976), it is possible that one or two follicle sizes (or daily growth increments) were not represented and so the rapid growth phase of the yolk may have been slightly longer. Using the yolk-ring counting method, Roudybush *et al.* (1979) obtained estimates of four to eight days for yolk formation in three species of shorebirds that laid slightly larger eggs than Robins.

From the dye-feeding experiment it was possible to determine during which stages of the breeding cycle yolk formation took place. The yolk of egg A was estimated to have been forming for three days before the dye was deposited, at which time (21 December) the bird was lining its nest. Because the bird began searching for a nest site the previous morning, it may be concluded that the rapid phase of yolk formation for this egg began before nest-building. Yolk deposition occurs simultaneously in several consecutive yolks of a clutch (King 1973, Roudybush *et al.* 1979) presumably with a difference of a day's growth between each for birds laying an egg each day. Therefore, in the case of the dye-fed Robin, all three follicles would have been undergoing the rapid phase of yolk depositon during the nest-building and prelaying stages. Earlier in the breeding season when these two stages lasted much longer, up to 13 days compared with four for female B-36287, the timing of yolk formation relative to the various stages may have been different.

Appendix 26. The monthly and total time-budgets (percentage of observation time) for male and female Robins during the incubation stage.

Month	Observation time (h)	Hours/day spent foraging	Behaviours[a]									
			F	Fst	Bm	V	R	P	Td	Ie	Nb	Inc
Male												
Aug.	12.8	8.8	84.35	0.60	4.33	0.79	5.06	3.73	0.46	0.68		
Sept.	19.1	8.6	82.62	0.22	4.56	2.08	3.73	5.42	0.60	0.77		
Oct.	15.7	9.0	76.11	0.41	7.09	3.96	3.66	7.02	0.99	0.76		
Nov.	9.7	11.5	78.75	0.75	3.64	2.84	5.62	5.95	1.49	0.96		
Dec.	15.4	10.8	70.49	0.40	15.91	1.39	5.31	5.21	0.31	0.98		
Total	72.7		78.44	0.43	7.35	2.22	4.52	5.50	0.72	0.82		
Female												
Aug.	11.3	1.2	11.49	0.05	3.38	0.05	2.87	2.35	0.00	0.18	0.12	79.51
Sept.	17.7	1.4	11.96	0.08	2.02	0.13	1.18	2.65	0.00	0.09	0.25	81.64
Oct.	27.8	1.5	11.42	0.00	4.55	0.00	1.62	1.19	0.23	0.44	0.50	80.05
Nov.	15.4	1.9	13.24	0.03	3.04	0.17	0.54	1.53	0.71	0.20	0.08	80.46
Dec.	22.5	2.4	15.80	0.03	3.74	0.08	0.84	1.53	0.23	0.28	0.15	77.32
Total	94.7		12.86	0.03	3.50	0.08	1.33	1.74	0.24	0.26	0.25	79.71

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Nb = nest-building, Inc = incubating.

Appendix 27. The diurnal patterns of behaviours (percentage of observation time/day-period) during three portions[a] of the breeding season for male Robins involved in the incubation stage.

Day-periods	Behaviours[b] F	Fst	Bm	V	R	P	Td	Ie	Observation time (h)
Early									
1	82.72	1.20	1.97	5.87	4.99	2.61	0.00	0.64	3.8
2	73.17	0.15	8.30	1.10	9.72	6.50	0.00	1.06	4.0
3	78.96	0.09	5.43	3.77	6.20	3.20	1.59	0.76	4.1
4	88.82	0.41	1.24	0.59	3.23	4.08	1.40	0.23	2.0
5	83.90	0.00	2.16	0.30	7.64	5.00	1.00	0.00	3.8
6	88.90	0.00	0.36	0.99	5.02	2.29	2.07	0.37	2.0
Middle									
1	75.11	2.79	1.56	6.15	2.54	6.84	3.58	1.43	3.5
2	74.77	0.00	2.64	8.71	6.89	5.87	0.00	1.12	2.7
3	70.64	0.00	9.51	5.67	6.07	6.43	0.40	1.28	4.0
4	78.85	0.00	5.13	1.26	7.06	5.65	0.11	1.94	4.7
5	71.97	0.00	9.26	4.58	6.20	7.22	0.00	0.77	3.4
6	77.05	0.00	13.03	0.95	0.28	7.95	0.00	0.74	1.0
Late									
1	73.20	2.28	1.33	10.13	1.30	11.65	0.00	0.11	0.8
2	70.03	0.71	10.16	0.85	4.22	11.01	1.81	1.21	1.9
3	66.09	0.59	16.46	2.16	7.29	7.21	0.00	0.20	3.1
4	70.44	0.00	13.21	1.54	9.11	4.96	0.17	0.57	3.3
5	86.08	0.00	8.65	0.00	0.83	2.52	0.00	1.91	1.9
6									–

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[a] Early = August and September, Middle = October and November, Late = December.

[b] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions.

Appendix 28. The diurnal patterns of behaviours (percentage of observation time per day-period) during three portions[a] of the breeding season for incubating female Robins.

	Behaviours[b]										Observation
Day-periods	F	Fst	Bm	V	R	P	Td	Ie	Nb	Inc	time (h)
Early											
1	15.83	0.11	2.07	0.41	0.83	2.38	0.00	0.13	0.00	78.24	4.8
2	14.56	0.00	0.90	0.00	1.26	2.79	0.00	0.07	0.26	80.16	5.3
3	7.43	0.25	3.26	0.04	1.97	3.38	0.00	0.24	0.46	82.97	5.8
4	20.37	0.00	1.70	0.20	4.79	1.03	0.00	0.20	0.00	71.71	2.9
5	6.65	0.00	2.06	0.00	0.73	3.11	0.00	0.00	0.35	87.10	4.9
6	8.72	0.00	4.04	0.00	2.19	1.53	0.00	0.11	0.00	83.41	6.4
Middle											
1	10.47	0.00	1.80	0.01	0.47	1.06	0.30	0.37	0.00	85.52	6.8
2	10.86	0.00	4.34	0.00	1.37	1.72	0.62	0.10	0.67	80.32	7.2
3	11.08	0.00	2.85	0.00	1.22	1.76	0.27	0.51	0.00	82.31	6.0
4	14.16	0.00	6.91	0.00	1.02	1.55	0.07	0.10	0.79	75.40	8.2
5	11.77	0.05	3.31	0.30	2.44	1.04	0.00	0.79	0.32	79.98	8.9
6	13.79	0.00	4.39	0.00	0.50	0.74	1.40	0.18	0.18	78.82	6.3
Late											
1	19.87	0.00	4.24	0.14	0.23	1.62	0.24	0.05	0.00	73.61	3.3
2	22.56	0.00	4.37	0.27	0.71	2.33	0.00	0.00	1.32	68.44	2.6
3	13.69	0.09	4.19	0.09	1.62	1.79	0.00	0.29	0.00	78.24	7.2
4	9.83	0.00	0.44	0.00	1.34	1.71	0.00	0.57	0.00	86.11	2.2
5	10.82	0.00	3.00	0.00	0.28	1.12	0.86	0.56	0.00	83.36	5.0
6	25.64	0.00	5.69	0.00	0.17	0.36	0.00	0.00	0.00	68.14	2.2

[a] Early = August and September, Middle = October and November, Late = December.

[b] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Nb = nest-building, Inc = incubating.

Appendix 29. The time-budgets (percentage of observation time) for male Robins raising nestlings of various age-groups (days) and brood sizes.

Age-groups (days)	Observation time (h)	Behaviours[a]									
		F	Fst	Bm	V	R	P	Td	Ie	Fp	Ns
1 nestling											
1-5	1.1	84.23	1.16	2.19	0.00	0.00	0.22	3.29	2.42	5.53	0.96
6-10	1.5	82.88	0.00	5.41	1.94	2.01	0.00	3.19	0.00	4.40	0.17
11-15	0.4	94.26	0.00	0.13	0.00	0.00	0.00	0.00	0.54	4.03	1.04
>15	1.6	86.75	0.00	2.09	3.14	5.57	1.44	0.00	0.08	0.93	0.00
2 nestlings											
1-5	4.6	85.14	0.00	2.36	1.20	1.45	1.78	1.73	0.93	4.10	1.31
6-10	1.3	78.40	0.00	2.00	0.06	9.29	0.86	0.00	0.67	7.40	1.32
11-15	1.5	83.41	0.00	6.62	0.59	3.79	0.24	0.00	0.80	3.15	1.40
>15	0.4	76.05	0.00	0.09	0.00	4.62	0.38	0.00	0.38	18.48	0.00
3 nestlings											
1-5	4.5	75.08	0.25	3.80	3.08	6.66	0.31	0.94	1.39	7.30	1.19
6-10	3.8	85.27	0.05	3.16	0.02	4.84	0.35	0.00	0.15	5.22	0.93
11-15	0.2	88.75	0.00	1.99	0.00	1.84	0.00	0.00	0.00	5.43	1.99
>15	1.6	83.71	0.00	1.09	3.99	1.86	0.54	0.00	0.61	6.21	1.99
Total	22.5	83.29	0.11	2.90	1.38	3.60	0.71	1.06	0.71	5.23	1.01

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Fp = feeding progeny, Ns = nest sanitation.

Appendix 30. The time-budgets (percentage of observation time) for female Robins rearing nestlings of various age-groups (days) and brood sizes.

Age-groups (days)	Observation time (h)	Behaviours[a]										
		F	Fst	Bm	V	R	P	Td	Ie	Fp	Ns	Brd
<u>1 nestling</u>												
1-5	4.1	27.72	0.00	1.22	0.00	0.48	0.08	0.47	0.00	0.89	1.01	68.13
6-10	8.1	22.73	0.00	2.38	0.00	0.93	0.22	0.00	0.16	0.88	1.09	71.61
11-15	2.1	31.34	0.00	22.64	0.00	5.95	0.06	0.00	0.00	1.77	0.14	38.10
>15	2.0	70.04	0.00	17.13	0.00	6.60	1.73	0.22	0.77	2.59	0.92	0.00
<u>2 nestlings</u>												
1-5	6.2	38.36	0.00	2.51	0.15	1.07	1.39	1.48	0.60	1.81	0.54	52.09
6-10	-											
11-15	5.3	53.05	0.00	9.96	0.00	4.39	0.92	0.00	1.74	1.64	2.07	26.23
>15	1.5	81.46	0.00	2.01	0.00	7.61	0.55	0.00	1.13	6.77	0.47	0.00
<u>3 nestlings</u>												
1-5	11.4	1.22	0.02	3.37	0.00	2.09	0.22	0.09	0.20	2.07	0.99	89.73
6-10	12.0	47.45	0.00	3.71	0.16	2.32	0.45	0.69	0.70	2.52	1.32	40.68
11-15	4.1	70.64	0.00	3.45	0.00	2.52	0.77	0.00	0.21	4.34	3.16	14.91
>15	6.2	73.38	0.26	3.50	0.00	3.28	1.39	0.00	0.22	5.04	2.24	10.69
Total	63.6	42.62	0.03	3.37	0.05	2.24	0.61	0.33	0.45	2.38	1.29	46.63

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Fp = feeding progeny, Ns = nest sanitation, Brd = brooding.

Appendix 31. The diurnal pattern of behaviours (percentage of observation time) for male and female Robins rearing nestlings.

Day-periods	Observation time (h)	Behaviours[a]										
		F	Fst	Bm	V	R	P	Td	Ie	Fp	Ns	Brd
Male												
1	1.7	82.30	0.00	2.23	0.57	5.88	0.92	0.00	0.69	6.58	0.83	
2	4.7	81.26	0.04	3.35	1.19	3.06	1.52	1.81	0.55	6.38	0.84	
3	5.3	81.26	0.00	1.50	2.04	6.19	0.43	2.26	0.32	5.17	0.83	
4	7.6	88.03	0.15	1.79	0.71	2.06	0.62	0.22	0.78	4.45	1.19	
5	3.8	80.12	0.00	5.90	3.01	3.53	0.27	0.00	1.30	4.73	1.14	
6	1.4	81.52	0.96	5.61	0.00	1.34	0.43	2.73	0.82	5.47	1.12	
Female												
1	7.9	46.71	0.12	2.64	0.00	1.20	0.76	0.10	0.29	3.30	2.19	42.69
2	14.7	44.60	0.04	3.49	0.17	2.00	0.88	0.40	0.34	2.45	1.14	44.49
3	11.5	44.56	0.02	2.49	0.03	3.26	0.40	0.27	0.57	2.72	1.47	44.20
4	17.1	41.38	0.00	3.03	0.00	2.00	0.53	0.50	0.67	2.01	1.24	48.64
5	10.4	38.86	0.00	1.37	0.00	2.91	0.48	0.15	0.23	2.29	0.80	52.91
6	3.5	34.96	0.00	14.92	0.00	1.40	0.68	0.27	0.55	1.12	1.05	45.05

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Fp = feeding progeny, Ns = nest sanitation, Brd = brooding.

Appendix 32. The monthly and total time-budgets (percentage of observation time) for male and female Robins rearing juveniles.

Month	Observation time (h)	Hours/day spent foraging	Behaviours[a]								
			F	Fst	Bm	V	R	P	Td	Ie	Fp
Male											
Sept.	8.3	9.5	80.75	0.02	3.79	3.82	4.49	1.68	0.24	0.98	4.23
Oct.	14.9	10.7	80.40	0.03	2.65	3.27	4.28	0.79	1.58	0.58	6.42
Nov.	16.6	11.5	78.93	0.07	3.97	5.76	5.10	0.55	0.94	0.48	4.20
Dec.	12.7	11.9	77.93	0.36	6.75	3.76	3.28	0.44	1.89	0.49	5.10
Total	52.5		79.39	0.12	4.24	4.27	4.33	0.77	1.24	0.59	5.05
Female											
Sept.	4.9	9.3	79.12	0.18	7.86	0.51	4.15	0.58	0.08	0.61	6.91
Oct.	4.4	10.8	81.47	0.00	8.77	0.00	4.93	1.51	0.00	0.06	3.26
Nov.	5.6	11.4	78.28	0.06	6.36	0.22	5.23	1.48	0.52	0.41	7.44
Dec.	5.6	13.6	88.67	0.00	1.50	0.32	0.56	0.36	0.82	0.11	7.66
Total	20.5		82.01	0.06	5.91	0.27	3.63	0.97	0.38	0.30	6.47

[a] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Fp = feeding progeny.

Appendix 33. The diurnal patterns of behaviours (percentage of observation time per day-period) during the breeding season for male and female Robins rearing juveniles.

		Behaviours[b]								
Day-periods[a]	Observation time (h)	F	Fst	Bm	V	R	P	Td	Ie	Fp
Male										
1	3.3	76.50	0.14	2.77	11.05	1.38	1.29	0.19	0.49	6.19
2	12.7	80.01	0.18	3.05	4.92	5.18	0.36	0.39	0.70	5.21
3	17.5	80.61	0.08	3.27	3.57	4.97	0.83	1.38	0.73	4.56
4	10.0	78.22	0.10	6.17	4.52	3.23	1.23	1.35	0.27	4.91
5	6.4	77.18	0.06	5.86	2.16	5.55	0.66	2.42	0.44	5.67
6	2.5	82.48	0.25	7.06	1.15	0.88	0.21	2.63	0.14	5.20
Female										
1	1.6	84.27	0.00	5.13	0.24	2.21	0.17	0.63	0.85	6.50
2	3.5	76.19	0.11	9.45	0.00	2.77	2.22	0.32	0.26	8.68
3	5.6	78.44	0.15	7.01	0.19	6.69	0.86	0.26	0.17	6.23
4	5.7	85.86	0.00	3.62	0.29	2.17	0.77	0.58	0.58	6.13
5	3.4	85.99	0.00	4.80	0.00	2.63	0.76	0.18	0.00	5.64
6	0.7	83.90	0.00	5.13	0.00	7.09	0.00	0.00	0.00	3.88

[a] The division of the daylight hours into six, equal length day-periods.

[b] F = foraging, Fst = food-storing, Bm = body-maintenance, V = vocalizing, R = resting, P = partner-interactions, Td = territorial defence, Ie = interspecific interactions, Fp = feeding progeny.

Appendix 34. Suggestions for future research.

The results of my study indicate several aspects which could be investigated further:

1. Robin weights.

It seems impractical quantitatively to assess the food available to Robins at Kowhai Bush because of the diversity of sites in which the birds forage and the variety of prey species they eat, but it may be possible to obtain some measure of food availability indirectly by weighing the birds. Such weighings would have to be done regularly, so conventional methods of capturing and weighing would be unsuitable, leading the birds to become timid. However, as a consequence of the bird's trusting nature I believe it would be possible to "train" them to perch on an automatic weighing device, perhaps enticed there by pre-weighed food offerings. The data could provide answers to questions such as the following:

> How do Robin weights vary as the year progresses and are the changes related to the proportion of time spent in foraging?
> Are immature Robins lighter than adults from January to June when immatures spend more time foraging than adults?
> In winter, do bachelors weigh less than paired adult males considering that the former sing more and forage less than the latter?
> Do Robins spend so much time foraging in winter because their bodily reserves are low, or are they increasing their fat deposits in preparation for breeding?

2. Time-budgets for other Robin populations.

From the comparison of the time-budgets for the Outer Chetwode Island and Kowhai Bush populations, it is apparent that there is a considerable degree of plasticity in the behaviour of the Robin. Therefore, it would be of interest to compare the time-budgets from this study with those for populations of Robins living elsewhere: for example, with those for populations in beech forests (*Nothofagus* spp.) at Arthurs Pass, western Canterbury and the Eglington Valley, Fiordland.

3. Factors that influence bachelor singing.

Recently, several studies concerning the influence of temperature on the singing of birds have been published: for example, Higgins, R.M.R. (1979) *Ibis* 121: 333-335 and Garson, P.J. & M.L. Hunter Jr. (1979) *Ibis* 121: 481-487. Since bachelor Robins spend so much time singing from conspicuous song-perches, the influence of weather factors and food availability on the proportion of time spent singing could be readily investigated at Kowhai Bush.

4. Features of nestling maturation.

Other than brief descriptive accounts of Robin nestling growth and behaviour (Flack 1973, 1979, in prep.), little information has been obtained about nestling maturation. Since breeding continues for six months and a pair of Robins can raise three broods in a season, there is plenty of scope to study such topics as:

Nestling growth rates and how these vary with the month of the breeding season, brood size and experience of the adults.
Ontogeny of nestling behaviour from hatching to independence.
Quantitative observations of the division of a brood of juveniles between the parents.
The food-trip rates to juveniles and how these change from fledging to independence.

5. Competition for prey species.

It is possible that Blackbirds and Song Thrushes compete with Robins for some prey. The timid nature of the *Turdus* species in Kowhai Bush precludes the adult birds being observed directly as they forage. However, by taking samples of food from their nestlings using neck collars it may be possible to compare their diets with those of Robin chicks. Placement of hides next to low Robin nests would be best carried out during the incubation stage in order to minimise the risk of desertions. Close observations from hides would enable the identification of many prey species fed to the chicks. At the same time, quantitative data could be collected on nest probing by female Robins and the question of how nestling begging influences parental feeding rates could be examined.

6. Adult Robin mortality.

Much work still needs to be carried out on the causes of adult mortality outside the breeding season. Two factors that could be investigated are:

Predation by mustelids - a trapping programme for mustelids over two to three years from January to July inclusive may help to reduce the numbers of these animals and elucidate the role of these predators in adult Robin mortality.
Starvation - some pairs could be supplied with food daily in autumn and winter. Such a study would also have interesting implications with regard to the extra food influencing the start of breeding and food-storing behaviour.