# Space use by passerine birds: a study of territory economics in robins *Erithacus rubecula* and dippers *Cinclus cinclus*.

Thesis submitted for the degree of
Doctor of Philosophy,

I.G.Johnstone.

Department of Biological and Molecular Sciences.
University of Stirling.
March 1994.

# Abstract.

1. Cost constraints in models of territory size are based on time/activity/laboratory estimates that predict birds using larger territories will incur higher energy costs. The predicted form of the cost constraint may be linear, accelerating or decelerating depending on assumptions inherent in the models. The aim of this study was to assess the reality and form of the cost constraint by making direct measurements of the energy costs of territory use in birds that occupy territories of different size and shape; polygonal territories represented by the robin *Erithacus rubecula*, and linear by the dipper *Cinclus cinclus*. Free-living energy expenditure was measured using the doubly-labelled water technique, whilst simultaneously recording patterns of territory use by radio-tracking.

2. Territorial robins concentrated their activity in one or more foraging patches located in bushes. Range polygons containing all the foraging patches used by an individual provided estimates of territory area, and were generally of high eccentricity. A small proportion of robins was classified as non-territorial based on range polygon areas. Furthermore, while territorial robins showed high fidelity to ranges over the short term (days), non-territorial individuals were nomadic. Over the longer term (months), however, some territorial robins showed range drift. Dippers similarly used preferred core regions within ranges, although there was no selection for particular habitat features.

3. Because robins occupied territory polygons which varied from polygonal to highly linear, work was focused on this species to allow intra-specific comparison. Robins tended to commute between foraging patches by flying. It was appropriate, therefore, to describe territories in terms of a number of patches linked by a network of flight paths. This generated two further measures of territory size; the number of patches used and the total flight distance between patches.

4. The robins exploited a renewing food supply. Predictions were tested concerning the temporal scheduling of visits to foraging patches within territories. Patches tended to be separated by flight paths of similar lengths, and were visited in a regular sequence. Although the number of foraging patches used varied, all territories had similar total core areas. Robins using many small foraging patches commuted between patches more often and covered a larger total flight distance during each foraging circuit of the territory. The configurations of foraging patches were used in a highly linear manner. This was true even if the territory containing them was of low eccentricity.

5. Changes in structure and pattern of use varied predictably with territory size, and could be described mathematically. Based on this and published time/activity budgets, a suite of models was developed to predict how energy costs would vary with number of patches used and total flight distance between patches. Models were tested by directly measuring the energy expenditure of robins using different territories. The number of patches used and total flight distance between patches were both significantly correlated with energy expenditure, while territory area was not. One of the models showed a significant fit to the observed data, and suggested that the form of the energy cost constraint on territory size was linear. The effect of territory shape on energy costs was minimal. The implications of these results for models of territory size are discussed.

6. The slope and elevation of the energy cost constraint varied with the morphology of territory occupants. Based on this, an association of morphology with territory size was predicted; robins of lower mass and wing-loading using larger territories. The observed data supported these predictions, and suggested a possible genetic predisposition to particular patterns of territory occupancy in the robin.

For my Parents, who only occasionally told me not to pick up dead things.

And my Grandmother, who always asked how my birds were, but sadly never saw the finished thesis.

# Acknowledgements.

This thesis represents the distilled essence of over four years of my life. The hardest thing I have ever done. It would not have been possible without the support and friendship of my colleagues in the Avian Ecology Group. The girls, with whom I shared an office for four years deserve a special mention; Maria-Alice Alvez provided staples and let me radio-track her sand martins; Chris Wernam provided endless cakes and buns in attempt to feed me up and looked up the names for Appendix 12; Lulu Stader made the coffee, my kidneys will never be the same again; and Sally Ward taught me the rudiments of SPSS$_x$, and with Robin introduced me to the thrills and spills of white water canoeing. All in all, I get the impression they found me just as interesting as I found them.

Many other members of the department played supporting roles; John Calladine helped radio-track robins and without his expert help in catching birds, my DLW sample would never have achieved the dizzy heights of eleven. Cara failed to lure me out to the pub on numerous occasions and with Kevin helped type and sort the bibliography. Other members of the group; Maimie, Ross, Helen, Anne and Steve in the early years, and later Rosli, Sari, John, and Sue helped out with various things over the years. The new boy, Jason, had the cheek to suggest something I hadn't thought of. I'm sure my birds will be safe in his hands.

Many landowners allowed me access to their land during the dipper work, and tolerated me wandering around at night. I would also like to apologise to the little old lady in Greenloaning, whose garden wall I accidentally destroyed late one night. The campus maintenance men and security guards were always helpful during the robin work and eventually got used to my creeping around in the bushes at night looking for roosting birds.

Jim Weir was my pilot to and from the reactor centre at East Kilbride on many occasions and taught me how to analyze my DLW samples. When he wasn't there, Susan helped out and stopped me blowing my self up. Nevertheless, I still managed to spill liquid nitrogen down my trousers and freeze my pubic hairs to the inside of my underpants. Derek in stores made things to catch birds, kept the department cars running and lent me tools when by bike broke down. Thankfully he never knew how close I came to losing one of the cars in the campus loch. Lewis provided an excellent photographic service, often at very short notice. Sandy, Carol and the other technicians were always on hand in the lab to tell me what I was doing was dangerous. Marilyn helped with computing problems and found ways to run my software. Jeff, of the Stirling Microprocessor Group designed and built the song playback

equipment and provided an expert soldering service to repair radio-tags which had been vandalised by the dippers.

Tony Derby provided a roof over my head and some interesting room mates. It was a bit like Arachnophobia meets Jurassic Park.

This work was funded by NERC studentship GT4/89/TLS/56. I am grateful to all those who provided facilities in the Department of Biological and Molecular Sciences at Stirling University and at the Scottish Universities Reactor Research Centre, East Kilbride.

Finally, Professor David Bryant, my supervisor, provided endless encouragement and advice, for which I express my thanks. He even forgave me when I set his lab on fire. It has been deeply rewarding experience to find out something new, however small, about another animal, and to be able to look out of my window at the garden robin and say: yes, I know why it behaves like that.

March 1994.

**Postscript.**

The appendices to some of the tables and figures were added voluntarily along with the required minor corrections after the viva.

The events surrounding my viva were strangely reassuring. The external examiner, flying up from southern England, forgot to catch the first flight, got stuck in a traffic jam and missed the second, and finally arrived thirty six hours late. It's nice to know even the best of us can mess up from time to time.

June 1994.

# Contents.

## 1. Introduction.

Page

- 1.1. Territoriality; background and current concepts. 1
  - 1.1.1. A definition of territory. 1
  - 1.1.2. The functions of territory. 2
  - 1.1.3. The concept of economic defendability. 3
  - 1.1.4. Costs, benefits and the optimal territory. 6
- 1.2. Measuring the energy cost constraints on territorial behaviour. 6
  - 1.2.1. Hypotheses to be tested. 6
  - 1.2.2. The study species. 7

## 2. General methods.

- 2.1. Introduction. 9
  - 2.1.1. Selection of study species. 9
  - 2.1.2. Summary of non-breeding ecology and behaviour. 9
    - 2.1.2.1.The robin. 9
    - 2.1.2.2.The dipper. 10
  - 2.1.3.Statistics and software. 11
- 2.2. The robin. 11
  - 2.2.1.Methods. 11
    - 2.2.1.1.The study site. 11
      - 2.2.1.1.1. Locations and aspect. 11
      - 2.2.1.1.2. Habitat structure and prey availability. 12
      - 2.2.1.1.3. Weather data. 12
    - 2.2.1.2. The examination of individuals. 12
      - 2.2.1.2.1. Capture techniques. 12
      - 2.2.1.2.2. Biometrics, ageing and sexing. 13
    - 2.2.1.3. Measuring the energy expenditure of free living birds. 13
      - 2.2.1.3.1. The doubly labelled water technique. 13
      - 2.2.1.3.2. Field protocol and analysis. 15
  - 2.2.2. Results. 16
    - 2.2.2.1. Weather data. 16
    - 2.2.2.2. Morphological variation between individuals. 17
      - 2.2.2.2.1. Structural body size. 17
      - 2.2.2.2.2. Wing morphology. 18
      - 2.2.2.2.3. The effects of age and sex. 18
    - 2.2.2.3. Physiological variation between individuals. 18
      - 2.2.2.3.1. Body composition and energetic condition. 18
      - 2.2.2.3.2. Variation in energetic condition. 21
  - 2.2.3. Radio-tagging methodology. 21
    - 2.2.3.1. Weight considerations and transmitter performance. 21
    - 2.2.3.2. Available options for attaching radio-tags to small passerines. 23
    - 2.2.3.3. Attaching radio-tags to robins using glue. 24
    - 2.2.3.4. Radio-tags attached to robins using tail-clips. 24

2.2.4. Results; the effect of radio-tags on the robin. . . . . 25
  2.2.4.1. Behaviour. . . . . . . . . 25
  2.2.4.2. Energetic condition. . . . . . . . 26
  2.2.4.3. Energy expenditure. . . . . . . . 27
  2.2.4.4. Survival. . . . . . . . . 28
2.2.5. Discussion. . . . . . . . . . 29
  2.2.5.1. Structural size. . . . . . . . 29
  2.2.5.2. Estimating the energetic condition of live birds. . . 29
  2.2.5.3. The effect of radio-tags on the robin. . . . 30
2.3. The dipper. . . . . . . . . . . 32
  2.3.1. Methods. . . . . . . . . . 32
    2.3.1.1. The study sites. . . . . . . . 32
    2.3.1.2. The study population. . . . . . 32
    2.3.1.3. Radio-tag attachment. . . . . 32
  2.3.2. Results; the effect of radio-tags on the dipper. . . . 33
    2.3.2.2. Behaviour. . . . . . . . . 33
    2.3.2.2. Energetic condition. . . . . . . . 34
    2.3.2.3. Energy expenditure. . . . . . . . 34
    2.3.2.4. Survival. . . . . . . . . 35
  2.3.3. Discussion. . . . . . . . . . 35

## 3. Territory and neighbourhood structure: the robin.

3.1. Introduction. . . . . . . . . . 36
3.2. Methods. . . . . . . . . . . 37
  3.2.1. Accuracy of location estimates. . . . . . 37
  3.2.2. Sampling protocol. . . . . . . . 37
  3.2.3. Locating roost sites. . . . . . . . 38
  3.2.4. Range shape. . . . . . . . . 39
  3.2.5. Defended area. . . . . . . . 39
3.3. Results. . . . . . . . . . . . 40
  3.3.1. Independence between ranges. . . . . . 40
  3.3.2. Selecting appropriate range estimators. . . . . 40
  3.3.3. Defining core regions. . . . . . . 41
  3.3.4. Core areas and range patchiness. . . . . . 42
  3.3.5. Defended-area and range use. . . . . . 43
  3.3.6. Characteristics of the usual-area. . . . . . 44
  3.3.7. Range fidelity. . . . . . . . . 46
  3.3.8. The individual within the neighbourhood. . . . . 48
  3.3.9. Excursive activity. . . . . . . . 51
  3.3.10. Roost selection. . . . . . . . 52
3.4. Discussion. . . . . . . . . . . 53
  3.4.1. Territory definition and structure. . . . . . 53
  3.4.2. Change in the location and extent of territories over time. . . 55
  3.4.3. Neighbourhood structure during day and night. . . . 56
  3.4.4. A probabilistic model of territory and neighbourhood structure. . 59
  3.4.5. Previous studies of territory in the robin
    in the light of radio-tracking results. . . . . . 60

## 4. Territory and neighbourhood structure: the dipper.

4.1. Introduction. . . . . . . . . . 62
4.2. Methods. . . . . . . . . . . 63
  4.2.1. Accuracy of locations estimates. . . . . . . 63
  4.2.2. Sampling protocol. . . . . . . . . 64
  4.2.3. Locating roost sites. . . . . . . . . 64
  4.2.4. Territory defense. . . . . . . . . 65
  4.2.5. Habitat structure. . . . . . . . . 65
4.3. Results. . . . . . . . . . . 65
  4.3.1. Independence between ranges. . . . . . . 65
  4.3.2. Deriving measures of range use. . . . . . . 66
  4.3.3. Characteristics of the usual-length. . . . . . . 67
  4.3.4. Individuals within the neighbourhood. . . . . . 69
  4.3.5. Roost selection. . . . . . . . . 70
4.4. Discussion. . . . . . . . . . 71
  4.4.1. Structure of the territory and neighbourhood in the dipper. . . 71
  4.4.2. Range use and habitat selection. . . . . . . 73
  4.4.3. Short and long term changes in the location and extent of territories. 74
  4.4.4. The selection of roost sites. . . . . . . . 75

## 5. Short term territory use in the robin; predictions and tests.

5.1. Introduction. . . . . . . . . . 76
5.2. The territory as a network. . . . . . . . 77
  5.2.1. Differential space use within the usual-area. . . . . 77
  5.2.2. The classification and shape of hypothetical networks. . . 78
  5.2.3. The quantification of network use from field data. . . . 80
5.3. The use of nuclei within networks. . . . . . . . 83
  5.3.1. Predation of a renewing food supply. . . . . . 83
  5.3.2. Methods. . . . . . . . . . 85
  5.3.3. Results. . . . . . . . . . 86
    5.3.3.1. Network structure. . . . . . . . 86
    5.3.3.2. Patch use within networks. . . . . . . 87
    5.3.3.3. Network use. . . . . . . . 90
  5.3.4. Discussion. . . . . . . . . . 92
    5.3.4.1. Network structure. . . . . . . . 92
    5.3.4.2. Patch use within networks. . . . . . . 92
    5.3.4.3. Network use. . . . . . . . 94
5.4. Intrusions and evictions. . . . . . . . . 95
  5.4.1. Methods. . . . . . . . . . 95
  5.4.2. Results. . . . . . . . . . 95
  5.4.3. Discussion. . . . . . . . . . 97
5.5. The defense component of territorial behaviour. . . . . . 100
  5.5.1. The consequences of hypothetical defense behaviours. . . 100
  5.5.2. Methods. . . . . . . . . . 104
  5.5.3. Results. . . . . . . . . . 106
  5.5.4. Discussion. . . . . . . . . . 107

## 6. The energy costs of territory use.

- 6.1. Introduction. 110
- 6.2. Modelling time/activity budgets for territorial robins. 111
  - 6.2.1. Time/activity budgets and network size. 111
  - 6.2.2. The effects of network shape. 113
- 6.3. Direct measurements of energy expenditure. 114
  - 6.3.1. Methods. 114
  - 6.3.2. Results. 114
- 6.4. A test of the models. 115
  - 6.4.1. Predicting energy budgets from their component costs. 115
  - 6.4.2. Energy expenditure and territory size. 117
  - 6.4.3. Discussion. 119
- 6.5. A test of the modified Model III. 123
  - 6.5.1. Territory size and the quality of owners. 123
  - 6.5.2. Discussion. 124

## 7. General discussion.

- 7.1. Radio-tracking small birds. 126
  - 7.1.1. Temporal scale of observations. 126
  - 7.1.2. The analysis of radio-tracking data; difficulties and solutions. 126
- 7.2. Territory and neighbourhood structure. 128
  - 7.2.1. Comparison with previous studies. 128
  - 7.2.2. Territory structure. 128
  - 7.2.3. Changes in territory over time. 129
  - 7.2.4. A measure of territory size. 130
- 7.3. The form of the energy cost constraint on territory size. 131
  - 7.3.1. Predicted exploitation and defense costs. 131
  - 7.3.2. The effects of territory shape. 133
  - 7.3.3. Evidence from direct measurements of energy expenditure. 133
  - 7.3.4. The effects of bird morphology. 134
  - 7.3.5. Implications for the cost constraint on territory size in the dipper. 135
- 7.4. Costs, benefits and the optimal territory. 136
  - 7.4.1. The form of the benefit constraint. 136
  - 7.4.2. The currency optimised. 137
  - 7.4.3. Non-economic costs and benefits. 137
- 7.5. Conclusions. 140

## 8. Bibliography.

## 9. Appendices.

## 10. Current publications based on the thesis.

Radio-tracking, like many other techniques, is seldom as easy as it looks.

Robert Kenward (1982).

# Chapter 1.

# 1. Introduction.

## 1.1. Territoriality; background and current concepts.

### 1.1.1. A definition of territory.

Territorial behaviour is one of the most conspicuous activities of many birds. Ownership of a fixed area, usually surrounded by clearly defined boundaries, is proclaimed with distinctive vocalizations, ritualised displays and not infrequently escalated fighting (Kaufman 1983). It is not surprising that such behaviour has attracted a large amount of study.

Before beginning an investigation of the behavioural ecology of territorial birds, a workable definition of territory must be established. Three concepts of territoriality have been pointed out by Kaufmann (1983). The first concept uses a behavioural approach for its definition. The specific use of the term "territory" to refer to a zoological phenomenon was begun by Atum (1868), who explained it as an area occupied by one male of a species which defends it against intrusion by other males of the same species and in which it makes itself conspicuous. Nobel (1939) simplified the definition to 'any defended area' and this has since been accepted by Hinde (1956), Tinbergen (1957) and many others. This has the advantage of being easily applicable to field studies by exploiting the defensive behaviour of territory owners (Dhondt 1966).

Secondly, a concept of territory more ecological than behavioural, has been advanced by Pitelka (1959). He defined a territory as an area of which the owner had more or less exclusive use, regardless of the means by which the area became identified with the occupant. This definition places the emphasis on the degree to which the members of a population partition the available habitat.

Thirdly, territoriality is a form of social dominance. This concept was first expressed by Emlen (1957), who defined territory as an area or space in which an individual is aggressive and largely, if not supremely dominant, with regard to certain categories of intruder. Further to this, Rand (1967) defined a territory as an area or space in which an individual dominates others who dominate it elsewhere.

When discussing what is meant by the term territory, it must be distinguished from the range of an individual. Range has been defined by Brown & Orians (1970) as "The area in which an individual normally lives, exclusive of migrations, emigrations, or unusual erratic wanderings". Thus the defended territory may only be part of a larger range, which may overlap with the ranges or even territories of neighbouring individuals, depending on the intensity of territorial defense, and also contain roost sites used communally by many individuals (Swann 1975).

### 1.1.2. The functions of territory.

Many early studies of territoriality were qualitative in nature, and concentrated on what different species were doing in their defended areas (eg Snow 1956, Gibb 1956). This comparative approach highlighted the great diversity of territorial behaviour and gave rise to various functional categories such as feeding territories and breeding territories (Hinde 1956). Many of these observations were supported by explanations which, however, had little theoretical basis. Ideas such as predator pressure (Errington 1946), patchy environments (Carpenter 1958), mate defending (Snow 1956) and psychological advantage (Carpenter 1934) were invoked but rarely measured.

Three functional hypotheses discussed by Verner (1977) offered more promise as general adaptive functions of territoriality. The density limitation hypothesis proposed that territoriality functions to limit population density below carrying capacity. This has been rejected by many biologists on the grounds of group selection (Wilson 1975). Territories may function to ensure an adequate supply of some resource; the sufficient resource hypothesis (Wilson 1975). Evidence is found in the negative correlation between territory size and the density of food, or some other important resource, found within the territory (Stenger 1958, Kodric-Brown & Brown 1978, Davies & Lundberg 1984). Finally the polygyny hypothesis (McLaren 1972) proposes that territoriality functions to allow males access to a number of females. However this fails to account for the breeding territories of monogamous species and non-breeding individual territories.

It was soon discovered however, that questions as to the function of territorial behaviour did not represent a very useful approach. This is because of the many conflicting selective pressures involved in the evolution of territoriality (Davies 1980).

### 1.1.3. The concept of economic defendability.

Brown (1964) proposed that the defendability of resources required for survival and reproduction (such as food supplies, mates and nest sites) is one of the most important determinants of the system of territorial behaviour which is attained through natural selection. Defendability should be conceived in terms of the time and energy spent in exploitation and defense activities (costs), and the advantages gained by exclusive access (benefits). Territorial behaviour should be expected when the benefits of being territorial are greater than the costs (Brown 1964). This concept of economic defendability has proved to be the corner stone of subsequent studies of territoriality.

Using this idea of the economic defense of a resource, a considerable amount of research has been carried out on birds which exploit a renewing food supply. That is a resource which, if left undisturbed for a period after exploitation, will recover to its initial level. Nectivorous birds in particular have been studied in detail, but also insectivorous birds such as the Pied Wagtail*.

The first investigation into the economics of feeding territoriality was carried out on the golden-winged sunbird (Gill & Wolf 1975). The nectar content of feeding territories comprising patches of flowers was measured, and from laboratory estimates of the energy costs of different activities, the amount of energy a sunbird expends in a day was calculated. When the daily energy costs were compared to the extra nectar gained by defending a territory and excluding competitors, it was found that the territorial individuals were making a slight net energetic profit. This was because the nectar level per flower inside a territory was higher than in undefended flowers, since other sunbirds were prevented from feeding. Thus the patches of flowers were economically defendable as territories.

Territory owners may not rely entirely on the aggressive eviction of intruders for territory defense. Paton & Carpenter (1984) produced evidence for a pattern of foraging by rufous hummingbirds which resulted in a higher net energy gain and lower food losses than if their foraging effort was distributed evenly over their territories. Their idea of peripheral foraging proposed that territory owners should feed on flowers around the edge of their territory during the first few hours of the morning, since nectar levels are high at dawn and the periphery of the territory is most vulnerable to intrusion and nectar stealing. During midday owners forage evenly over their territories, and in the territory cores in the late afternoon when they are heaviest and therefore have the highest flight costs. Such "defence

---

* All scientific names are given in Appendix 12.

by exploitation" (Paton & Carpenter 1984) may be common when food resources are being defended and should be considered along with aggressive exclusion of intruders in the overall strategies of territorial animals.

A study of pied wagtails by Davies (1976) supported these findings. Some single birds or pairs defended permanent territories along a river, consisting of a series of muddy bays where debris containing food items was washed up, and where feeding was predictably good. The total area suitable for feeding was about the same in each territory. Other birds fed in flocks and exploited temporary patches of abundant food. Further study of the economics of territorial defense in the pied wagtail (Davies & Houston 1981), explained why an owner sometimes tolerated another individual feeding on its territory. Since insects washed up on the river banks in the territory formed a renewing food supply, after a stretch had been depleted time was needed for prey abundance to return to a profitable level. An individuals' feeding rate, therefore, depended on the time that had elapsed since the stretch was last depleted of prey, termed the "return time". Territory owners increased their return times and therefore feeding rates by a systematic search of the territory and by evicting intruding competitors when encountered. When intruders did land undetected they had a lower feeding rate than owners since they had no knowledge of the time since particular stretches were last exploited. They also reduced the owners feeding rate by depleting areas just before it arrived. Intruders landing on a recently depleted stretch, however, were often not evicted even though they were noticed, since their feeding rate was very low. They often left quickly of their own accord. Davies & Houston (1981) viewed this as "defence by depletion".

Most studies of territoriality have assumed that the cost and benefits of defence are primarily determined by attributes intrinsic to each individual territory, such as resource levels. However a growing literature suggests that factors extrinsic to the territory may also affect the defense costs of the owner (Krebs 1971). In particular the position of a territory with respect to neighbouring territories and the nature of the habitat surrounding the group of territories may have significant effects on territory sizes, overlap and the densities of territory owners (Stamps & Beuchner 1985, Stamps *et al* 1987).

### 1.1.4. Costs, benefits and the optimal territory.

The type of quantitative studies discussed above sought only to discover whether territoriality was of net economic benefit in terms of exploitation and defense costs. For a thorough understanding of avian territorial systems, however, it is necessary to know whether territoriality is more profitable than alternative strategies, and how the economics of defence vary with changes in the value of the defended resource, intruder pressure or territory size.

More recently, attempts have been made to tackle these problems in a more quantitative manner by the use of optimization theory. If territorial behaviour is a result of natural selection then it can be interpreted in terms of the contribution it makes to an individuals' survival and reproductive success. It is assumed that an animal will exhibit territorial behaviour that maximizes its Darwinian fitness, (Pyke *et al* 1977). Like all optimization problems, it may be split into three stages; a) choosing a currency; what is to be maximized or minimized; b) choosing the appropriate cost and benefit functions (constraints); c) solving for the optimum, (Arnold 1988). The optimal solution can then be compared with what is observed in the field. If the predictions of the model correspond with observations, then it can provisionally be concluded that the selective pressures responsible for the behaviour have been correctly identified. If the model fails, then the discrepancy can be used as a source of information for devising alternative models, as a prelude to further observations and experiments. The aim is not to test whether an individual is behaving optimally; this is an assumption. Instead, the aim is to test whether the optimization criteria and constraints used to construct the model have been identified correctly (Krebs & Davies 1987).

For individual feeding territories, the benefit constraint in models of territorial behaviour has usually been described as a decelerating function with territory size. This is because benefits will increase as first and then level off, as the resource becomes superabundant in relation to the animals needs (Kodric-Brown & Brown 1978; MacLean & Seastedt 1979; Myers *et al* 1981; Davies & Houston 1984; but see Pyke 1979). The parameters of this constraint are relatively straightforward to estimate, in terms of energy gains, from observations of foraging behaviour and information on the energy content and assimilation efficiencies of the food. Territory size can be adjusted in response to changes in the constraints, in order to provide sufficient resources for continued survival (constant resource territories; Stephens & Dunbar 1993). Territory size may be changed in order to track short-term optima (Davies & Houston 1984). Alternatively, the failure of owners to track short-term changes in costs and benefits by changing territory size, may suggest that long-term optima, for example maximising the chances of overwinter survival, are most important (Davies & Houston 1981).

The costs constraint on territory size has never previously been quantified directly, owing to the inability until recently to measure directly the free-living energy expenditure of animals, and the absence of information concerning specific defense activities, such as boundary patrolling. Previous studies have resorted to estimating the form of the cost constraint, based on various assumptions (Davies & Houston 1984). This has led to a variety of contradictory functions being used in models of optimal behaviour (Table 1.1.). Three possible variants are illustrated in Fig.1.1. to show how the constraints on costs and benefits can be used to make predictions about the territory size that optimises different currencies.

## 1.2. Measuring the energy cost constraint on territorial behaviour.

### 1.2.1. Hypotheses to be tested.

Until the recent advent of the doubly labelled water technique (Lifson & McLintock 1966), no direct method of measuring the free-living energy expenditure of animals was available. The use of this technique in directly measuring the form of constraints on territorial behaviour has been advocated by Bryant (1989), and has the advantage of framing both costs and benefits in a common currency (energy).

All of the studies in which the form of the cost constraints on territory size have been described, have included the cost of territory defense in addition to the cost of territory exploitation (Kodric-Brown & Brown 1978; MacLean & Seastedt 1979; Myers *et al* 1981; Schoener 1983; Davies & Houston 1984; Stephens & Dunbar 1993). Although activities such as boundary patrolling have frequently been invoked, the nature and cost of these behaviours have never been quantified.

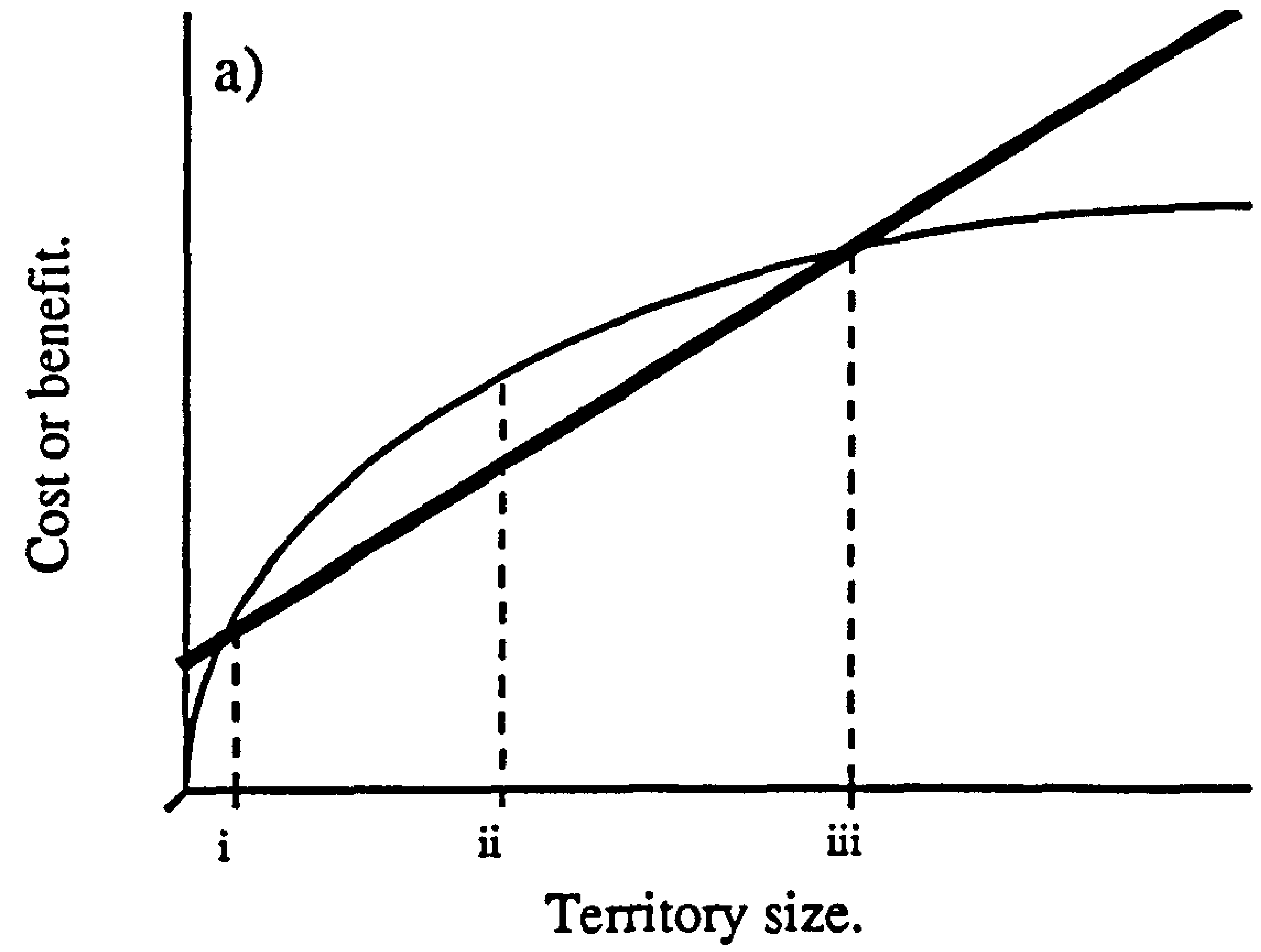
Field studies of territorial energetics have largely concentrated on estimating the energy costs and benefits from the time/activity budgets of occupants (Gill & Wolf 1975, Carpenter & MacMillan 1976, Pyke 1979). Exploitation and defense are, however, behaviours which require an occupant to move between different regions within a territory. This pattern of time/space budgeting can now be recorded in detail for small birds, with the aid of recently developed miniature radio-transmitters (Kenward 1987).

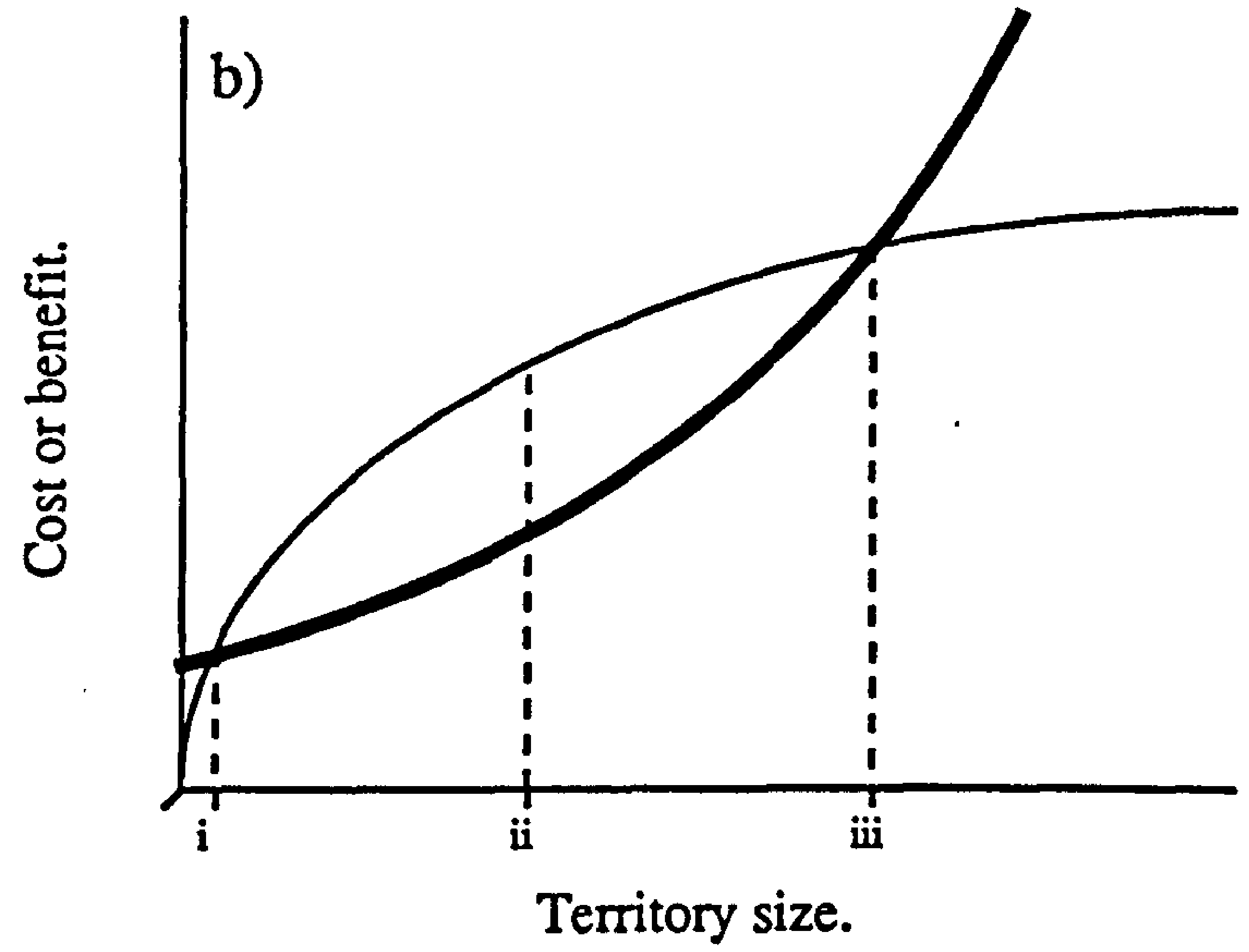
The costs of exploiting and defending large or small territories should differ; large territories being more costly to maintain than small (Davies & Houston 1984). Furthermore, the slope of the cost constraint on territory size would be expected to differ for territories of

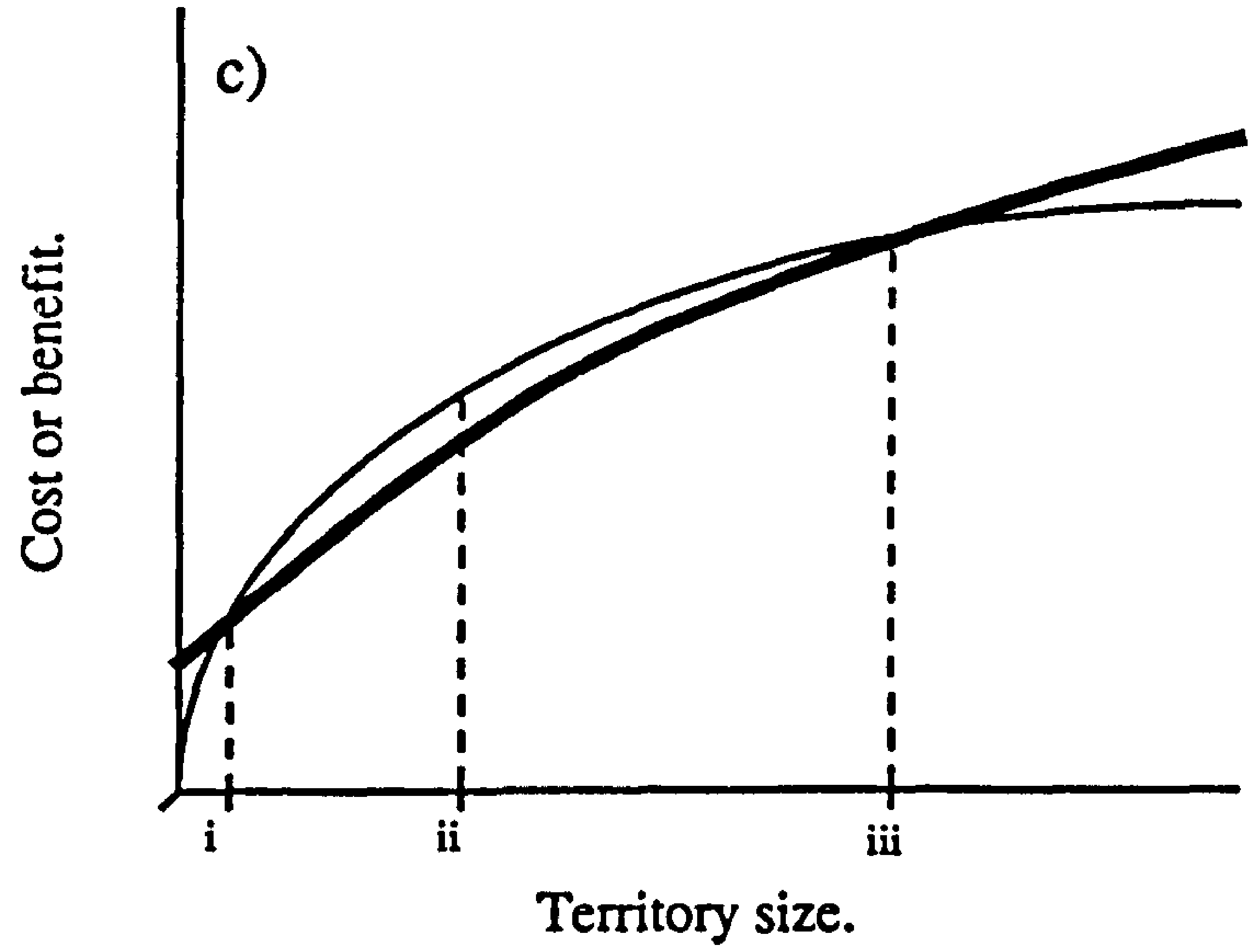
**Table 1.1.** A selection of previous studies in which a form of the cost constraint function in models of territory size has been proposed.

| Source | Nature of paper | Form of cost function | Justification |
|---|---|---|---|
| Kodric-Brown & Brown (1978) | Field study of the rufus hummingbird *Selasphorus rufus* | Begins at a positive value (maintenance cost) and increases as a linear or accelerating function with territory area | Costs must increase with the number of flowers in the territory, in order to reflect energy spent on foraging and defense |
| MacLean & Seastedt (1979) | Theoretical | Increases as a linear function with territory area, but could be different | Territorial defense time is a function of the mean distance between all possible points in the territory |
| Myers, Connors & Pitelka (1981) | Field study of the sanderling *Calidris alba* | Accelerating function with territory area | Intruder rate and cost per chase should increase with the area defended and the average chase distance |
| Davies & Houston (1984) | Theoretical | Accelerating function with territory area | More intruders will come into a larger territory and the owner will also have to patrol over larger distances |
| Stephens & Dunbar (1993) | Theoretical | Decelerating function with territory area | Dimensional analysis of previous cost/benefit models |
| Schoener (1983) | Theoretical | Linear, accelerating or decelerating function with territory size | Various assumptions |

**Fig.1.1.** The forms of different cost constraints on territory size that have been predicted by previous studies. All are shown with the same decelerating benefit constraint. In (a) the cost function is linear (Kodric-Brown & Brown 1978; MacLean & Seastedt 1979). The cost function in (b) is accelerating (Myers *et al* 1981, Davies & Houston 1984). Finally (c) shows a decelerating cost function (Stephens & Dunbar 1993). In each case the benefit function begins at the origin, while the cost function begins at a minimum maintenance cost (Kodric-Brown & Brown 1978, Myers *et al* 1981). The optimal territory size is indicated for three different currencies; (i) minimise cost, (ii) maximise net benefit, (iii) maximise gross benefit.


a)
Cost or benefit.
i
ii
iii
Territory size.


b)
Cost or benefit.
i
ii
iii
Territory size.


c)
Cost or benefit.
i
ii
iii
Territory size.

different shape. For example, the percentage area that is accessible from the centre of a circular or polygonal territory is greater than the percentage area within a highly linear territory (Fig.1.2.). It follows therefore, that the occupants of polygonal territories will incur lower costs when moving between foraging areas or boundaries, compared to the occupants of linear territories. The gradient, or rate of increase in gradient of the cost constraint should consequently be higher for the occupants of linear territories.

A comparison of the energy costs of using territories which differ in both size and shape will establish the reality and form of the energy cost constraint on territorial behaviour, and allow its significance for energy balance and territory maintenance to be assessed.

Consequently, the basic questions and hypotheses which this thesis will attempt to test may be summarised as follows:

1) In terms of temporal scheduling of visits to different parts of their territories, how do small passerines achieve territorial exploitation and defense?
2) Do the occupants of large territories incur higher energy costs than the occupants of small territories, and do the costs differ between territories of different accessibility (shape)?
3) What is the mathematical form of the energy cost constraint on territory size, and what are the implications of this for existing optimal models?

### 1.2.2. The study species.

Most studies of territorial animals have viewed owners as being separated from neighbours by a discrete territory boundaries. The location of these boundaries dictates how territories may be classified in terms of their shape. This concept is typified by two studies of territorial waders. The breeding pectoral sandpiper occupies territories which are separated from neighbours by a continuous boundaries. These are defined by dyads of neighbours as they signal their ownership to each other on the flat and uniform tundra habitat. These territories may be classified as highly polygonal, often forming the shape of a regular hexagon (Grant 1969). A hexagon would be expected if territories were packed as closely together as possible. Sanderlings wintering on uniform tidal sand flats are territorial when this is the most economic way to forage (Myers *et al* 1981). Under these conditions individual sanderling defend sections of shore line against conspecifics which may intrude by aggressive chases and evictions. Because the invertebrate prey exploited by sanderling are constrained by the tidal

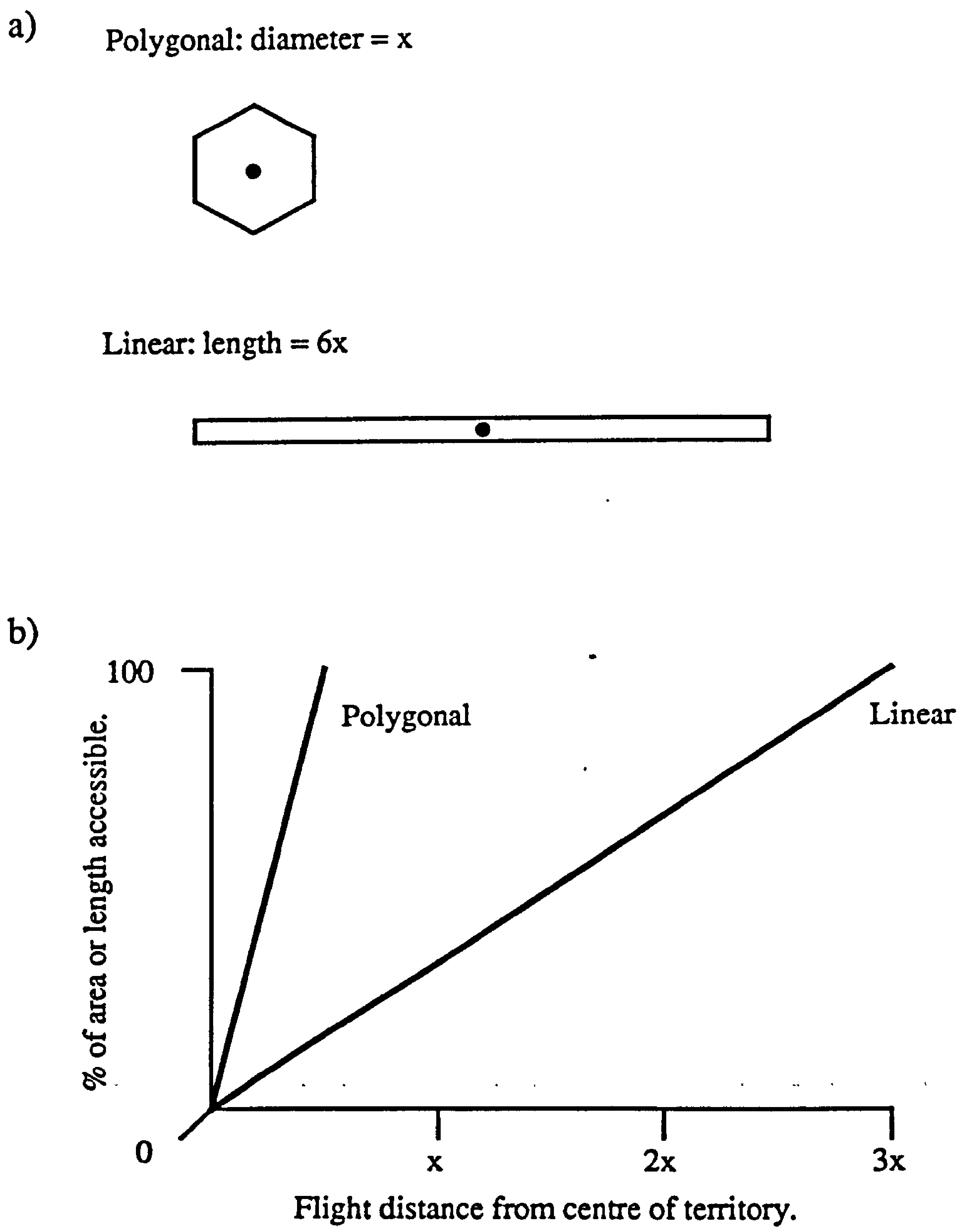


**Fig.1.2.** The effect of differences in territory shape on the accessibility of the space within territories. The two extremes of territory shape are polygonal which approaches circular and linear (a), the centre of each territory is marked by a solid symbol. In (b) it is apparent that the occupant of a polygonal territory would be able to reach foraging sites or intruders from the territory centre in a much shorter flight distance than the occupier of a linear territory.

cycle into a zone running along the shore, these territories may be considered highly linear, and result in the shore line being divided into short lengths separated by defended boundaries, beyond which owners will not venture (Myers *et al* 1981).

In these examples the defended resource is distributed in a uniform habitat, producing apparently simple territorial systems that are easily defined by shape. Such systems are however often difficult to study. For example, the behaviour of breeding sandpipers represents a compromise between several conflicting goals which often vary between the sexes. The goal of males is to guarantee paternity of his mates offspring while that of females may be to ensure copulations with the highest quality males available (Birkhead & Moller 1990). Furthermore, breeding territories are usually occupied by a male and female, making quantification of the costs and benefits of territorial behaviour more complex. Although these considerations do not affect the behaviour of wintering sanderlings occupying individual territories, defendability of their territories is governed by the 12 hr cycle of the tides, making long term monitoring or manipulation of individuals using the same territory difficult. Individuals must abandon their territories during high tide during which prey populations may redistribute themselves.

The choice of study species which conform to these two main criteria of easily observable territorial behaviour (display and aggressive evictions) and long term individual territoriality, and occupy polygonal and linear territories are met by a number of British species. The techniques employed to measure space use and energy expenditure, however, impose certain other requirements. Individuals must be large enough to be suitable for doubly labelled water measurements of energy expenditure, and to carry radio-tags for prolonged periods. Furthermore, frequent recaptures are necessary for replacing radio-transmitters during measurements of space use, and for labelling and sampling the body the water pool for the stable isotope technique. Finally the species must be sufficiently abundant for territorial interactions to be frequent and for information to be available on the consequences for the population of the territorial energetics of individuals.

During winter, the European robin and the dipper fulfil all of these requirements (Lack 1965, Cramp 1988). Based on the literature these species appeared to defend polygonal and linear territories respectively.

# Chapter 2.

# 2. General methods.

## 2.1. Introduction.

### 2.1.1. The non-breeding ecology and behaviour of the study species.

2.1.1.1. The robin.

The race of European robin to inhabit Britain is *Erithacus rubecula melophilus* (Cramp 1988), and represents the western end of a cline in progressively darker plumage across Europe. British and Irish birds show more olive mantles and richer orange breasts than European populations (Cramp 1988). There is no sexual dimorphism in plumage in this small passerine, although some studies report statistical differences in the wing-chord, tail and tarsus lengths between sexes when measured from skins, males being larger then females (Cramp 1988). The average life span of the robin has been estimated to be 13.3 months (Lack 1965), although a small proportion of birds may live for several years. Annual mortality is 62 % for adults and 72 % for juveniles (Lack 1965).

The robin preys predominately on small mobile invertebrates (Lack 1948, Grajetsky 1993), collected from the ground by hopping, or by dropping from perches once items have been located (East 1982). In severe weather, when the preferred foraging habitat may be frozen or covered by snow, individuals may take berries and even exploit ground disturbed by other animals including man (Harper 1984, Lack 1965). Birds living close to human habitations will readily exploit artificial food sources on bird tables (Lack 1965).

Harper (1986) describes most habitat occupied by robins as containing at least some mature trees, robin densities being low in poorly wooded areas of the British Isles. Lack (1948) recorded a preference by robins for woodland edges, suggesting a requirement for something other than mature trees alone. An analysis of wintering densities around Oxford suggested that the presence of abundant cover within two metres of the ground is an important factor in the suitability of habitat for wintering robins (Harper 1984b). A positive correlation between the density of the shrub layer and reproductive success has also been recorded (Hoelzel 1988).

Territories are maintained by singing and the aggressive eviction of intruders (Lack 1965, Chantrey & Workman 1984). Display involves adopting poses which exaggerate the orange breast patch. It has been suggested that the colour and extent of the breast is important in determining the relative dominance between dyads of birds (D.Harper pers. comm.). In this way robins may usually be able to settle aggressive interactions without fighting, although robins will kill opponents during struggles for territory ownership (Lack 1965, Harper 1984)

Non-breeding individual territories are established and defended by both sexes from the end of the annual moult in adults (July-August) or independence of fledged young, until the onset of spring song in the following spring. In the south of England the spring song surge may take place in early January (Lack 1965) while in central Scotland this is delayed until late February (this study). Females then abandon their individual territory and pair with males. The latter appear to enlarge their non-breeding territory, occasionally by fusing their territory with that of a neighbouring female (Lack 1965).

The robin is a partial migrant (Lack 1943). Typically males defend the same territory for their entire life (Lack 1965), while the majority of females and some males migrate varying distances to winter in a different location from that in which they breed. These movements are usually less than five kilometres (Mead 1984). A greater proportion of the population is migratory in the northern part of its range (Lack 1943). The tendency of individuals to be migrants or residents is genetically determined (Biebach 1983). Furthermore, the proportion of a population that is migratory depends on the nature of the habitat they occupy (Adriaensen & Dhondt 1984).

### 2.1.1.2. The dipper.

The mainland British race of the dipper *Cinclus cinclus gularis* (Cramp 1988) is an exclusively aquatic forager. Insect larvae constitute the main food items, supplemented with molluscs and small fish (Ormerod & Tyler 1986). Food is obtained by wading and diving in fast flowing water. This passerine is highly adapted to exploit this foraging niche, being of stocky build with powerful legs, and feet with sharp claws for clinging to boulders and stones to resist the full force of the water (Cramp 1988).

Owing to these foraging adaptations, typical sites occupied by the dipper are fast flowing streams and rivers, where preferred prey are abundant. Although in common with most small passerines mortality is high during the first few months of life, thereafter individuals may expect to survive for several years (Newton 1989). The dipper exhibits sexual dimorphism of body size. Males are larger than females, with insignificant overlap (Ormerod, Tyler & Lewis 1986).

The dipper has frequently been described as showing year round territorial defense

(Cramp 1988). Non-breeding territories are established after the late summer annual moult in adults, and after post fledging dispersal in young birds. Both males and females exhibit non-breeding territoriality. Individuals defend a length of suitable water course by the aggressive eviction of intruders (Cramp 1988). Dominance during encounters between owners and neighbours or owners and transients is influenced by relative body size and the intensity and extent of chestnut colouring on the belly (Newton 1989). Females abandon their territories in early spring and pair with males on larger breeding territories. Some populations show altitude-related seasonal movements, upland areas being abandoned during the winter (Cramp 1988).

### 2.1.2. Statistics and software.

Statistical procedures generally follow Zar (1974) and were carried out using $SPSS_X$. Normality of data was assessed by examination of histograms and by correlation with normal probability scores. Samples of data with correlations greater than 0.95 were considered to be normally distributed. Transformations were applied, where appropriate, to achieve normality. Small samples sizes and those which were not normally distributed were analyzed using non-parametric techniques. Unless otherwise stated, the five percent probability level for two-tailed tests was accepted as the value at which significance was achieved.

A large proportion of the space use statistics were obtained using the Ranges IVm application, issue 1.5 (Kenward 1990). Additional software used were the Static and Dynamic programs of Doncaster (1990). Software was run on an IBM compatible PC under the MS-DOS operating system. Data were entered and edited in WordPerfect® before being imported to the packages in ASCII format.

## 2.2. The robin.

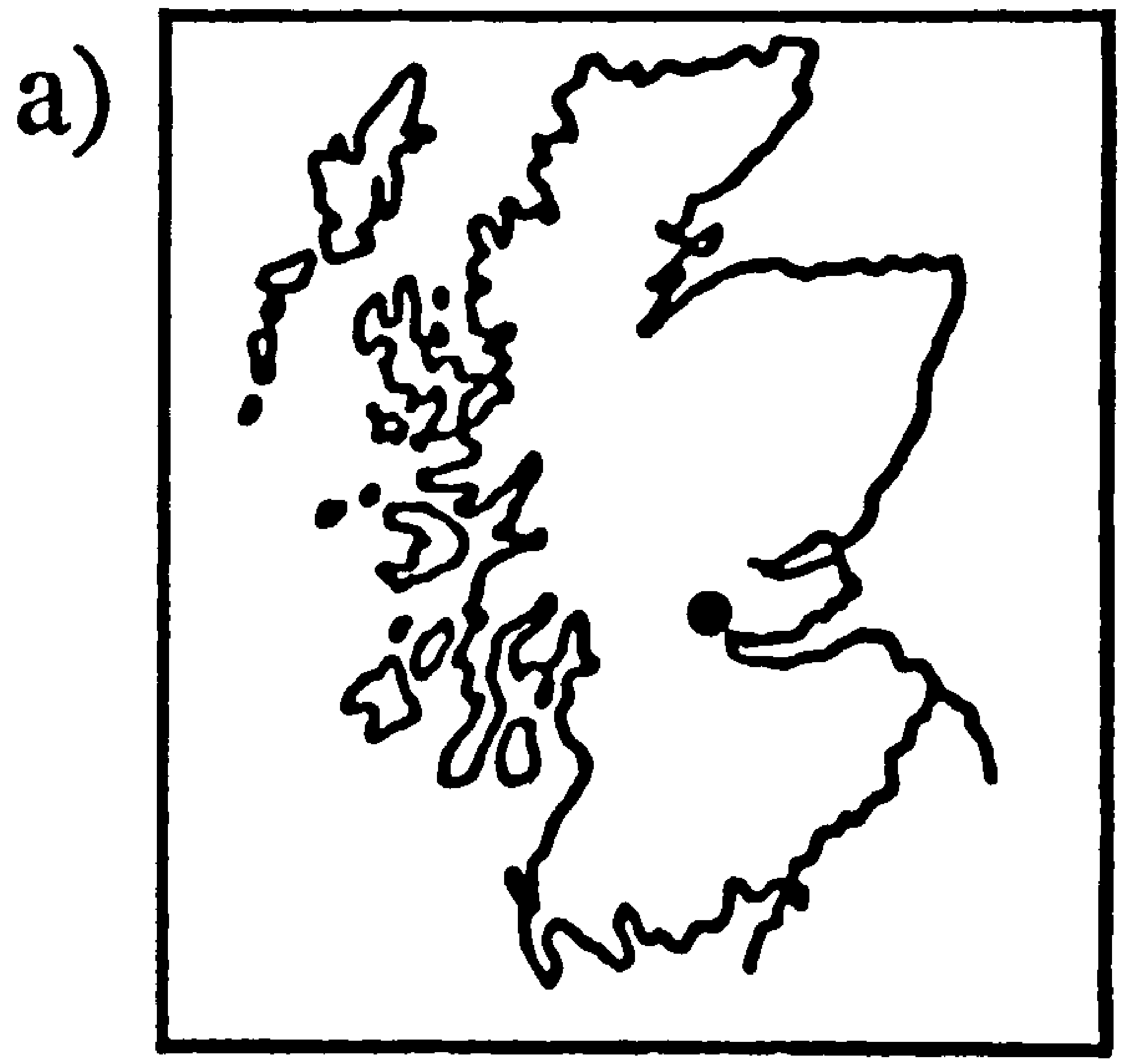
### 2.2.1. Methods.

#### 2.2.1.1. The study site.

#### *2.2.1.1.1. Location and aspect.*

The study population of robins was located on the campus of the University of Stirling in central Scotland. Although backed by the Ochil Hills to the north, the altitude of the study site was only 30-50 m above sea level. The two areas within which fieldwork was concentrated are shown in relation to major boundaries and buildings, in Fig 2.1.

**Fig.2.1.** The study area shown in relation to Scotland (a), and in more detail (b). The rectangles outline the two main study areas, within which the habitat structure is indicated. Solid indicates shrubs and bushes; stippled, tree canopy and open denotes grass. Thin lines represent field boundaries and buildings. North is towards the top of the figure.




b)
Spital Hill
Boilerhouse Wood
0
200
Scale (m)
©I.G.T. 1993

#### *2.2.1.1.2. Habitat structure and prey availability.*

The habitat within the study site could be divided into four zones. The major plant species and other important ground cover occurring within these zones are summarised in Table 2.1. The extent of the canopy, shrub layer and short grass within the main plots are also indicated on Fig.2.1.b. and summarised in Table 2.2. The dense shrub layer and more open areas within woodland are illustrated in Plates 2.1. and 2.2.

Prey availability was sampled using pitfall traps containing formaldehyde diluted in water, since these were likely the capture the mobile invertebrates which are preyed on by robins. Traps were placed in the ground so that their rim was at ground level. The circumference of the circular traps was 30 cm. Trap contents were inspected 24 hrs after being set.

#### *2.2.1.1.3. Weather data.*

A daily record was made of minimum and maximum temperature, rainfall and windspeed at the Parkhead weather recording station on the University campus during the course of each field season. Midpoint temperature was calculated as the midpoint value of the maximum and minimum temperature on each day.

### 2.2.1.2. The examination of individuals.

#### *2.2.1.2.1. Capture techniques.*

Robins were captured using a variety of techniques. Most favoured, because of the minimum of disturbance to the habitat, were walk-in cage traps. These were placed in dense cover, baited with cheese, porage oats or meal worms and regularly inspected for captured birds. The robins entered through a funnel shaped opening and once inside could not find the opening again. Up to 10 traps could be set at once to either trap different individuals over a large area or to saturate a small area with traps to increase the chances of capturing a particular individual. Occasionally more than one robin was found in a particular trap. Fights between robins in the confined space were however, very rare. In over 550 robin captures using traps, only 2 birds (0.4 %) died while in a trap. Of these, one injured its self while trying to escape, while the other was killed by another robin which had entered the same trap.

**Table 2.1.** Plant species and other important ground cover present in the different vegetation zones within the areas occupied by the robin study population.

| Vegetation zone | Approximate height range (m) | Species & nature of ground cover * |
|---|---|---|
| Herb layer & other ground cover | 0 | Short grass<br>Leaf litter<br>Nettle *Urtica dioica* #<br>Fern *Dryopteris felix-mas* # |
| Shrub layer | 0-3 | *Rhododendron ponticum*<br>Various ornamental spp.<br>Bramble *Rubus fruticosus*<br>Gorse *Ulex europaeus*<br>Broom *Cytisus scoparius*<br>Holly *Ilex aquifolium*<br>Yew *Taxus baccata* |
| Under story | 3-6 | Elder *Sambucus nigra*<br>Hawthorn *Crataegus monogyna*<br>Hazel *Corylus avellana* |
| Canopy | 6-9 | Oak *Quercus robur*<br>Horse Chestnut *Aesculus hippocastanum*<br>Sycamore *Acer pseudoplantanus*<br>Birch *Betula pendula*<br>Beech *Fagus sylvatica*<br>Ash *Fraxinus excelsior*<br>Elm *Ulmus laevis* |

* Ranked by approximate abundance.

\# Patchy abundance in early Autumn only.

**Table 2.2.** The area and % area of the habitat blocks indicated in Fig.2.1. that is accounted for by different habitat types. Since some habitat types overlap (eg bushes under canopy), the percentage habitat areas will sum to greater than 100.

| Habitat type | Boilerhouse Wood | | Spital Hill | |
|---|---|---|---|---|
| | Area (ha) | % total | Area (ha) | % total |
| Bushes & shrubs | 1.8 | 3 | 1.0 | 3 |
| Canopy | 13.2 | 22 | 9.2 | 34 |
| Buildings | 0.9 | 1 | 0.2 | 1 |
| Open grass | 49.1 | 76 | 19.6 | 65 |
| Total | 65.0 | | 30.0 | |

**Plate 2.1.** A section of the Boilerhouse Wood study area showing large *Rhododendron* bushes separated by more open areas.

**Plate 2.2.** A view through the Spital Hill study area. Although wooded, there were few bushes and shrubs.

Trapping efforts using cage-traps were supplemented with conventional mist netting when necessary. Using these techniques all robins using the study area could be captured or recaptured within a few hours, or occasionally with particularly wary individuals after a few days.

#### *2.2.1.2.2. Biometrics, ageing and sexing.*

Once captured robins were subjected to a detailed examination and a number of characters measured. These are described in Table 2.3. The standard diagrams used to quantify body fat deposits are summarised in Fig. 2.2. Although no confirmatory data are presented here, measurements were known to be highly repeatable. All birds were fitted with B.T.O. numbered aluminum leg rings and individual combinations of colour rings.

Over the course of the study a sample of dead robins was collected for the purposes of carcass analysis. These were subjected to a more rigorous examination, including measurement of wing span and area and determination of sex by dissection (Table 2.3.).

### 2.2.1.3. Measuring the energy expenditure of free-living birds.

#### *2.2.1.3.1. The doubly labelled water technique.*

The metabolic rate and energy expenditure of animals during calorimetry studies has often been determined from the rate of carbon dioxide production. The doubly labelled water technique is a method of indirect calorimetry which can be used to measure the energy expenditure of animals while free-living in their natural environment, in terms of carbon dioxide production estimated from rates of stable isotope turnover (Lifson & McClintock 1966). This measure of energy expenditure includes the costs of basal metabolism, thermoregulation, postural muscle activity, energy assimilation and locomotion.

The doubly labelled water technique was developed after the observation that inhaled oxygen rapidly achieved isotopic equilibrium with the oxygen in the body water pool (Lifson *et al* 1949). This is due initially to the combination of inspired oxygen and hydrogen ions in the body to form water, and the breakdown of body water to produce carbon dioxide during the Krebs cycle. The oxygen atoms from the liberated carbon dioxide and the body water are brought into isotopic equilibrium in the blood and ultimately exhaled gases, by reactions catalysed by the enzyme carbonic anhydrase (Speakman & Racey 1988).

**Table 2.3.** Summary of characters recorded during examination of live robins and during post mortem.

| Character | Description of measurement | Method | Units and resolution | |
|---|---|---|---|---|
| Wing chord | Flattened and straightened to give chord length (method 3, Svensson 1984). | Stopped rule | mm | 1 |
| Wing span * | Following Pennycuick (1989) | Rule | mm | 1 |
| Wing area * | Following Pennycuick (1989) | Area of traced outline | mm$^2$ | 25 |
| Tarsus length | Maximum length from rear of tarsal joint to base of digits, with tarsal joint and and digits flexed. | Callipers | mm | 0.1 |
| Head & bill length | Measured along the midline. | Callipers | mm | 0.1 |
| Bill length | Furthest extent of feathering on forehead to bill tip. | Callipers | mm | 0.1 |
| Bill depth | Vertical measurement at distal end of nostril. | Callipers | mm | 0.1 |
| Keel length | Segment length between point at which furcula joins sternum and posterior rim of sternum measured along the midline. | Callipers | mm | 0.1 |
| Body mass [$] | Total body mass of live bird. | 30 g spring balance | g | 0.1 |
| Body fat deposits [$] | Examination of tracheal pit and anterior abdominal regions to assess the extent of visible fat deposits. | Comparison of each region with standard diagrams | Scale of 0-4 | Nearest whole value |
| Age | Individuals were categorised as either adults of unknown age or 1$^{st}$ year birds, when captured for the first time. | Palate colour and plumage characters (Svensson 1984) | - | - |
| Sex [#] | Individuals catagorised as male, female or unsexed. Sex was determined by dissection during post mortems. | Cloacal protruberance, brood patch and behaviour | - | - |

* Only measured post mortem.

\# Only possible for live robins while birds were in breeding condition. Individuals which had been monitored in a previous Autumn and survived to breed could thus be sexed retrospectively.

$ Recorded for every recapture.

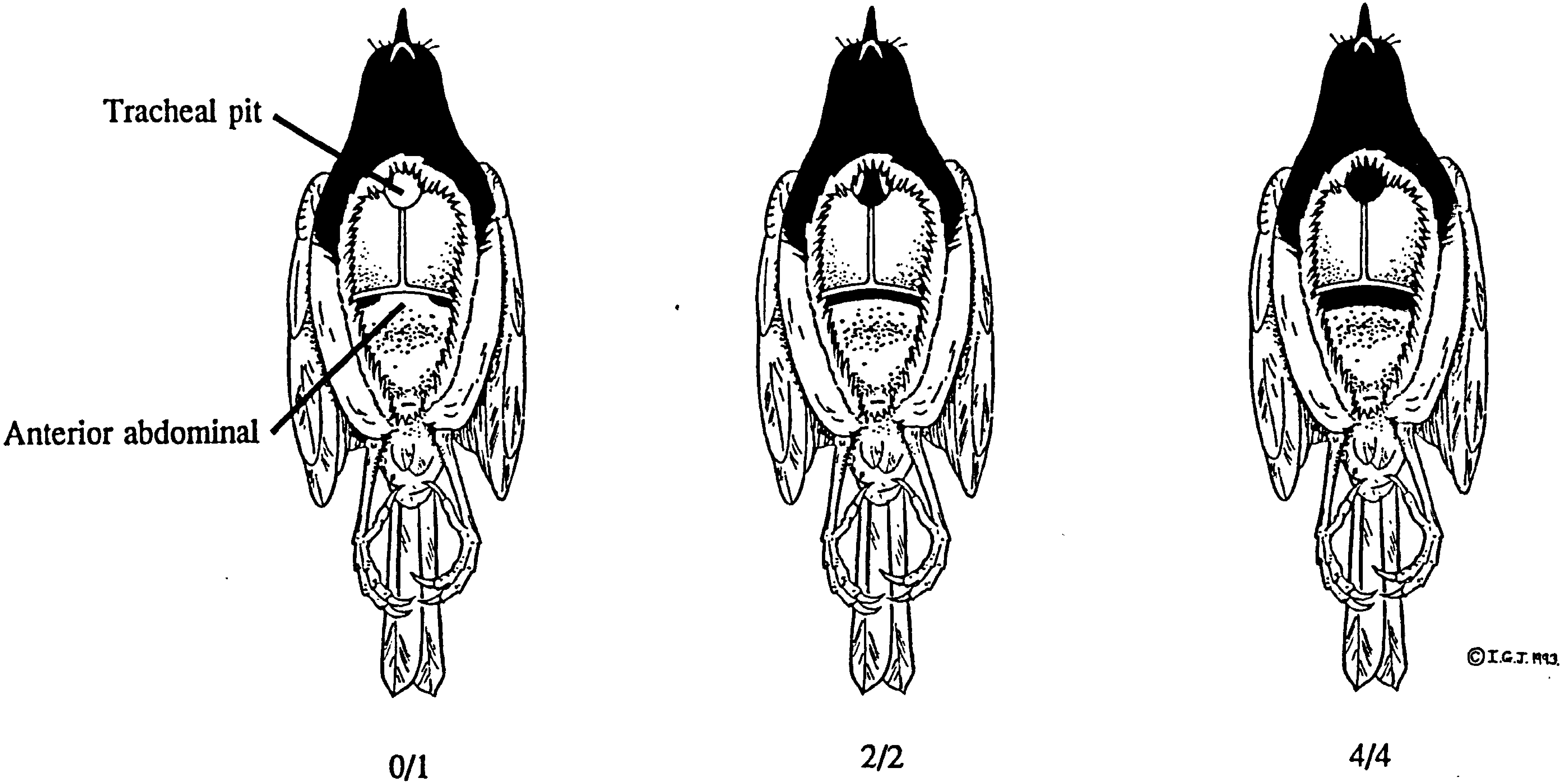


**Fig.2.2.** Diagrams showing the range of visible fat scores in the robin. The two main areas of fat deposition are indicated, with their associated scores for each bird shown (tracheal pit score/anterior abdominal score).

The technique involves labelling the body water pool with stable isotopes of hydrogen $^{1}H$ and oxygen $^{16}O$. These are deuterium $^{2}H$ and heavy oxygen $^{18}O$ respectively. Doubly labelled water is made up by mixing $^{2}H_2{}^{16}O$, a source of deuterium, and $^{1}H_2{}^{18}O$, a source of heavy oxygen. A period is allowed for the complete equilibration of these isotopes with the water within the subjects body, after which a sample of body fluid, normally blood, is taken. A second sample is taken some multiple of 24 hrs later, from which rates of isotope turnover are calculated.

The principle routes of loss of the $^{18}O$ label are in water and respiratory carbon dioxide. The $^{2}H$ is required to determine the amount of $^{18}O$ lost when combined with hydrogen to from water. Once this is known, the amount of $^{18}O$ lost as metabolic carbon dioxide can be determined from the turnover rates of the oxygen and hydrogen isotopes in the body (equation 1-3, Table 2.4.). The rate of carbon dioxide production is used to determine the average daily metabolic rate (A.D.M.R. $cm^3CO_2g^{-1}\ hr^{-1}$) (equation 4, Table 2.4.). Daily energy expenditure (kJ $day^{-1}$) may be calculated (equation 5, Table 2.4.) using an assumed value of the respiratory quotient RQ to determine the calorific equivalent of the volume of carbon dioxide produced.

Energy expenditure is often expressed in terms of metabolic intensity (M). This is the energy expenditure (kJ $hr^{-1}$) divided by the basal metabolic rate (kJ $hr^{-1}$). Since basal metabolic rate increases with the amount of metabolising tissue, this controls for differences in body mass when comparing energy expenditures between individuals or species.

Calculation of metabolic rate and energy expenditure from the rate of isotope turnover involves several assumptions which are not normally violated to an extent sufficient to introduce serious error in the results (Tatner & Bryant 1989). The assumptions are listed in Table 2.5. The principles and assumptions of the doubly labelled water technique have been discussed in more detail by Lifson & McClintock (1966), Nagy (1980), Speakman & Racey (1988), Tatner & Bryant (1989) and Speakman (1990).

Validation of the doubly labelled water technique against other techniques for estimating energy expenditure, such as laboratory based infra-red gas analysis and field based time/activity/laboratory studies, has yielded differences ranging from 3 % to 13 % (Bryant *et al* 1985). The mean absolute discrepancy in vertebrate studies however, is generally less than 10 % (Tatner & Bryant 1989).

**Table 2.4.** Formulae for calulation of energy expenditure from the initial, final and natural abundances of the stable isotopes $^2H$ and $^{18}O$ (ppm).

K = ln(Initial isotope excess) - ln(Final isotope excess) 1/(Measurement period) (ppm $hr^{-1}$)................1.

N = mass x Body water fraction x $(1000/18)^*$ (m Mol)..................2.

$rCO_2 = (N/2.08^{\#})(K_o-K_d) - (0.015\ K_d\ N)^{\$}$ (m Mol $hr^{-1}$)............3.

ADMR = $(rCO_2 \times 22.4^{\dagger})$/mass ($cm^3CO_2\ g^{-1}\ hr^{-1}$).....4.

DEE = ADMR x mass x $24^{\ddagger}$ x $(26.44/1000)^{\S}$ (kJ $day^{-1}$)................5.

**Where:**

Isotope excess = Differences between initial or final isotope abundance and natural abundance (ppm).
Measurement period = Period between initial and final samples (hrs).
K = Isotope turnover rate ($K_o$ for $^{18}O$, $K_d$ for $^2H$).
mass = mean body mass during measurement period (initial mass + final mass )/2.
Body water fraction = proportion of body mass that is water. Using data from Tatner & Bryant (1989), % Body water = 88.5 - 1.25 mass
N = Size of body water pool

---

* Converts g to Mol.
\# Product of a fractionation and stoichiometric factor.
$ Fractionation effects of evaporative loss assuming this accounts for 50 % water loss (Lifson & MacClintock 1966).
† Converts mMol to $cm^3$.
‡ Converts $hr^{-1}$ to $day^{-1}$.
§ Heat equivalent (kJ) of 1 $cm^3$ $CO_2$ (Brody 1945) based on an assumed value of RQ for a winter robin of 0.75 (Tatner & Bryant 1986).

**Table 2.5.** The assumptions inherent in the doubly labelled water technique (after Tatner & Bryant 1989).

1. *The body water pool is of constant volume during the measurement period.*
   Calculated $CO_2$ output is insensitive to naturally occuring changes in the body water fraction (Nagy 1980).
2. *Rates of water flux and carbon dioxide production are constant.*
   This will not be true for animals which show cycles of activity. To ensure that the result is not biased by the inclusion of a disproportionate amount of the active or resting phase, the measurement period should be as close to a multiple of 24 hrs as possible.
3. *Isotopes label only water and carbon dioxide within the subject's body.*
   Isotope exchange between body tissues such as lipid deposits and the body water pool is small and probably very slow (Schoeller *et al* 1986b).
4. *Isotopes leave the body only as water and respiratory carbon dioxide.*
   Loss of isotopes in ratios of $D:O^{18}$ other than 2:1 is minimal where investigated (Nagy 1980, Schoeller *et al* 1986).
5. *The specific activities of the isotopes in water and carbon dioxide leaving the body are the same as in the body water pool.*
   Even if the subject has a high fluid intake, the overestimate in the rate of $CO_2$ production due to fractionation is likely to be insignificant (Weathers & Nagy 1980).
6. *Water or carbon dioxide do not enter the animal across the skin or lung surfaces.*
   Evaluation of the technique with a mammal under humid conditions suggested no departure from the values of $CO_2$ production produced by other methods (Gettinger 1983).

### *2.2.1.3.2. Field protocol and analysis.*

Robins were captured during the late afternoon and weighed. The volume of doubly labelled water required for isotope concentrations to be detectable above natural abundance after 48 hrs was calculated from body mass using a dosage per gram of 20 µl. For most individuals this required a dose of approximately 0.2 $cm^3$. Labelled water consisted of a mixture of 20.6 atom % $^1H_2O^{18}$ and 99.8 atom % $^2H_2{}^{16}O$. The labelled water was introduced intraperitonially by injection. The injection site was midway between the anterior rim of the sternum and the pubis, off the mid line to avoid the ventral medial vein and dorsal aorta.

Once the stable isotope has been loaded, the robins were held in a bird bag in a quiet place for approximately one hour to allow the isotopes to reach equilibrium with the body water pool. The initial sample of body fluid, represented by a blood sample, was collected by pricking a vein with a sterile syringe needle. Two such sites were used to obtain samples of blood; inside and slightly distal to the tarsal joint; and the brachial vein in the wing where it lay exposed over the humerus-ulna joint. Sites were first swabbed with ethanol to reduce the chances of introducing pathogens and afterwards smeared with an antiseptic ointment. Great care was taken to prevent the surrounding feathers from becoming matted with blood as this would compromise the birds insulation. Eight to ten blood samples of approximately 5 µl were collected in 10 µl graduated glass capillaries, which were flame sealed within five minutes. The concentration of stable isotopes contained within these samples represented the initial abundances. The bird was then released in the same location as it was caught. By capturing birds in the late afternoon they could be released after equilibration around the time of dusk, at which time most birds settle down to roost. Because all robins were therefore inactive at the time of release, individuals could if necessary recover from the loading and sampling procedure without being at a competitive disadvantage relative to other robins in the neighbourhood.

The robins were recaptured as close as possible to the full period of measurement. This was normally 24 hrs but occasionally 48 hrs. The birds were reweighed and the second blood samples taken using the same methodology. The isotope concentrations in these samples represented the final abundances after having followed normal free-living activity for the duration of the measurement period. Samples of blood were taken from two unlabelled individuals at the start and end of the period during which doubly labelled water measurements were carried out. The deuterium and heavy oxygen concentrations in these samples represented the natural abundance of the isotopes in the study population.

The sealed blood samples could be stored at room temperature indefinitely prior to analysis of isotopic composition. The concentrations of $^{18}O$ and $^{2}H$ were measured by isotope ratio mass spectrometry, in the Life Sciences Laboratory at the Scottish Universities Reactor Research Centre, part of the National Engineering Laboratory at East Kilbride.

The concentration of $^{18}O$ label was measured by conversion of the water in the sample to carbon dioxide via reactions with guanidine chloride and phosphoric acid (Dugen et al 1985). The ratio of $^{18}O$ to $^{16}O$ in the sample of carbon dioxide was measured using a VG SIRA 10 isotope ratio mass spectrometer.

The concentration of $^{2}H$ was determined by reduction of the water in the sample to hydrogen gas in a uranium furnace at 600°C (Wong & Klein 1986). The gas was collected on activated carbon for analysis of hydrogen/deuterium ratios using an OPTIMA isotope ratio mass spectrometer. Samples were processed in ascending or descending order of deuterium concentration based on whether they were initial or final samples, in order minimise problems with the memory effect of the furnace which retains a small amount of the previous sample. Calibration equations used to determine the concentrations (ppm) of $^{18}O$ and deuterium from the delta raw values produced by the mass spectrometers were determined by running standard samples containing known concentrations of isotopes. On each run samples were compared to a standard reference gas of known isotopic content, which remained the same throughout the analysis.

Two capillaries from each sampling occasion were analyzed consecutively for each labelling isotope. A further replicate was analyzed if duplicate samples did not produce concentrations of the labelling isotope, ideally within 3 % of one another. This was not always possible, although 85 % of oxygen samples and 92 % of hydrogen samples did conform to this level of replication. The remaining replicates were within 5 %.
The mean of the closest pair of values from replicate samples was used in equation 1 (Table 2.4.).

### 2.2.2. Results.

#### 2.2.2.1. Weather data.

The correlations between the different weather variables during this period are shown in Table 2.6. All three temperature measures were highly positively correlated. Midpoint

**Table 2.6.** Pearson correlation coefficients between daily weather variables recorded at the University weather station, during the period between August and the onset of spring song in February for the years 1989/90 and 1991/92 (n=520).

| | $T_{min}$ (°C) | $T_{max}$ (°C) | $T_{mid}$ (°C) | Rainfall (mm) | Wind speed (knots) |
|---|---|---|---|---|---|
| $T_{max}$ (°C) | 0.81 *** | | | | |
| $T_{mid}$ (°C) | 0.94 *** | 0.96 *** | | | |
| Rainfall (mm) | 0.06 | 0.01 | 0.03 | | |
| Wind speed (knots) | -0.15 *** | -0.13 ** | -0.15 *** | 0.10 | |
| Day of year # | -0.72 *** | -0.79 *** | -0.80 *** | 0.12 * | -0.07 |

* P<0.01 ** P<0.005 *** P<0.001

\# Day one equals 1st August.

temperature was negatively correlated with windspeed, but was not correlated with rainfall. Midpoint temperature was also strongly negatively correlated with day of year as was rainfall. To summarise, as late summer progressed into autumn and winter, it became colder, wetter and windier.

The mean number of invertebrates captured by three pitfall traps positioned in the different habitat types in a 24 hr period was not correlated with the midpoint temperature recorded on the same day (r=0.23 ns n=20). Mean numbers of invertebrates captured were, however, correlated with the mid point temperature on the previous day (r=0.43 p<0.05 n=20), and most correlated with the midpoint temperature averaged over the previous five days (r=0.66 p<0.001 n=20). There were therefore more mobile invertebrates entering pitfall traps when the temperature was higher.

### 2.2.2.2. Morphological variation between individuals.

#### *2.2.2.2.1. Structural body size.*

Body size has been defined as the amount of total attachment surface available for metabolising tissues and the size of support structures for internal organs (Freeman & Jackson 1990). A measure of body size for each individual is required in order to control for differences in structural size when quantifying variables such as energetic condition, and when investigating the consequences of structural body size on the extent of territories and their pattern of use. Such a measure based on several characters is advantageous in that it reduces variation due to developmental abnormalities, abrasion or measurement error in single characters (Freeman & Jackson 1990).

The summary statistics for measures of structural size from all robins in adult plumage are presented in Table 2.7. The correlation matrix in Table 2.8. shows the strengths of the relationships between these different structural measures. Significant correlations were found between keel length and wing chord, keel length and head & bill length.

A principal component analysis was carried out on the measures of structural size recorded from each robin. The factor loading scores and percentage of variance in body size explained by each the three principal components extracted by the analysis are shown in Table 2.9. On average individuals of large structural size should be more massive than individuals of small structural size. The relationships between body mass, the individual measures of structural size and the composite measures of structural size represented by the

**Table 2.7.** Summary statistics for biometrics of robins in full adult plumage.

| | Mean (mm) | S.D. | n |
|---|---|---|---|
| Wing chord | 73.8 | 2.0 | 74 |
| Tarsus | 28.9 | 1.9 | 74 |
| Head & bill | 33.7 | 0.7 | 74 |
| Bill length | 8.4 | 0.5 | 73 |
| Bill depth | 3.4 | 0.2 | 74 |
| Keel | 16.5 | 0.8 | 72 |

**Table 2.8.** Pearson correlations between the measures of structural size (mm) in the robin. Only measurements taken from birds in full adult plumage were included, sample sizes in brackets.

| | Wing chord | Tarsus | Head & bill | Bill length | Bill depth |
|---|---|---|---|---|---|
| Tarsus | -0.01<br>(74) | | | | |
| Head & bill length | 0.28<br>(74) | 0.15<br>(74) | | | |
| Bill length | -0.06<br>(73) | 0.21<br>(73) | 0.10<br>(73) | | |
| Bill depth | 0.17<br>(74) | 0.04<br>(74) | -0.07<br>(74) | -0.14<br>(73) | |
| Keel | 0.32 **<br>(72) | 0.09<br>(72) | 0.26 *<br>(72) | 0.05<br>(71) | -0.03<br>(72) |

* $p<0.05$ ** $p<0.01$

**Table 2.9.** Factor loading scores from PCA of measures of structural size in robins (n=71). The % variance explained is the % of total variance in body size explained by each principal component.

| | **PC1** | **PC2** | **PC3** |
|---|---|---|---|
| Wing chord | 0.74 | -0.18 | 0.30 |
| Tarsus | 0.08 | 0.81 | 0.20 |
| Head & bill | 0.68 | 0.22 | -0.13 |
| Bill length | 0.01 | 0.72 | 0.25 |
| Bill depth | -0.01 | -0.01 | 0.94 |
| Keel | 0.75 | 0.04 | -0.06 |
| % variance explained | 27.4 | 21.6 | 16.8 |

principal components are shown in Table 2.10. Only keel length was significantly correlated with body mass. In multiple regression analysis with body mass as the dependent variable, keel length and bill depth were included at the five percent level of significance (Table 2.11.). Together these accounted for 14 % of the variation in body mass (Table 2.11.). This was considerably more than the 4 % accounted for by regression of the best composite measure of body size (PC1) on body mass.

#### *2.2.2.2.2. Wing morphology.*

The wing chord was significantly correlated with wing span but not wing length for the individuals measured post mortem (Table 2.12.). Wing span was however highly correlated with wing area (Table 2.12.). Wing span could not be measured on live robins because of the risk of injury and so it was predicted using the equation derived from the regression of wing span on wing chord (Table 2.13.). The minimum and maximum wing span and wing area recorded during the post mortems of 28 robins are shown in Fig.2.3. to illustrate the size range of the aerodynamic surfaces.

#### *2.2.2.2.3. Effects of age and sex.*

There were no significant differences between the individual measures and composite measure of structural size between male and female and adult and first year birds (Table 2.14.). Males were larger then females in three out of seven measures with one being equal, and adults being larger then juveniles in one out of seven, with three being equal. In addition, there were no significant differences between the composite measures of structural size represented by the principle components (T-tests all ns at $p<0.05$, same sample sizes). Any attempt to determine the age and sex of live robins, for example using a discriminant function analysis with the measures of structural size, was therefore liable to yield an unreliable sexing technique.

### 2.2.2.3. Physiological variation between individuals.

#### *2.2.2.3.1. Body composition and energetic condition.*

Energetic condition is a measure of the extent of an individuals' energy reserves. These may take the form of deposits of fat or protein within the body, and can be used to investigate when food shortage or other stresses occur (Marcström & Kenward 1981). In order

**Table 2.10.** Pearson correlation coefficients between body mass (g), and individual measures (mm) and principle components of structural size. All correlations except that indicated were non-significant at the 5 % level.

| | r | n |
|---|---|---|
| Wing chord | 0.04 | 74 |
| Tarsus | 0.06 | 74 |
| Head & bill | 0.14 | 74 |
| Bill length | 0.18 | 73 |
| Bill depth | 0.21 | 74 |
| Keel | 0.30 * | 72 |
| | | |
| PC1 | 0.20 | 71 |
| PC2 | 0.16 | 71 |
| PC3 | 0.17 | 71 |

* $p<0.01$

**Table 2.11.** Multiple linear regression analysis of body mass on the measures of structural size (n=72). Only coefficients significant at the 5 % level are shown. Independent variables that were non-significant were; wing chord, tarsus, head & bill, and bill length.

| Dependent variable | β | Independent variable | α | Cumulative $r^2$ | F | Significance |
|---|---|---|---|---|---|---|
| Body mass (g) | 0.676 | Keel length (mm) | | 0.08 | 7.15 | $p<0.01$ |
| | 2.392 | Bill depth (mm) | | 0.14 | 6.63 | $p<0.005$ |
| | | | 0.063 | | | |

β Regression coefficients.
α Elevation.

**Table 2.12.** Pearson correlation coefficients between measures of wing size recorded from robins during post mortems (n=28). Wing span and wing area were not significantly correlated with any non-wing measure of structural size at the 5 % level.

| | Wing chord (mm) | Wing span (mm) |
|---|---|---|
| Wing span (mm) | 0.50 * | |
| Wing area ($mm^2$) | 0.33 | 0.75 ** |

* $p<0.01$ ** $p<0.005$

**Table 2.13.** Regression statistics for the relationship between wing span and wing chord for robin carcasses examined during post mortem (n=27).

| Dependent variable | $\beta$ | Independent variable | $\alpha$ | $r^2$ | F | Significance |
|---|---|---|---|---|---|---|
| Wing span (mm) | 1.15 | Wing chord (mm) | 143.37 | 0.22 | 8.51 | $p<0.01$ |

$\beta$ Slope.
$\alpha$ Elevation.

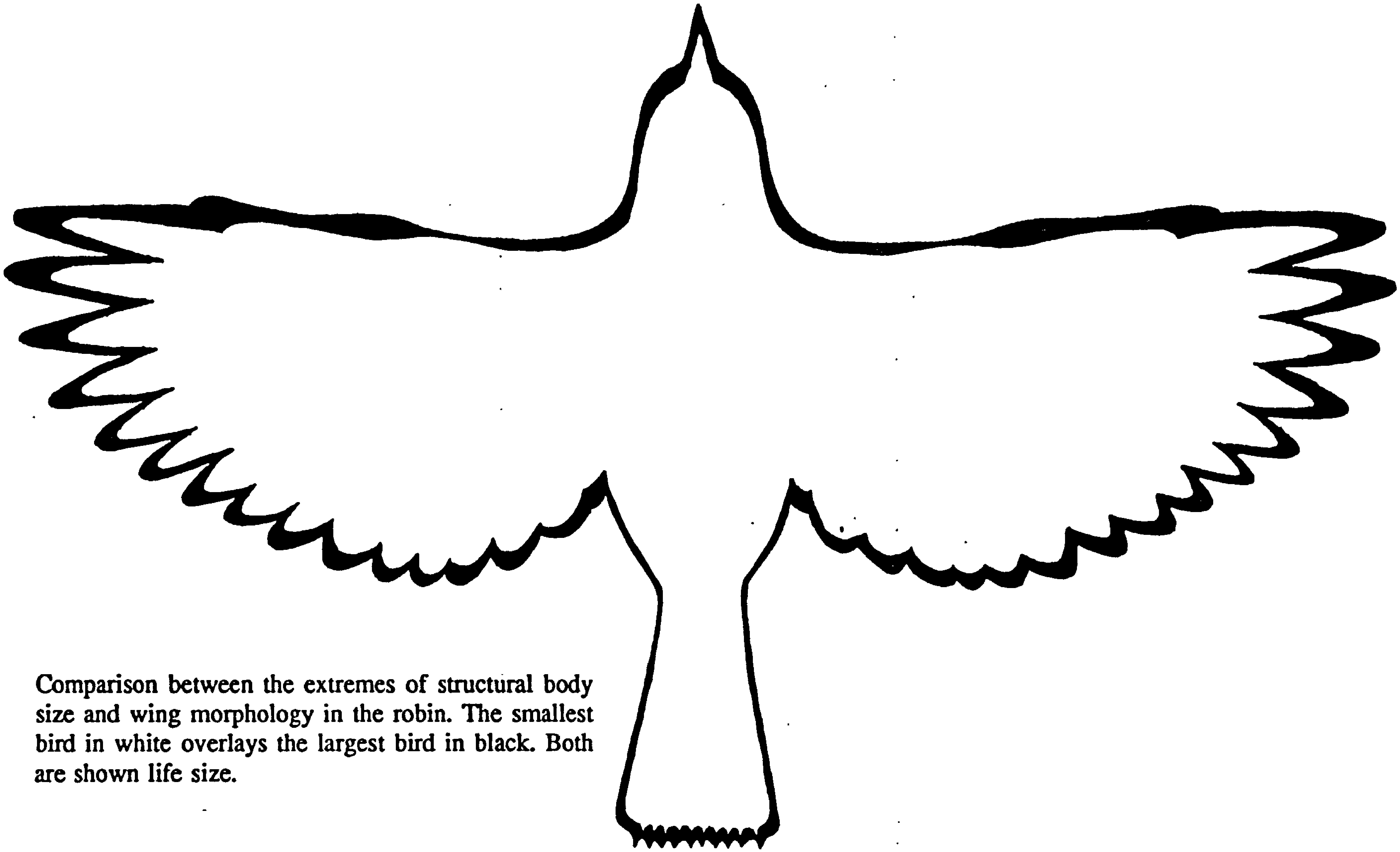


**Fig.2.3.** Comparison between the extremes of structural body size and wing morphology in the robin. The smallest bird in white overlays the largest bird in black. Both are shown life size.

**Table 2.14.** Comparisons between the measures of structural size (mm) of robins of different sex and age measured when in full adult plumage. T-tests between sex and age all ns at $p=0.05$. Data for each individual refer to the age when first captured.

| | Male | | | Female | | | Adult | | | 1st year | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | SD | n | Mean | SD | n | Mean | SD | n | Mean | SD | n |
| Wing chord | 74.1 | 2.1 | 17 | 72.7 | 2.0 | 14 | 74.1 | 2.1 | 32 | 73.6 | 2.0 | 42 |
| Tarsus | 28.4 | 0.7 | 17 | 29.0 | 1.0 | 14 | 28.8 | 0.9 | 32 | 28.9 | 2.4 | 42 |
| Head & bill | 33.7 | 0.7 | 17 | 33.8 | 1.0 | 14 | 33.7 | 0.7 | 32 | 33.7 | 0.8 | 42 |
| Bill length | 8.2 | 0.4 | 17 | 8.5 | 0.4 | 14 | 8.4 | 0.5 | 31 | 8.5 | 0.5 | 42 |
| Bill depth | 3.4 | 0.2 | 17 | 3.4 | 0.1 | 14 | 3.4 | 0.2 | 32 | 3.4 | 0.2 | 42 |
| Keel | 16.3 | 0.8 | 17 | 16.2 | 1.0 | 14 | 16.4 | 0.7 | 31 | 16.5 | 0.8 | 41 |
| Predicted mass * | 19.2 | 0.7 | 17 | 19.0 | 0.5 | 14 | 19.3 | 0.7 | 31 | 19.3 | 0.6 | 41 |

* Predicted mass=0.063+0.676 keel+2.392 Bill depth.

to quantify the energetic condition of live robins of known structural size, from the extent of their fat deposits or body mass, it is necessary to compare these estimates with the measured body composition of a sample of birds.

A sample of 27 robin carcasses collected over the course of the study and stored in a frozen state were analyzed to determine their composition in terms of fat, water and lean components. The mass at death was recorded before freezing. After thawing, the carcasses were examined and the characters described in Table 2.3. were measured and recorded as for live birds with the inclusion of further wing measurements and determination of sex by dissection. The stomach and intestine were dissected out to remove any effects of gut contents, and the carcasses reweighed to give the gut-free mass. Carcasses were then freeze dried to constant mass and reweighed to give the dry gut-free mass. The mass of water in the gut-free carcass was calculated as the difference between the gut-free mass and the dry gut-free mass. The fat contained within the carcasses was dissolved by reflux in a soxhlet apparatus for 24 hrs using a 5:1 dimethylether:chloroform mixture as the solvent. The carcasses were then further freeze dried and weighed for a final time to give the gut-free lean dry mass. The results are summarised in Appendix 1.

The fat scores were not normally distributed, 18 out of the 27 individuals (66 %) being scored zero for both tracheal pit and anterior abdominal regions. Because of this the data could not be normalised.

The relationship between fat score and measured fat content for the dead robins was nonlinear, fat content following a decelerating function with fat scores. After $\mathrm{Log}_{10}$ transforming the fat scores to linearise the relationship, the correlation between fat content and fat score was positive and highly significant (Fig.2.4.). Using the tracheal pit score alone, the correlation was slightly more significant ($r_s$=0.76 p<0.001 n=27) than that for the anterior abdominal region alone ($r_s$=0.74 p<0.001 n=27). The highest correlation however was obtained by using the sum of the two regions ($r_s$=0.77 p<0.001 n=27). Fat scores were an estimate of the visible area of fat relative to the structural size of individuals. Therefore the bodies of robins which scored highly on an assessment of their visible fat deposits did contain a high fat component on both absolute and relative scales.

The expected body mass of individuals of a particular structural size can be predicted from the equation in Table 2.11. Robins which contained relatively greater reserves of fat and protein will have a greater body mass than that predicted from their keel lengths and bill

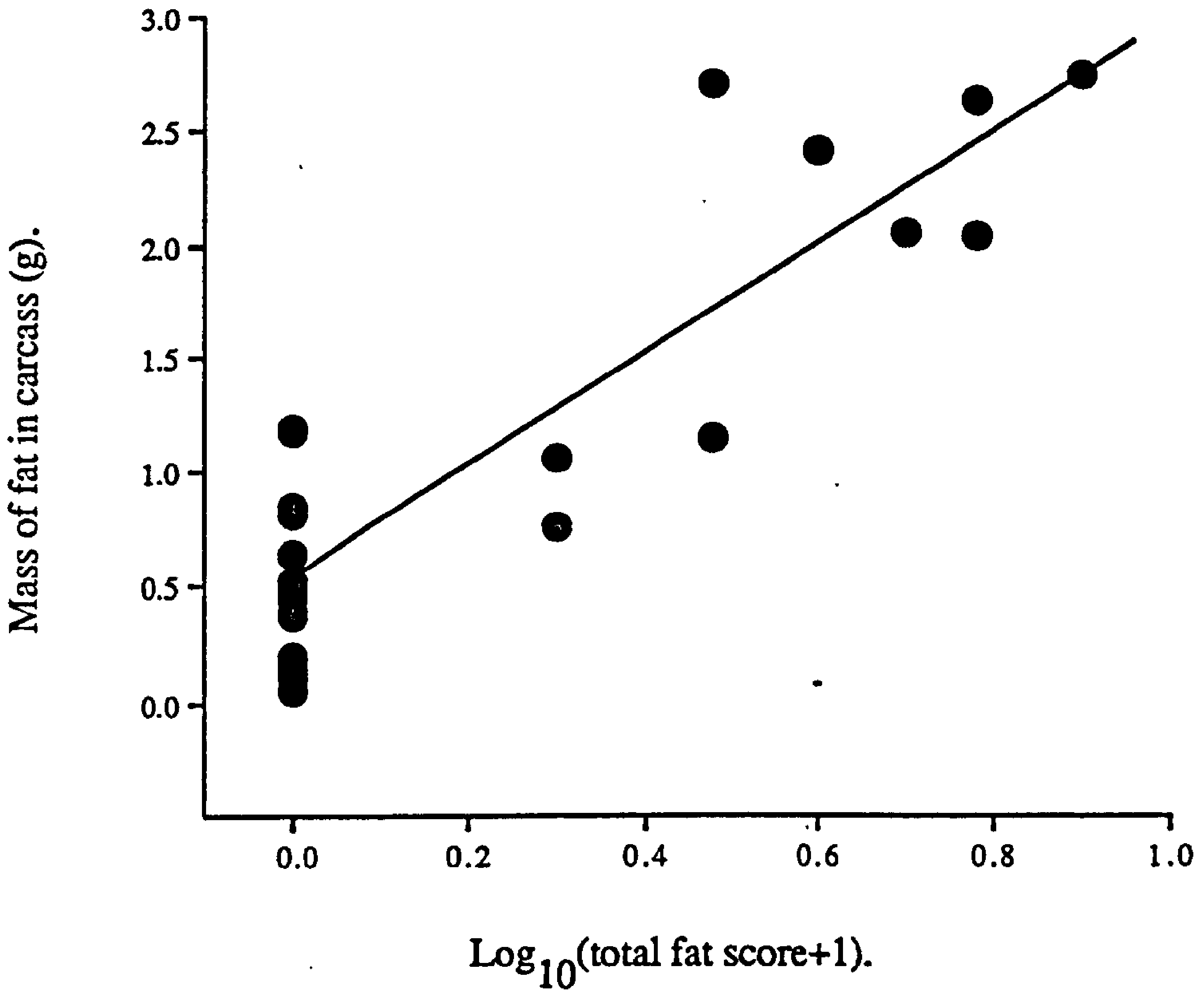


**Fig.2.4.** The relationship between total fat score and mass of fat (g) in robin carcasses ($r_s$=0.77 $p<0.001$ n=27). The line shows the fitted regression;

Fat mass=2.55 $\text{Log}_{10}$ (Total fat score+1)+0.46

depths. An index of body condition may therefore be obtained by subtracting the predicted body mass from the observed body mass (Ormerod & Tyler 1990). Values for the condition index will be positive for birds heavier then predicted from their structural size and negative for those lighter then predicted. The condition indices therefore control for much of the differences in body size (Ormerod & Tyler 1990).

Correlation analysis of the proportion of body mass at death made up by each body component (arcsine-square root transformed to normalise) with condition (Table 2.15.), indicated that robins that were heavier than expected from their structural size contained higher levels of fat, and robins which contained a large fat component did so at the expense of their proportional water and lean components. The relationship between change in fat content as measured by fat score and body mass is illustrated in Fig.2.5. for a sample of live birds reweighed after a mean period of 28 days (range 3-239 n=18). Mass change between captures was positively correlated with change in total fat score, the correlation explaining 33 % of variation in the data ($r=0.59$ $p<0.01$ $n=18$). Since each variable could be considered as the dependent, the trend is illustrated with a geometric mean regression line.

Robins which increased or decreased their total fat scores also increased or decreased their body mass. Total fat score and condition were therefore measures of body energy reserves and thus energetic condition.

The causes of death of the dead robins were known and could be categorised. These are shown in Appendix 1., along with definitions of the categories to which they were assigned. In summary four were taken under licence; six were found dead; seven died in accidents and seven were predated by domestic cats. Based on an analysis of body mass and total fat score, there were differences between individuals which had died from different causes. Robins which were collected under licence were assumed to represent healthy average birds. Their median body mass was only 1.0g (5 %) less than the median of all live individuals captured (n=74). Robins which were found dead were on average 2.45 g (14 %) lighter than these, while those predated by domestic cats were on average 2.41 g (13 %) heavier. The birds which had suffered accidental deaths were however only 0.81 g (4 %) heavier than those taken under licence. The data are shown in Fig.2.6.a. Although the differences between groups were significant (Kruskal Wallis ANOVA $H=11.21$ $p<0.005$ $df=3$ $n=4,6,7,7$), Tukey multiple comparisons between classes were barely significant at the five percent level (Table 2.16.). There were no differences between the structural size of the birds

**Table 2.15.** Pearson correlation coefficients between body condition and the four main components of body composition for robins (n=16). Condition is the observed body mass minus the body mass predicted by keel length and bill depth. The carcass components are the proportion of the observed mass accounted for by each of the components, arcsine-square root transformed to normalise.

| | Condition (g) | Gut component | Water component | Fat component |
|---|---|---|---|---|
| Gut component | 0.41 | | | |
| Water component | -0.64 ** | -0.63 ** | | |
| Fat component | 0.69 **** | 0.10 | -0.74 *** | |
| Lean component | -0.81 **** | -0.74 *** | 0.66 ** | -0.50 ** |

* $p<0.05$ ** $p<0.01$ *** $p<0.005$ **** $p<0.001$

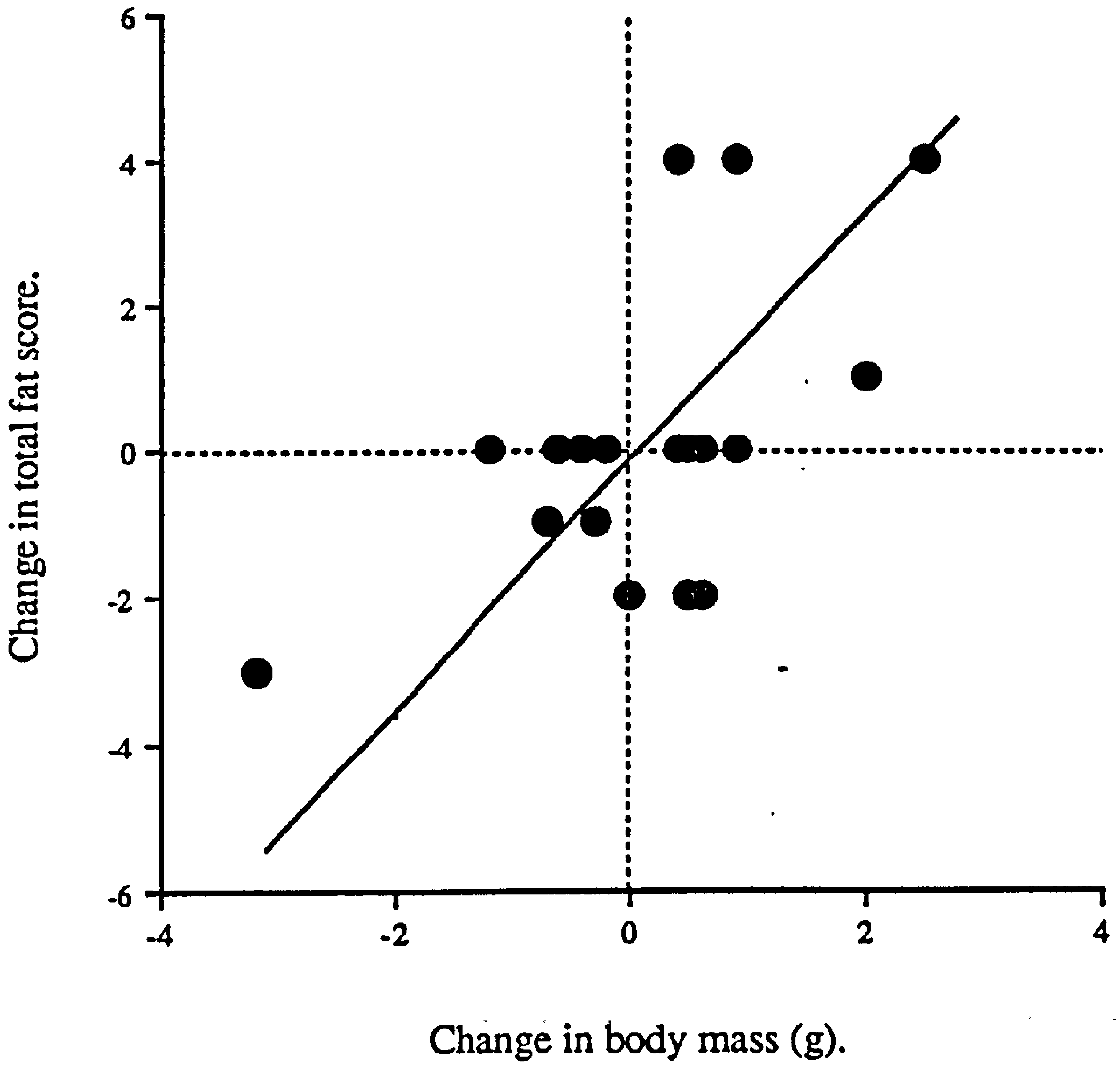


**Fig.2.5.** The relationship between change in body mass (g) and change in total fat score ($r=0.59$ $p<0.01$ $n=18$). The line indicates the geometric mean regression;

Change in fat score=1.67 Mass change-0.18
($r^2=0.30$ $F=8.44$ $p<0.01$ $n=18$)

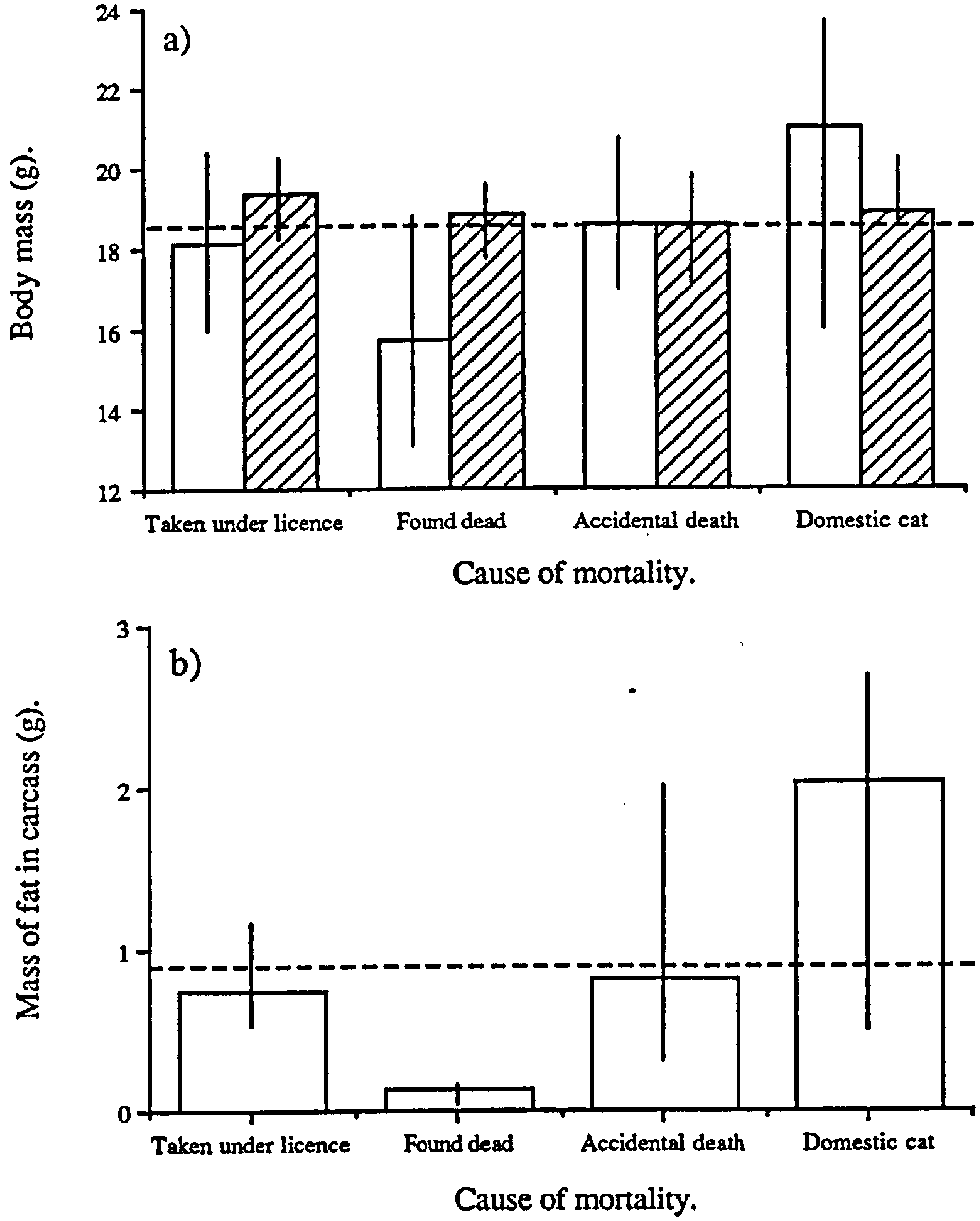


**Fig.2.6.** Body condition and causes of mortality. In (a) is shown median body mass at death (open) and median body mass predicted from structural size (hatched). The median fat content of carcasses is shown in (b). Error bars indicate range of data, and dashed lines the mean of the group means of the observed data. Samples sizes; taken under licence n=4; found dead n=6; accidental death n=7; domestic cat n=7. See text and Tables 2.16 and 2.17 for accompanying statistics.

**Table 2.16.** Critical values (q) and probability levels for relevant Tukey multiple comparisons between the body mass at death of robins which died of different causes.

| | Found dead (n=6) | Accidental death (n=7) | Domestic cat (n=7) |
|---|---|---|---|
| Taken under licence (n=4) | 2.826 | 0.962 | 2.862 |
| Accidental death (n=7) | 4.364 *** | - | 2.228 |

* p<0.2 ** p<0.1 *** p<0.05

**Table 2.17.** Critical values (q) and probability levels for relevant Tukey multiple comparisons between the fat content at death of robins which died of different causes.

| | Found dead (n=6) | Accidental death (n=7) | Domestic cat (n=7) |
|---|---|---|---|
| Taken under licence (n=4) | 2.694 | 0.198 | 3.786 * |
| Accidental death (n=7) | 3.345 ** | | 4.218 *** |

* p<0.2 ** p<0.1 *** p<0.05

which had died in different ways (Kruskal Wallis ANOVA H=5.29 ns df=3 n=4,6,7,7). The same pattern of differences between causes of death were shown by the total fat scores (Fig.2.6.b.). The differences were more significant (Kruskal Wallis ANOVA H=16.13 $p<0.001$ df=3 n=4,6,7,7), as were the multiple comparisons between classes (Table 2.17.).

### *2.2.2.3.2. Variation in energetic condition.*

Condition was not correlated with daylength or time of capture (as a percentage of daylength elapsed)(arcsine square root transformed; r=-0.12 ns n=66, r=0.15 ns n=66). Similarly, total fat score was not correlated with time of capture (r=0.01 ns n=49). However, it was negatively correlated with day length (r=-0.54 $p<0.001$ n=49). Hence robins tended to have larger fat deposits when days were short. The small annual variation in body mass from late summer through to mid winter is illustrated in Fig 2.7.

The correlations between condition, total fat score and various weather variables are shown in Table 2.18. Both condition and fat score were most consistently and strongly correlated with the weather averaged over the previous five days with temperature being most important.

## **2.2.3. Radio-tagging methodology.**

### 2.2.3.1. Weight considerations and transmitter performance.

Attaching a load to a volant animal will cause a reduction in its flight performance, specifically by increasing its weight and increasing the drag on its body (Obrecht *et al* 1988). Such effects may be highly significant for animals which include flight as part of their normal time/activity budgets. The often-cited 10 % and 5 % of body mass limits (Brander & Cochran 1969, Cochran 1980) have been applied in many studies when determining the maximum mass a device may be in order to prevent any deleterious effects on a subject. The rationale for selecting these limits however, has seldom been discussed.

In most flying animals the power available from the flight muscles ($P_a$) is greater then the power required for flight at the maximum range velocity ($P_{mr}$); the most economic velocity for level flight (Caccamise & Hedin 1985). The difference between $P_a$ and $P_{mr}$ represents the surplus power ($P_s$) available for a bird to use in flight over and above $P_{mr}$. A portion of $P_s$ is used whenever a bird accelerates, manouvers, gains altitude or transports an additional load such as fat deposits, large food items or an electronic device (Caccamise & Hedin 1985).

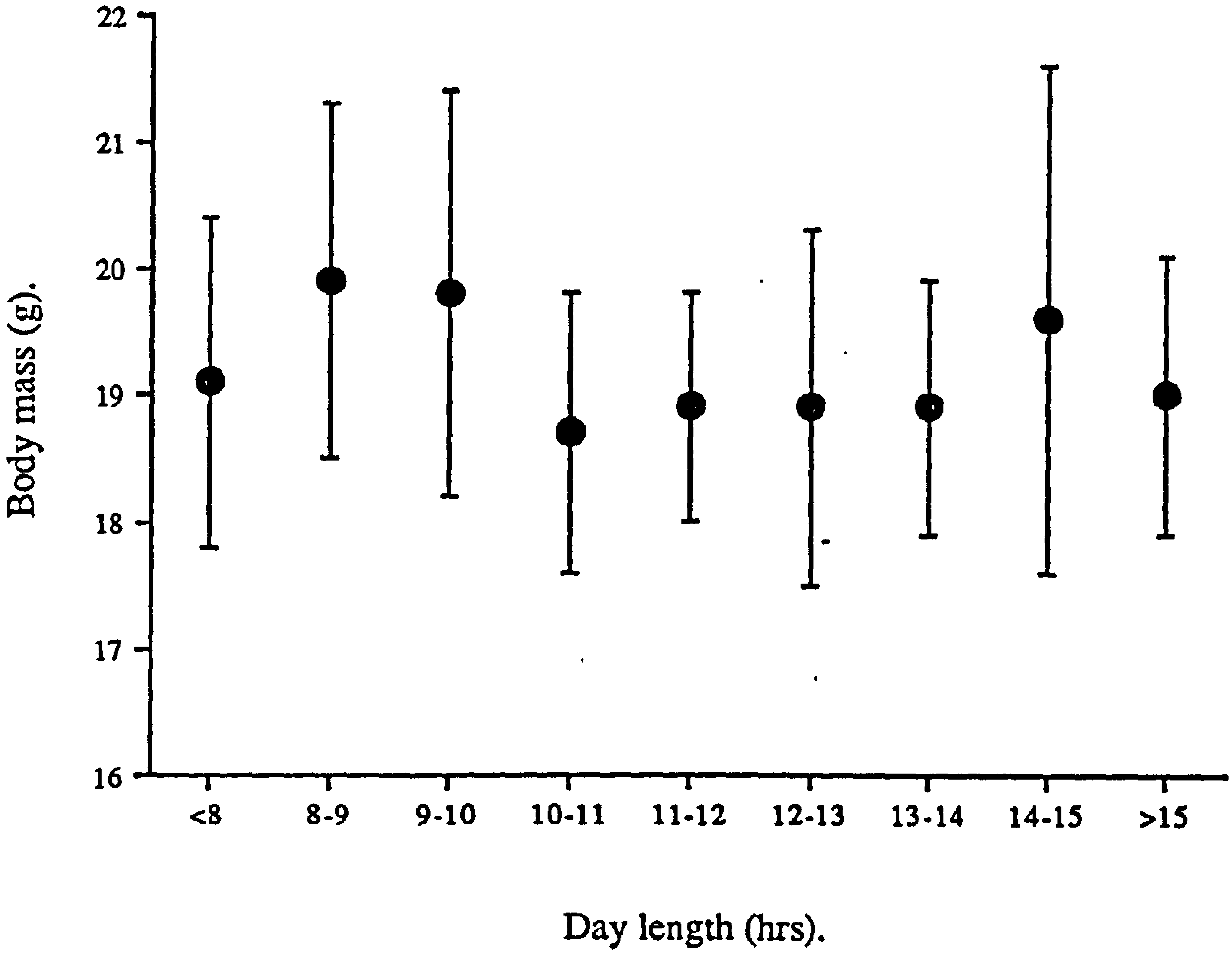


**Fig.2.7.** Variation in mean body mass with daylength (±SD). Although data were independent within each daylength class, some individuals were included in several different classes to achieve acceptable sample sizes. Sample sizes for daylength classes, starting with the shortest; n=47,34,31,29,19,26,25,39,12.

**Table 2.18.** Correlations between measures of weather variables, body condition total fat scores for robins between August and the onset of spring song in February (mass n=76, fat score n=54). Mass was normally distributed. Fat scores were not normally distributed and could not be normalised by transformation. Condition is the observed body mass minus the body mass predicted from keel length and bill depth.

| | Weather on day of capture | | Weather on previous day | | Weather averaged over previous five days | |
|---|---|---|---|---|---|---|
| | Condition # | Fat score $ | Condition # | Fat score $ | Condition # | Fat score $ |
| $T_{mid}$ (°C) | -0.21 | -0.51 **** | -0.16 | -0.49 **** | -0.26 * | -0.49 **** |
| Rain (mm) | -0.06 | -0.26 * | 0.05 | -0.19 | -0.01 | -0.38 *** |
| Wind speed (knots) | 0.00 | -0.37 *** | -0.30 ** | 0.06 | -0.03 | -0.41 **** |

* $p<0.05$ ** $p<0.01$ *** $p<0.005$ **** $p<0.001$

\# Pearson correlation.

$ Spearman correlation.

Furthermore, for a given reduction in $P_s$ a small bird can carry a greater proportion of its body mass than a large bird (Caccamise & Hedin 1985).

A radio-tag represents just such an additional load to a bird, and because of this a compromise must be sought between minimising the device mass and maximising its usefulness in the field. A large and heavy power cell can drive a transmitter of high signal range or long transmitting life, but represents a larger load to the bird. All radio-tags used in the present study were based on Biotrack SS-1 single stage transmitters powered by silver cells and potted in epoxy resin. While the predicted transmitting life was two to four weeks, field life was frequently longer.

The completed radio-tags weighed 1.8 g compared to the mean of 19.3 g (range 15.0-23.5 n=74) for the body mass of the robin in the present study. Radio-tags therefore represented on average 9 % of body mass. For the lightest bird however, this represented 12 % and for the heaviest 7 % of body mass. The reduction in the surplus power available to robins of this range of body mass are shown in Table 2.19. with accompanying data in Table 2.20. $P_{mr}$ was calculated using the computer programs of Pennycuick (1989), metabolic variables being set to the default values (see Appendix 2.). The radio-tag was assumed to be covered by feathers with zero increase in drag. Examples of the output for two simulations are shown in Appendix 2. Variation in the mass of the pectoral muscles of the robin accounted for 71 % of the variation in body mass (Table 2.20.). If flight muscles of different mass are assumed to have the same power availability ($P_a$), then as predicted by Caccamise & Hedin (1985) birds of higher body mass will use more of their $P_s$ in carrying devices than birds of low mass (Table 2.19.). If $P_a$ from the flight muscles covaries with their mass however, then it is the low mass and under-powered individuals which must use more of their $P_s$ to carry a device such as a radio-tag (Table 2.19.). In both cases however, the reduction in $P_s$ is less then two percent. In terms of available mechanical power produced by the flight muscles therefore, an 1.8 g radio-tag falls well within the capabilities of the robin to carry additional loads in level powered flight.

During the short flights typical of foraging robins, the total chemical power required (25.6 $kJhr^{-1}$; Tatner & Bryant 1986) is twice $P_a$ (Table 2.19), since birds are operating at speeds less than $V_{mp}$. Although some of this is due to basal metabolism, thermoregulation and the legs during takeoff and landing (Tatner & Bryant 1986), $P_s$ will be substantially reduced with associated reduced load carrying capacity. Nevertheless, the chemical power required by

**Table 2.19.** Percentage change in the surplus power available for flight by robins of similar size but different body mass engaged in powered flight, with and without 1.8 g devices attached.

| | Body mass (g) | $P_a$ (kJhr$^{-1}$) * | No device carried | | 1.8 g device carried | | %$\Delta P_s$ † |
|---|---|---|---|---|---|---|---|
| | | | $P_{mr}$ (kJhr$^{1}$) # | $P_s$ (kJhr$^{-1}$) $ | $P_{mr}$ (kJhr$^{-1}$) # | $P_s$ (kJhr$^{-1}$) $ | |
| **Assuming mechanical power available from flight muscles is constant and based on their mean mass** | 15.0 | 12.82 | 1.12 | 11.70 | 1.25 | 11.57 | -1.1 |
| | 19.3 | 12.82 | 1.57 | 11.25 | 1.74 | 11.08 | -1.5 |
| | 23.5 | 12.82 | 2.07 | 10.75 | 2.24 | 10.58 | -1.6 |
| **Assuming mechanical power available from flight muscles varies with body mass.** | 15.0 | 9.07 | 1.12 | 7.95 | 1.25 | 7.82 | -1.6 |
| | 19.3 | 12.82 | 1.57 | 11.25 | 1.74 | 11.08 | -1.5 |
| | 23.5 | 17.06 | 2.07 | 14.99 | 2.24 | 14.82 | -1.1 |

* Mechanical power available from flight muscles $P_a=m_f fQ$ (Jhr$^{-1}$). Where $m_f$ is the wet mass of the flight muscles (g) (see Table 2.20.),f is the wing beat frequency (26 beats sec$^{-1}$ for tits; Burton 1990, and assumed not to vary with body mass) and Q is the work done in one contraction per gram of muscle (Pennycuick 1989), equal to 57Jkg$^{-1}$ (Caccamise & Hedin 1985).

# Maximum range power $P_{mr}$ is the mechanical power required to fly at the most efficient velocity $V_{mr}$ (Pennycuick 1989).

$ Surplus mechanical power $P_s=P_a-P_{mr}$ (Caccamise & Hedin 1985).

† Percentage change in surplus power.

**Table 2.20.** Flight characteristics of robins of minimum, mean and maximum body mass and mean wing span.

| Body mass (g) | Pectoral muscle mass* (g) | Wingdisc loading$ ($g\ mm^{-2}$) |
|---|---|---|
| 15.0 | 1.7 | 0.00115 |
| 19.3 | 2.4 | 0.00148 |
| 23.5 | 3.2 | 0.00181 |

* Pectoral muscle mass=0.81 Body mass-1.05 ($p<0.0001$ $F=38.5$ $r^2=0.71$ $n=16$), (pectoral muscle mass was not correlated with body size, as predicted from keel length and bill depth, $r=0.25$ ns $n=16$).

$ Body mass divided by $\pi(\text{wingspan}/2)^2$ (Feinsinger & Chaplin 1975). Wing Chord set to mean value of 228.2mm (see section 2.2.2.2.2.).

the muscles of a 19.3 g robin to carry the 1.8 g device at $V_{mp}$ only increases from 5.29 to 5.83 kJhr$^{-1}$ (10 %)(Appendix 2.). For 15 g and 23.5 g birds this is 12 % and 8 % respectively. Here chemical power refers to the rate that energy must be metabolised in order to provide mechanical power in the form of muscle contraction. Approximately 77% of the chemical power will be lost as heat.

Following a theoretical study of load carrying in small bats, Aldridge & Brigham (1988) concluded that a 1:1 relationship existed between percent device load and percent decrease in manouverability. The robin has a relatively high wing loading and aspect ratio compared with other birds of a similar body mass or wing area (Tatner & Bryant 1986, this study), which implies an inherent high acceleration and manouverability (Pennycuick 1989). Consequently, this implies that robins equipped with 1.8g packages could likewise incur a 7-12 % reduction in their manouverability depending on their body mass.

The radio signal was broadcast through a 10 cm whip antenna and was in the 173-174 MHz range. The range over which the signals could be detected with RX-81 receivers and three-element yagi antennas was up to one kilometre, but depended on the height of birds above ground level. The range was greatest at night when the birds were stationary and usually some distance above the ground while roosting. The poorest range was experienced from birds which roosted in rabbit burrows. Even when transmitters were shielded by up to 50 cm of earth, however, signals could be detected at over 100 m.

### 2.2.3.2. Available options for attaching radio-tags to small passerines.

Radio-tags have frequently been attached to larger birds in the form of a back pack using harnesses made from elastic, leather or neoprene (reviewed by Kenward 1987). This technique however, has been rarely used to attach radio-tags to small birds. Out of 13 studies of birds of body mass less than 70 g (Table 2.21.), only 1 (8 %) used a harness. Problems associated with the use of harnesses include the possibility of snagging on vegetation; disruption of the aerodynamic profile of the bird and the generation of a thermal window in the plumage around the device and along the harness straps, causing failure of water proofing or excessive heat loss in cold environments. Harnesses are also permanent unless a bio-degradable element is included.

The technique used most often on small birds has been to attach radio-tags using glue, usually to an area of trimmed feathers in the interscapular region (8 out of 13 studies, 62 %,

**Table 2.21.** Previous studies of small free living volant animals (<70 g) which have used radio-tracking. Dashes indicated information not stated or not available. Continued on next page.

| **Foraging guild**<br>Species | Body mass (g) † | Wingdisc loading (g mm$^{-2}$) # | Total mass of Radio-tag package (g) $ | Method of attachment and location of package | Reported effects | Source |
|---|---|---|---|---|---|---|
| **Intertidal probers** | | | | | | |
| * Purple sandpiper | | | | | | |
| *Calidris maritima* | 68.0 | 0.00050 | 2.0 | Cyanoacrylate, dorsal | 1 out of 5 deserted clutch and later predated | Cresswell & Summers (1990) |
| * Dunlin | | | | | | |
| *Calidris alpina* | 53.0 | 0.00058 | 1.1 | Epoxy resin, posterior dorsal | 9 % could not fly, increased predation during first 3 days. | Warnock & Warnock (1993) |
| **Oceanic surface dippers** | | | | | | |
| * Storm petrel | | | | | | |
| *Hydrobates pelagicus* | 30.0 | 0.00035 | 1.5 | Cyanoacrylate and thread, central tail rectrice | No effect on the survival and reproduction of one individual | Nygard & Einavik (1992) |
| **Vegetation and ground gleaners** | | | | | | |
| * Northern Cardinal | | | | | | |
| *Cardinalis cardinalis* | 47.0 | - | 1.4 | Cyanoacrylate, mid dorsal | No evidence for increased mortality or impared behaviour | Johnson, Pebworth & Krueger (1991) |
| * Northern Orioel | | | | | | |
| *Icterus galbula* | 30.8 | - | 2.1 | Cyanoacrylate, mid dorsal | - | Williams (1990) |
| Bullfinch | | | | | | |
| *Pyrrhula pyrrhula* | 23.5 | 0.00050 | 2.2 | - | - | Grieg-Smith (1985) |
| Chaffinch | | | | | | |
| *Frigilla coelebs* | 21.0 | 0.00035 | 1.5 | Elastic harness, mid dorsal | - | Hanski & Haila (1988) |
| * Reed bunting | | | | | | |
| *Emberiza schoeniclus* | 20.0 | 0.00043 | 1.3 (0.3) | Dorsal tail-clip | 1 out of 5 died within 24hrs | C.Buose (pers. comm.) |
| Great tit | | | | | | |
| *Parus major* | 19.1 | 0.00046 | 2.2 (0.4) | Dorsal tail-clip | Excessive preening by 1 out of 4 individuals | East & Hoffer (1986) |
| New-Holland Honeyeater | | | | | | |
| *Phylidonyris novaehollandiae* | 18.9 | - | 1.5 | Latex adhesive, mid dorsal | Initial discomfort | O'Connor & Pyke (1987) |
| * Kirtlands warbler | | | | | | |
| *Dendroica kirtlandii* | 13.8 | - | 1.1 | Latex adhesive, mid dorsal | - | Sykes, Carpenter, Holzman& Geisler (1990) |

Table 2.21. Continued.

| **Foraging guild** Species | Body mass (g) † | Wingdisc loading (g mm$^{-2}$) # | Total mass of Radio-tag package (g) $ | Method of attachment and location of package | Reported effects | Source |
|---|---|---|---|---|---|---|
| **Diurnal aerial forager** | | | | | | |
| Swallow | | | | | | |
| *Hirundo rustica* | 18.2 | 0.00024 | 0.9 | Cyanoacrylate, mid dorsal | Fewer longer foraging bouts by incubating females | Brigham (1989) |
| * Sand martin | | | | | | |
| *Riparia riparia* | 12.7 | 0.00019 | 1.3 (0.3) | Ventral tail-clip | No effect on body mass, brood provisioning rates or survival | Alves & Johnstone (in press) |
| **Nocturnal aerial forager** | | | | | | |
| Greater horseshoe bat | | | | | | |
| *Rhinolophus ferrumequinum* | 13-34 | 0.00015-0.00028 | 2.0 | Epoxy resin, mid dorsal | No effect on survival of different mass classes | Stebbings (1982) |
| * Brown longeared bat | | | | | | |
| *Plecotus auritus* | 6-12 | 0.00014-0.00019 | 0.9 | Neck collar | - | Furmann & Seitz (1992) |

† Ranked by decreasing body mass in each foraging guild.

# Wingdisc loading equals body mass divided by $\pi$(wingspan/2)$^2$ (Feinsinger & Chaplin 1975).

$ Where relavent mass of tail-clip given in brackets.

* Study published or carried out after the methods for the present study had been determined.

Table 2.21.). Radio-tags attached to small birds in this way are seldom aerodynamic and also present similar thermal window problems. Glue-mounted devices do however always fall off of their own accord, although the duration of attachment is frequently unpredictable.

In some studies, radio-tags have been attached to small birds using miniature tail-clips (2 out of 13, 15 %, Table 2.21.). There are distinct advantages to using this method. Tail-mounted packages hidden under the tail coverts do not disrupt the aerodynamic profile of the birds or generate a thermal window through which heat may be lost. Furthermore, tail-clips remain on the bird until removed or are lost naturally during the annual moult.

### 2.2.3.3. Attaching radio-tags to robins using glue.

Radio-tags were attached using cyanoacrylate to the centre a piece of gauze of approximately four times the area of the tag. This had negligible effect on the mass of the package. A small area of feathers on the central dorsal tract between the scapulae and above the centre of gravity of the bird was trimmed down to short stumps and the gauze and radio-tag glued to these using latex adhesive or cyanoacrylate, after first degreasing the plumage with ethanol. The antenna projected down the midline and beyond the tail. The process was difficult to perform single handed on such a small bird and once fitted, radio-tags could not be easily removed by hand, remaining on the bird for very unpredictable periods (mean=7 days, range 1-12 n=9). This was largely similar to the retention times achieved by previous studies (1-4 days on swallows; Brigham 1989, mean 24 days on captive yellowthroats; Sykes *et al* 1990, mean 5 days on northern cardinal; Johnson *et al* 1991). Furthermore, radio-tags fitted this way tended to bond to the feathers more readily than the skin so that they were not securely anchored and liable to unbalance the bird during movement. The number and fate of radio-tags attached to robins using this technique are shown in Table 2.22.

### 2.2.3.4. Radio-tags attached to robins using tail-clips.

The initial design of tail-clip used on free-living robins consisted of two one millimetre thick perspex plates clamped together using nylon bolts, based on the design of East & Hoffer (1986). The dimensions of the plates are shown in Appendix 3. With the radio-tags attached to the tail-clips, the total package weighed 1.8 g. They were attached to robins by threading the two central tail rectrices between the plates, tucking a further rectrice between the plates on each side and tightening the bolts. The clip was fitted so that the bulk of the package was beneath the tail and hidden by the under tail coverts(Fig.2.8.Plate 2.3.a-c.). This ensured that the radio-tag was as close to the centre of gravity of the bird as possible while being securely anchored, and did not disrupt the aerodynamic profile of the bird. There is a possibility, however, that such an off axis load may affect flight performance. The extent of this could not be assessed.

This basic design was later modified so that the upper tail-clip plate was made of one millimetre thick rubber backed by a nylon load spreading washer. This cushioning eliminated the small tendency for tail rectrices to break off after having their shafts crushed by over tightened bolts. The arrangement of the rectrices in and alongside the tail-clip is illustrated in Fig.2.9.

During the fitting of tail-clips robins were restrained by wrapping them in black cloth (Plate 2.4.). Using this technique tail-clips could be fitted or removed by one person and the bird released within two minutes. The number of radio-tags fitted to robins using tail-clips and the numbers recovered in different ways are shown in Table 2.22. During August, some adult robins were still undergoing their annual moult. Because of this the tail rectrices had not fully emerged from their sheaths, and were insufficiently hardened to carry a tail-clip without damage. These individuals could only be radio-tagged using glue-on techniques.

### 2.2.4. Results; the effect of radio-tags on the robin.

#### 2.2.4.1. Behaviour.

The radio-tagging procedure and subsequent presence of the package may cause the robins to behave differently after release. The effect may be temporary, lasting minutes to hours or chronic, lasting many days. Effects may range from initial discomfort to altered foraging behaviour, changes in metabolic rate and decreased survival (reviewed by Calvo & Furness 1992).

Upon release, robins radio-tagged using both glue-on and tail-clip techniques flew strongly with an apparently normal bounding flight gait. Occasionally birds were unbalanced when landing on perches for the first few times, however after this they quickly adjusted to the small change in centre of gravity caused by the presence of the back or tail-mounted package. This was particularly apparent when tags were removed, as some individuals still allowed for the mass of the radio-tag when first landing and over balanced.

The distances between successive two minute relocations of four radio-tagged robins

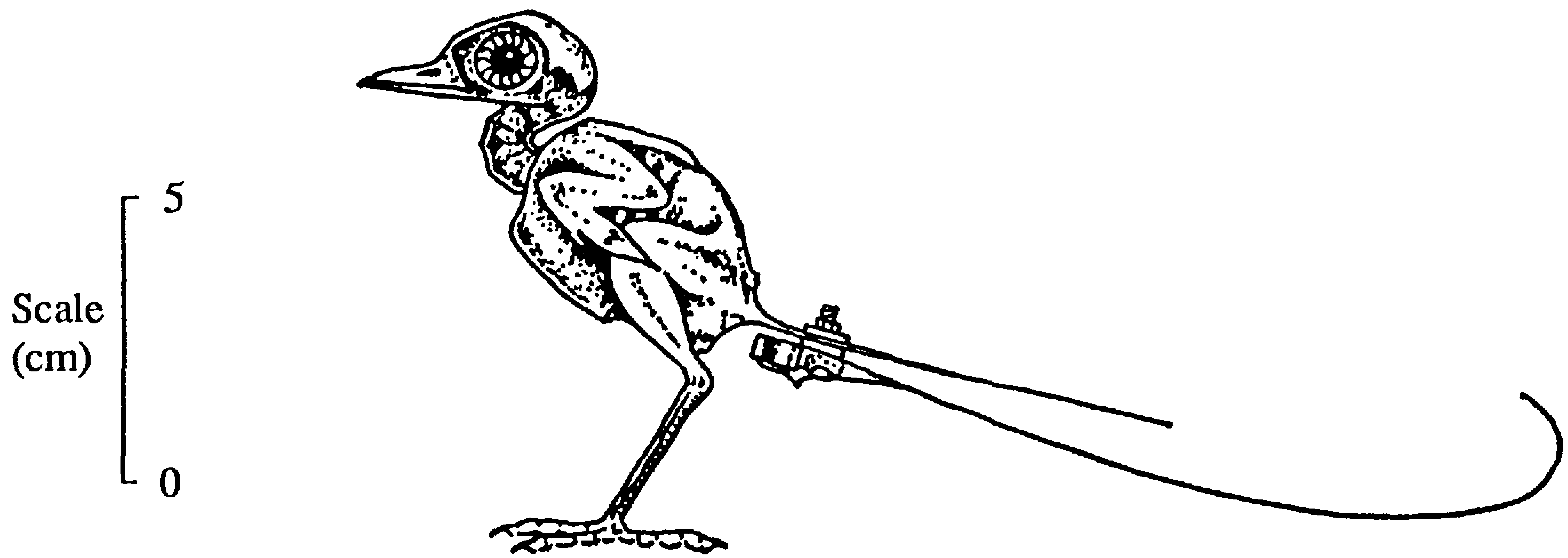
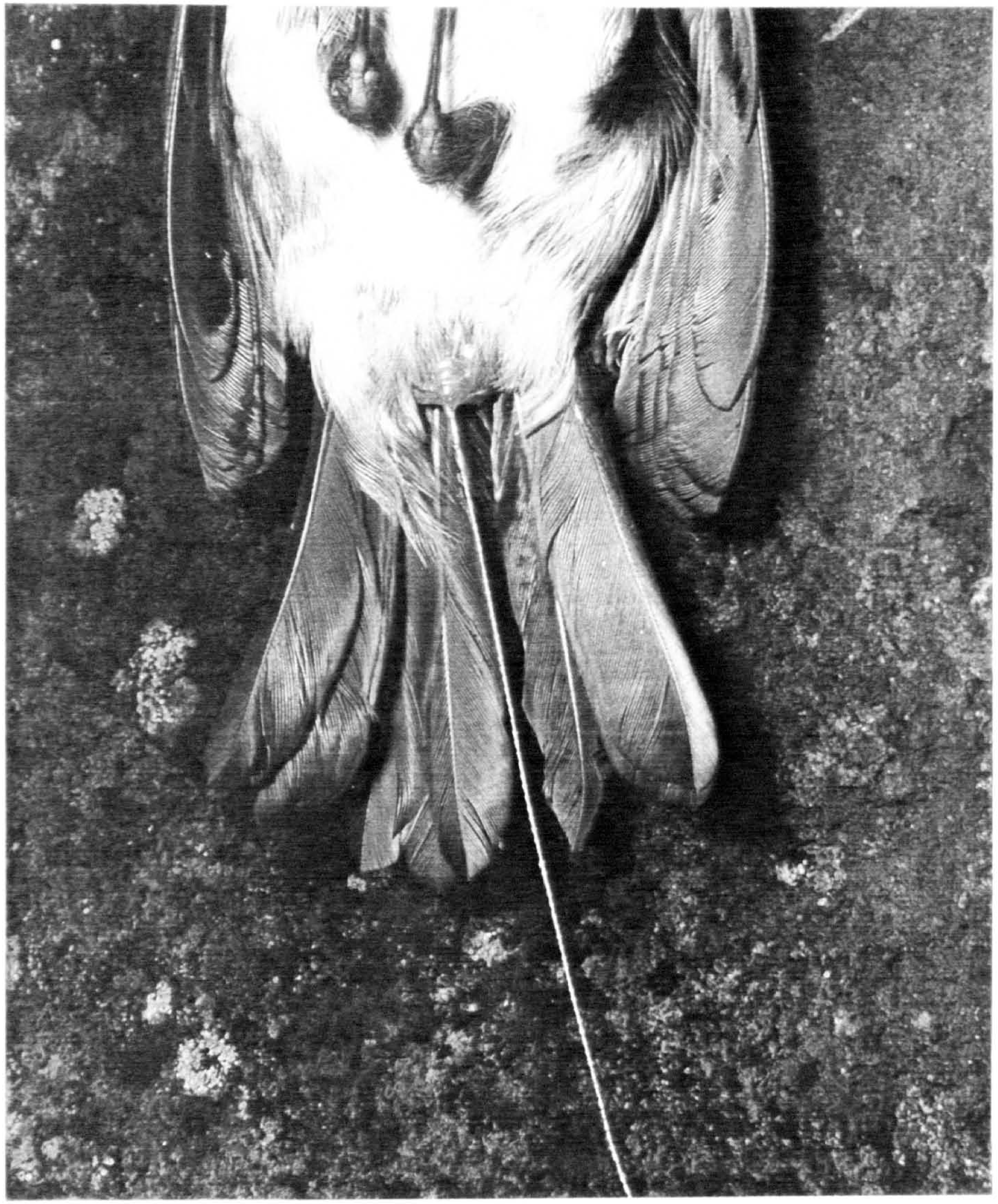
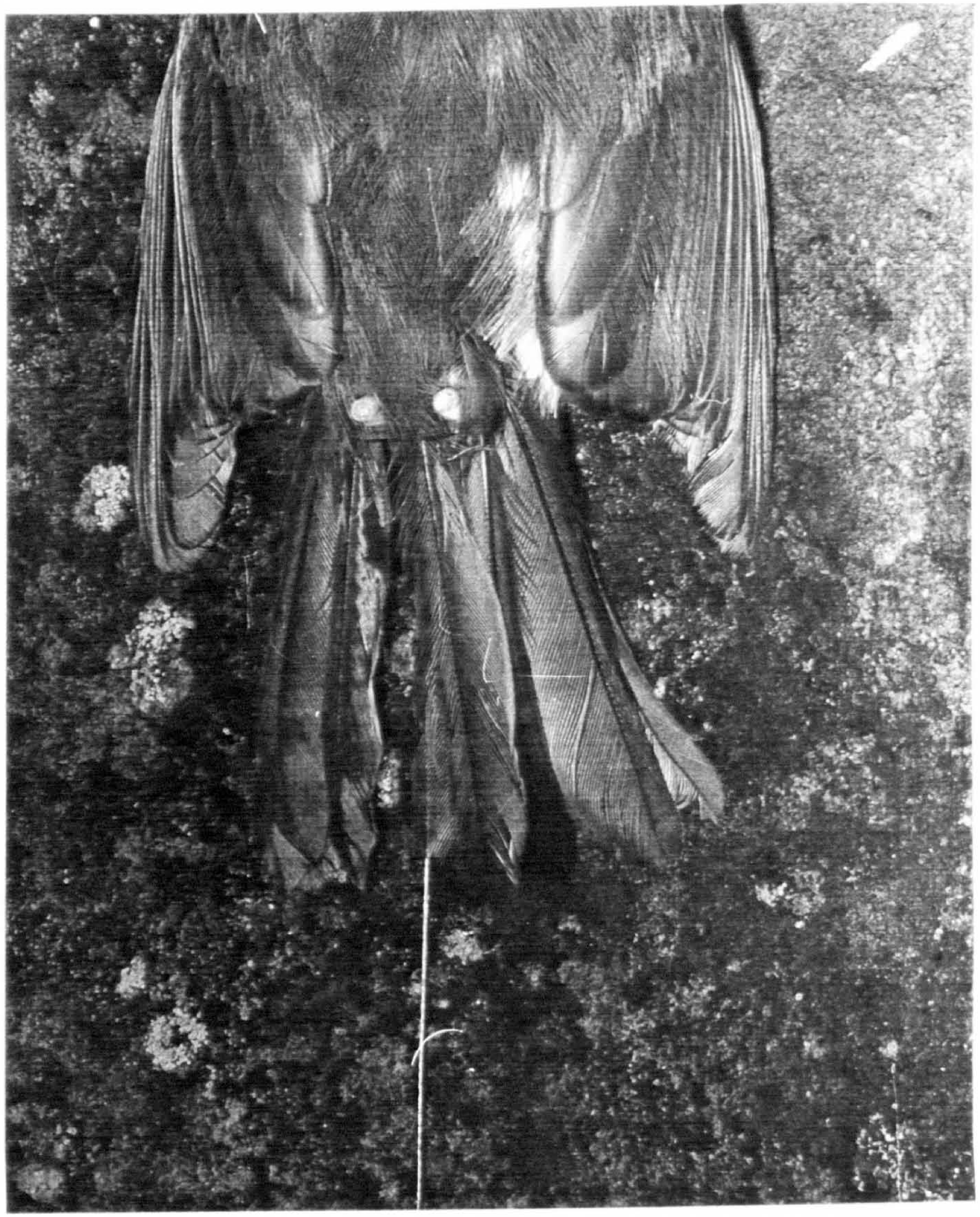


Fig.2.8. Diagram of a robin showing the position of the ventrally mounted tail-clip and radio-tag in relation to the structural anatomy of the bird.

**Plate 2.3.** The ventrally mounted tail-clip and radio-tag attached to a robin.
(a) Ventral view showing how well the package is hidden by the under tail coverts.

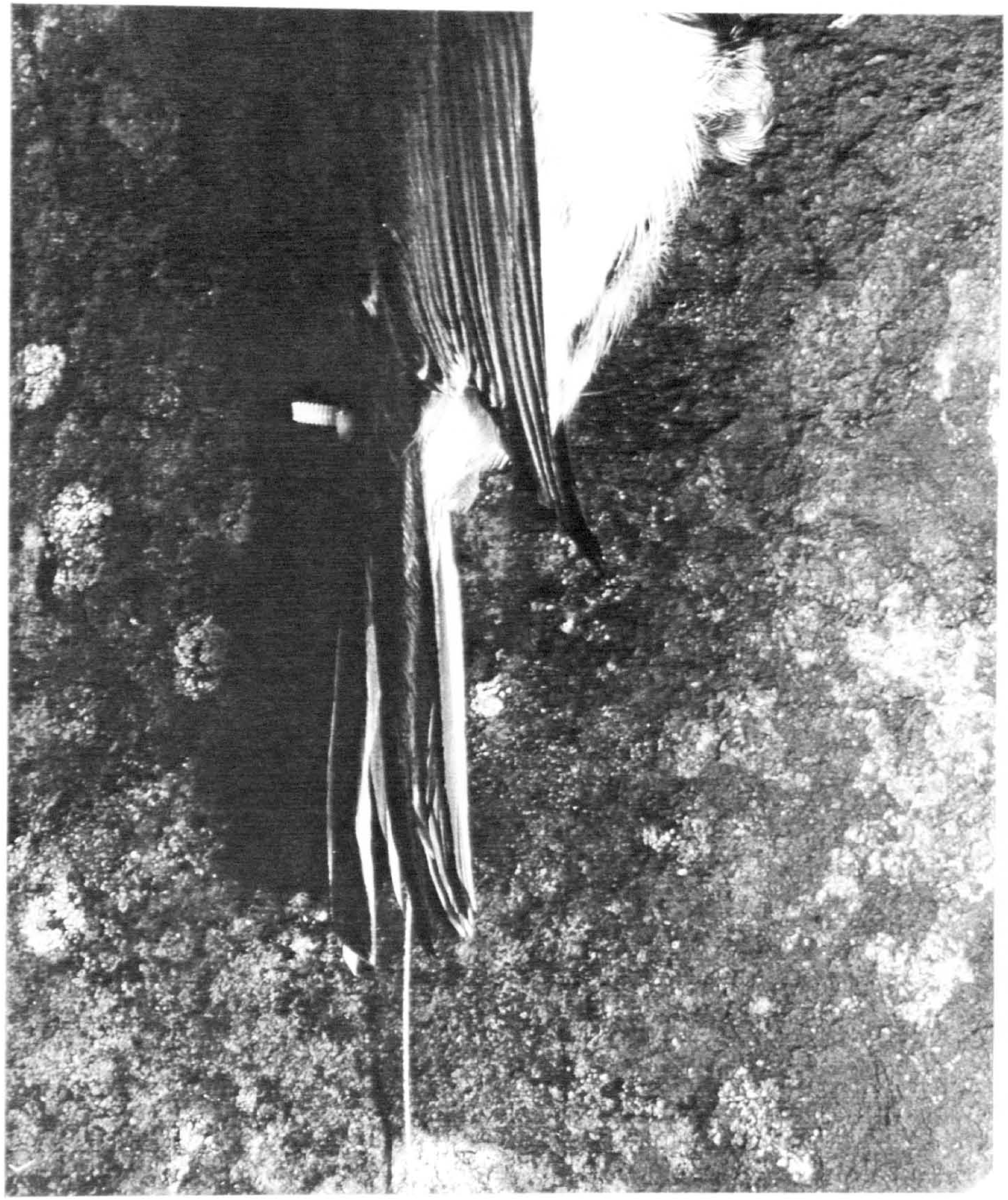
(b) Dorsal view showing the upper plate of the tail-clip and the nylon bolts which clamp the two plates together. Once fitted the tail-clips cause the tail rectrices to be spread further than normal, although this had no apparent effect on the birds.





(c) Side view showing how little the under tail package affected the aerodynamic profile of the bird.

**Plate 2.4.** A robin restrained in cloth during the fitting of a tail-mounted radio-tag.



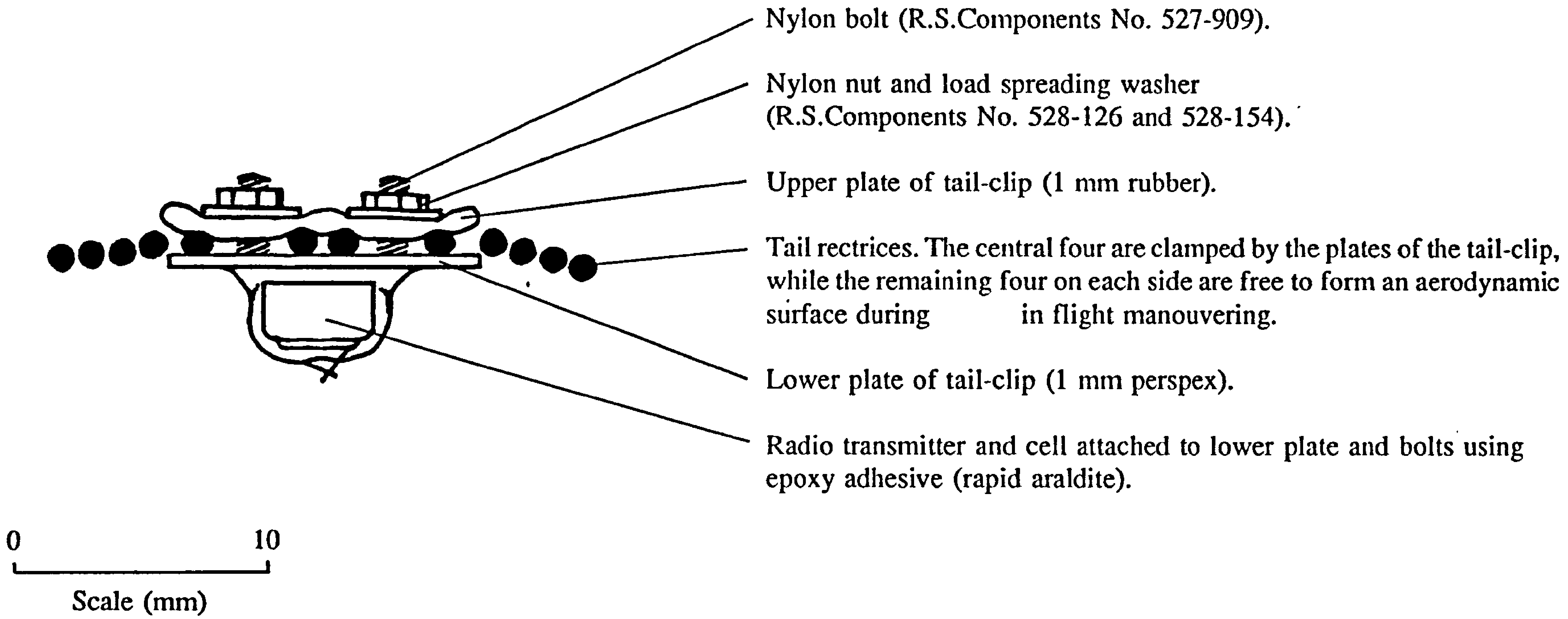


**Figure 2.9.** Diagram illustrating the construction of tail-clips, and how they were attached to the tail rectrices of robins.

**Table 2.22.** Numbers of radio-tags deployed on robins using different techniques and details of their recovery.

| Method of attachment | No. occasions on which radio-tags were fitted | No. recovered from live birds | No. moulted or slipped off | No. pulled out by entanglement of antenna in trap | No. pulled out by entanglement of antenna in vegetation | No. recovered from dead birds | No. not recovered $ |
|---|---|---|---|---|---|---|---|
| **Glued on** | 9 | 2 | 7 | 0 | 0 | 0 | 0 |
| Percentage | | 22 | 78 | 0 | 0 | 0 | 0 |
| **Tail-clips** | 87 | 48 | 18[*] | 4 | 1[#] | 10 | 6 |
| Percentage | | 55 | 21 | 5 | 1 | 11 | 7 |

[*] The majority of these cases occured when using two solid tail-clip plates.

[#] This individual would have died had the radio-tag been attached using a harness.

[$] These individuals migrated or could not be recaptured during the transmitting life of the radio-tag. Four birds were known to have lost their radio-tags during the annual moult, the two others (2% of total) were migrants and remained unaccounted for at the end of the study.

were measured for each of three consecutive 20 min periods after release, and for 20 min at approximately the same time on the following day. Distances between relocations were in this situation considered to be statistically independent. There were no differences in the inter-location distances moved by robins between the four time periods for each of the four individuals (Kruskal Wallis ANOVA all $H<3.6$ ns $df=3$ $n=10$). The results for two individuals are shown in Fig.2.10. The lines join the median values, indicating that bird (b) did show decreased activity for a short period after release, although this was not significant. Radio-tagged robins were regularly seen in flights of several hundred metres across open fields when moving between areas.

Some robins briefly pecked at the radio-tag on release. After birds had been equipped with tail-clips for several weeks, antennae were frequently bent over at the tip, foreshortening the length and reducing the range. This was probably done during the preening of the tail rectrices from which the antenna projected. After carrying tail-clips, the tail rectrices were always clean and well preened.

Robins sang and evicted intruders while radio-tagged with no apparent difficulty. Furthermore, the tail-flicking behaviour associated with tic-calling (Cramp 1988) was unaffected. Because there was huge variation in song output between individuals and the eviction of intruders by owners was very rarely observed, it was not considered feasible to attempt to quantify the effects of radio-tags on such advertisement behaviour. Radio-tagged robins sometimes spent up to 20 min sitting quietly in dense cover, sometimes on the ground. This was interpreted as normal resting behaviour that would otherwise have gone un-observed. Similar behaviour was recorded by East (1982). It was often difficult to distinguish radio-tagged robins from un-tagged conspecifics when they were in close proximity.

### 2.2.4.2. Energetic condition.

The change in body mass over time of a robin with a radio-tag glued to its back is illustrated relative to an un-tagged control bird in Fig.2.11. and serves to contrast the effect of glue-on techniques and tail-clips. Clearly the radio-tagged bird lost mass relative to the control bird. The experiment was carried out during February when time available for foraging was short and temperatures low, and had its rate of mass loss continued the tagged bird would have surely reached a mass below which starvation was inevitable. A few radio-tags were attached to moulting robins in August using the glue-on technique. The mean mass

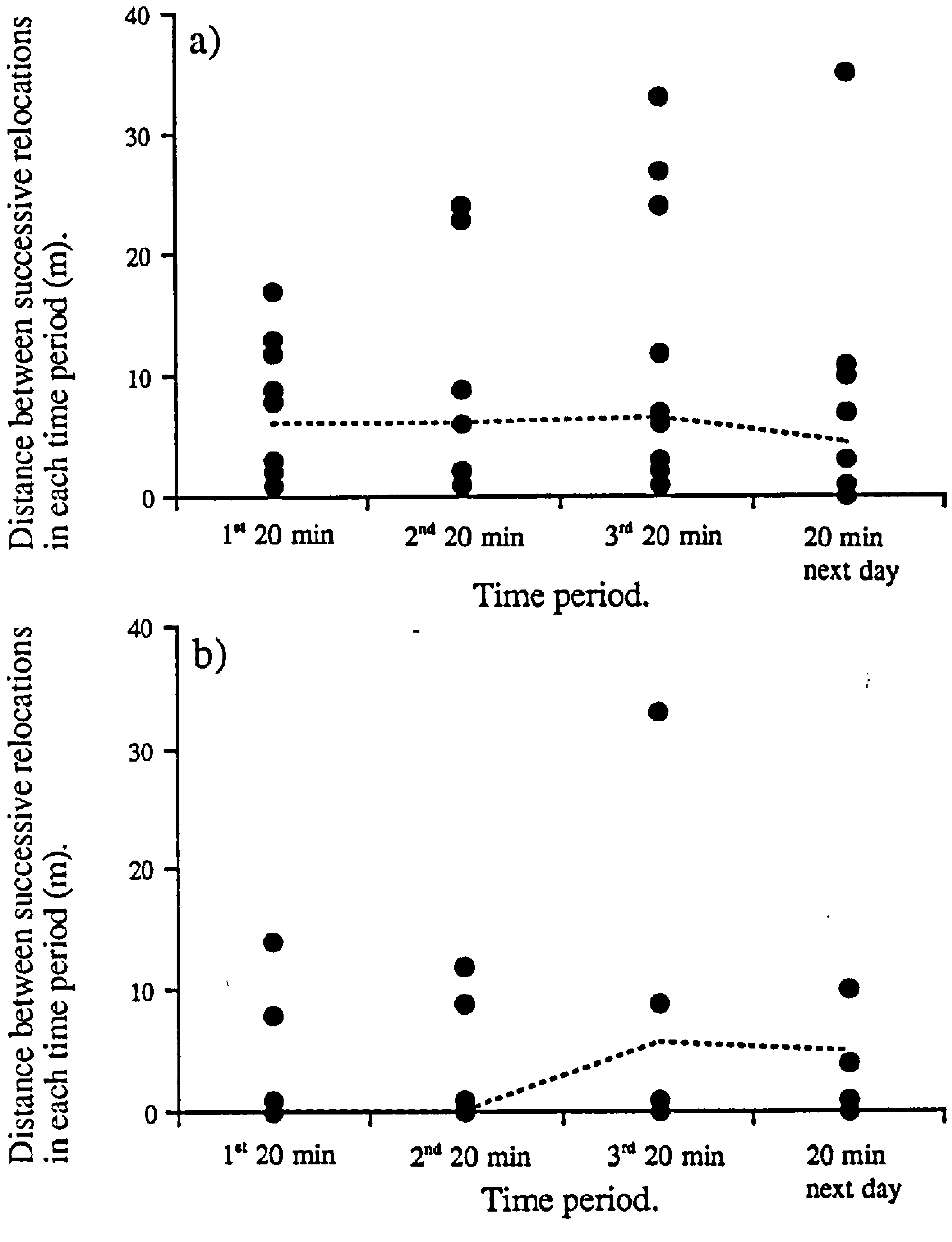


**Fig.2.10.** Short term changes in the rates of movement shown by robins during the period immediately after having a radio-tag fitted. In the first example (a) the individual shows no change in movement, while the example in (b) suggests relative inactivity during the first 40 min post release. Both were, however, non-significant (Kruskal-Wallis ANOVA H<3.6 ns). Each time period is represented by the distances between 11 consecutive relocations of the radio-tagged bird, and the lines join the median distance between successive locations in each time period.

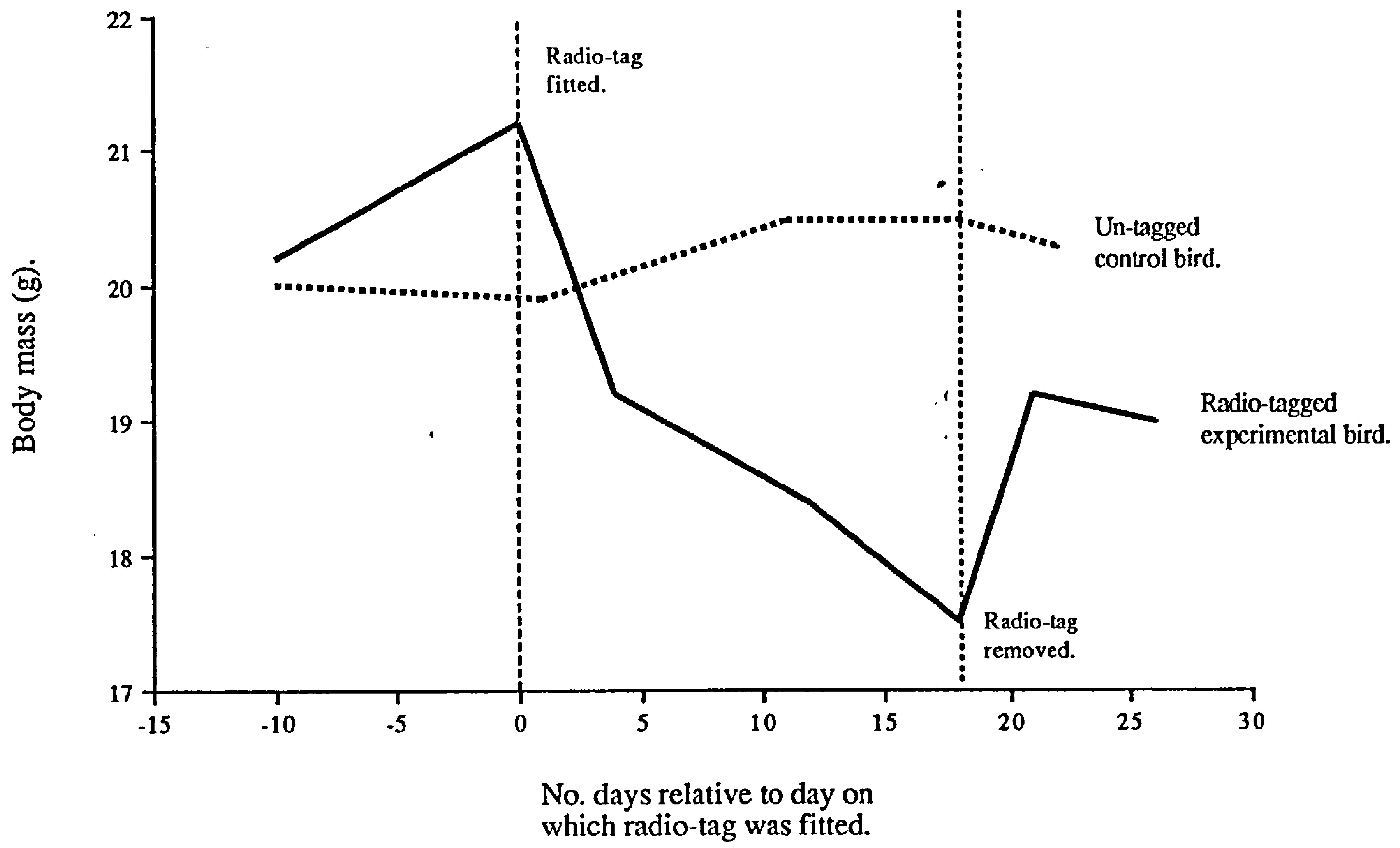


**Fig.2.11.** Change in body mass for a robin radio-tagged using a glue-on technique compared to a control bird during February.

change in these birds was 0.4 g (range 0-0.8, n=2) over a mean duration of 4.5 days (range 2-7, n=2).

Although the sample size was small there was no difference in the mass change between matched pairs of robins radio-tagged using tail-clips and untagged control birds over a median period of 6.5 days (range 3-12) (Wilcoxon Matched-pairs Signed-rank test Z=-0.10 ns n=6, tagged median=0.15 g range -2.4-1.4, control median=0.15 g range -2.6-2.0).

Body mass was most closely correlated with the temperature averaged over the previous five days (section 2.2.2.3.2.). Variation in temperature explained 15 % of the variation in body mass. Using the regression equation: Mass=19.85-0.12 Temperature ($p<0.001$ $F=14.42$ $r^2=0.15$ $n=76$), body masses could be corrected using residuals, to values that would be expected at 5°C, the approximate mid point of the temperature range. This allowed direct comparison of body masses measured on days when temperatures were different.

The change in body mass, previously corrected to that at 5°C, was not correlated with the duration that the tail-clips were carried (square root transformed to normalise) (r=0.14 ns n=38, mean duration=30 days range 1-239, Fig 2.12.). Similarly, the change in total fat score was not correlated with the duration over which tail-clips were carried (r=0.01 ns n=18, mean duration=28 days range 3-239). Although change in fat score was normally distributed, the total fat score was not, and therefore could not be corrected to that at 5°C using a regression equation.

### 2.2.4.3. Energy expenditure.

A ventrally mounted tail-clip will produce negligible additional drag. The cost to a robin of mean body mass (19.3 g) and wing span (228 mm) of carrying such a 1.8 g tail-mounted radio-tag was consequently calculated to represent an increase of 10 % in the chemical power required for level powered flight at the minimum power speed, using the computer program of Pennycuick (1989)(Appendix 2.). The effect on daily energy expenditure of this predicted additional cost will be tiny however, since robins spend less than one percent of their activity period in flight (East 1980). Increase in the energy required for hopping caused by the additional mass of the radio-tags was impossible to estimate, but would be considerably less than that for flight considering the different energy requirements of the activities (Tatner & Bryant 1986). In contrast to hopping or flying, the cost of perching

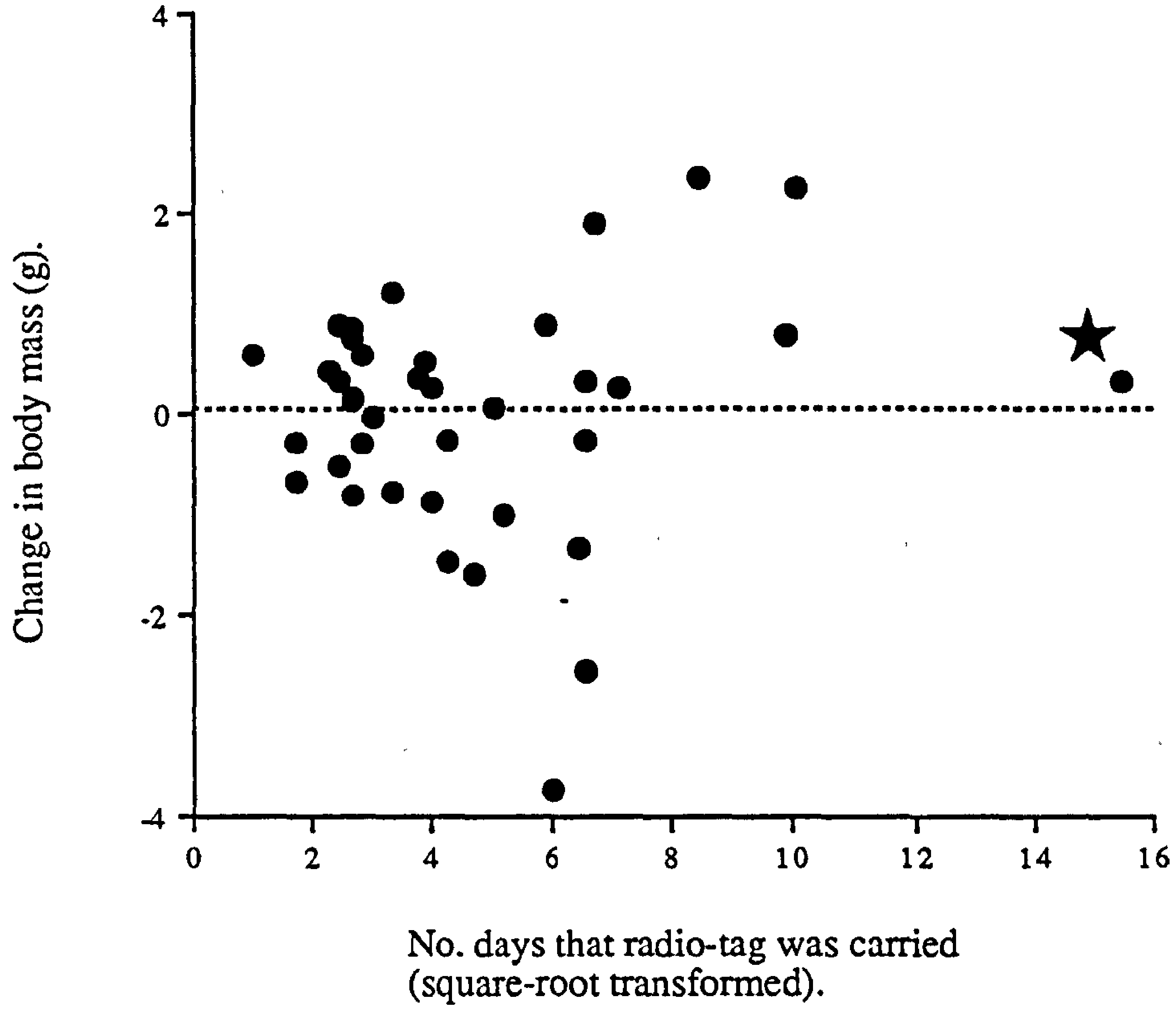


**Fig.2.12.** Change in body mass in robins that were equipped with tail-mounted radio-tags over the period that they were radio-tagged (r=0.14 ns n=38). Body mass was first corrected to that at 5°C (see text). The star indicates a migrant female which returned, still radio-tagged, to the study area over 200 days after first being equipped

quietly is predominately that of thermoregulation. Therefore since unlike back mounted radio-tags, the ventrally mounted tail packages do not disrupt the insulating qualities of the plumage, they will have minimal effect on the energy required for thermoregulation and the total cost of perching quietly.

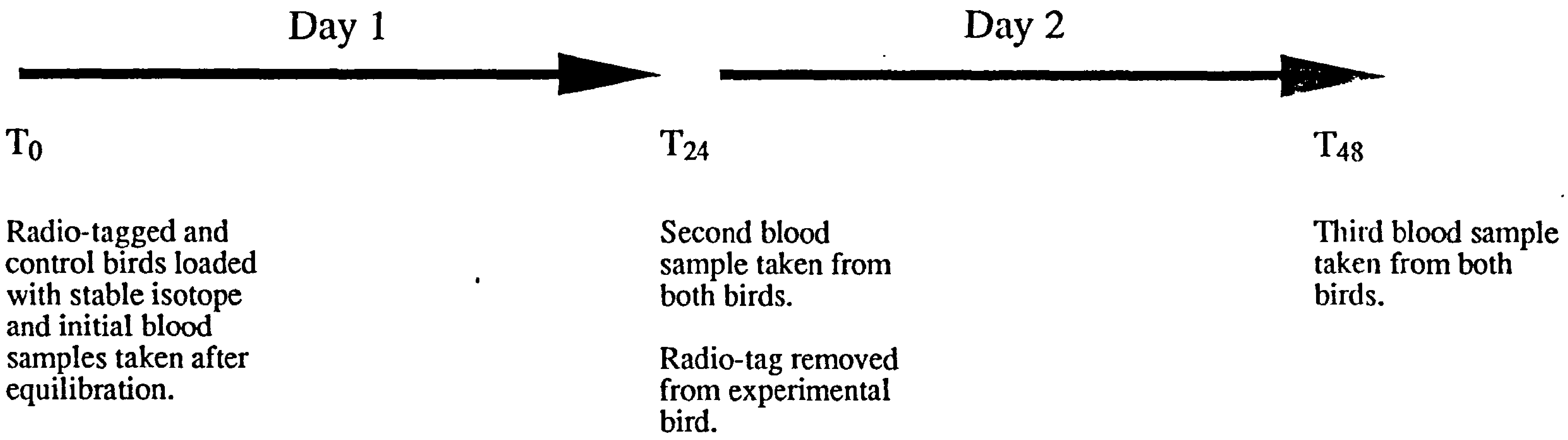
The cost of carrying a 1.8 g radio-tag attached by tail-clip was measured using the doubly labelled water technique. The experimental protocol is summarised in Fig.2.13. The energy expenditure was measured for experimental radio-tagged and un-tagged control birds over day-1, at the end of which the radio-tag was removed from the experimental bird. The energy expenditure for day-2 therefore represents that for un-tagged birds. This was carried out for two pairs of birds, each containing an experimental and control individual. The experimental birds had previously carried a radio-tag for at least seven days and so will have habituated to it short term effects, reducing the chance of including some additional cost of, for example increased preening.

The results are shown in Table 2.23. Natural abundances of $^{18}O$ and $^{2}H$ were 1990.80 and 145.19 ppm respectively. These were within 0.03 and 0.19 % of the values for winter robins predicted by an isotopic tracer study (Tatner 1988). In response to the removal of the tail-clip from the experimental birds, their ADMR increased by 6 % (range 4-12) relative to the control birds. This value falls within the $\pm$10 % error inherent in the doubly labelled water technique (Tatner & Bryant 1989). It must be concluded therefore that there was no evidence for an effect of the radio-tags on free-living energy expenditure.

### 2.2.4.4. Survival.

There was a slight but non-significant tendency for more robins to die while radio-tagged compared to the number of un-tagged birds which disappeared ($\chi^2$=0.114 ns df=1 n=52, Table 2.24.). Similarly there was a slight but not significant tendency for robins which survived carrying a radio-tag at least once to subsequently disappear before the onset of spring song relative to the number of birds which were never radio-tagged but had disappeared by the same date ($\chi^2$=0.912 ns df=1 n=40, Table 2.25.).

The causes of mortality reported for recoveries of ringed birds which had died (Mead 1984); the recovery of carcasses by Harper (1984); the dead robins obtained for body composition analysis; and the robins which died while radio-tagged are summarised in Table 2.26.



Radio-tagged and control birds loaded with stable isotope and initial blood samples taken after equilibration.

Second blood sample taken from both birds.

Radio-tag removed from experimental bird.

Third blood sample taken from both birds.

**Fig.2.13.** Field protocol for measuring the energy costs of carrying a tail-mounted radio-tag. T indicates time (hrs).

**Table 2.23.** Mid point and range of energy expenditures for experimental and control robins during determination of the energy cost of carrying a radio-tag (n=2). Experimental birds carried radio-tags on and prior to day 1.

| Period over which energy expenditure was measured | Experimental | | | Control | | |
|---|---|---|---|---|---|---|
| | A.D.M.R. ($cm^3CO_2g^{-1}hr^{-1}$) | D.E.E. ($kJ\ day^{-1}$) | M * | A.D.M.R. ($cm^3CO_2g^{-1}hr^{-1}$) | D.E.E. ($kJ\ day^{-1}$) | M * |
| Day 1 | 5.13<br>(4.43-5.82) | 65.64<br>(58.13-73.14) | 2.32<br>(2.02-2.62) | 6.40<br>(6.28-6.52) | 80.66<br>(77.33-83.99) | 2.90<br>(2.83-2.96) |
| Day 2 | 5.65<br>(5.35-5.94) | 68.64<br>(68.28-68.99) | 2.52<br>(2.42-2.62) | 6.67<br>(6.51-6.83) | 81.66<br>(80.67-82.64) | 2.97<br>(2.94-3.00) |
| % change | 10<br>(2-21) | 5<br>(-6-17) | 7<br>(0-20) | 4<br>(-2-9) | 1<br>(-2-4) | 2<br>(-1-6) |

* Metabolic intensity M=energy expenditure ($kJhr^{-1}$) divided by BMR, where BMR=5.03 $Mass^{0.726}$ ($cm^3CO_2\ hr^{-1}$) (Aschoff & Phol 1970). Multiply by 26.44/1000 to convert to $kJhr^{-1}$.

**Table 2.24.** Contingency table for number of occasions on which radio-tagged and un-tagged matched control robins survived, or died or disappeared. $\chi^2$=0.114 ns.

| | Radio-tagged | Un-tagged control | Total |
|---|---|---|---|
| Survived | 20 | 21 | 41 |
| Died or disappeared | 6 | 5 | 11 |
| Total | 26 | 26 | 52 |

**Table 2.25.** Contingency table for number of occasions on which robins which had or had not been equiped with radio-tags disappeared. Data from the population during 1991/92. Birds were classed as survivors if they were still alive during the spring song surge (a few days either side of 16th February). $\chi^2$=0.912 ns.

| | Survived being radio-tagged | Never radio-tagged | Total |
|---|---|---|---|
| Survived | 8 | 13 | 21 |
| Disappeared | 10 | 9 | 19 |
| Total | 18 | 22 | 40 |

### 2.2.5. Discussion.

#### 2.2.5.1. Structural size,

Most studies of small birds and of robins in particular have described body size using a single structural measure, usually wing chord length or tarsus length (Harper 1985, Karlson *et al* 1986). The most important predictor of overall structural body size in the present study was keel length. This measurement was not recorded for birds captured in the previous studies. The sternal keel forms the origin of the pectoral muscles, the major muscle block in small birds. Furthermore, the sternum forms the ventral wall of the thoracic cavity, containing heart, liver and lungs. Because of this, keel length is intuitively to be preferred over wing chord or tarsus since it is much more likely to reflect the amount of metabolising tissue present in an individual.

An error in a single measure of structural size will produce a greater error in the value for structural size than a composite measure derived from principle component or, as in this case, multiple regression analysis. This is because an error in a single measurement will contribute less to the measure of overall size. Consequently body size predicted by keel length and bill depth was considered a robust estimate of the structural size of individual robins.

#### 2.2.5.2. Estimating the energetic condition of live birds.

Fat deposits comprise stored energy to be used when food availability is limited (Houston & McNamara 1993). Total fat score was a accurate estimate of the fat content of individuals. Since fat scores were an estimate of area of visible fat deposits relative to the area of each particular anatomical region, they were independent of body size. The extent to which individuals were heavier than expected based on their structural body size is a crude index of their energetic condition. Heavier birds contained proportionally larger fat deposits at the expense of their proportional water and lean components. In addition, the condition index and fat scores of individuals were directly proportional. Consequently for the purposes of this study, condition indices and fat scores were considered good estimates of the extent of the energy reserves of the robin*.

From the analysis of birds found dead, mortality in the robin was mass dependent (section 2.2.2.3.1.). Birds that were of lower than average condition were at greater risk of dying of starvation, while birds that were of higher than average condition were more likely to be predated. It is intuitive that birds of low body mass and fat score, and therefore low energy reserves, will be at a greater risk of dying during a period of high energy demand such as a cold night than birds of average condition. Although a central tenet of much recent theory (Houston & McNamara 1993), the increased susceptibility to predation of birds with higher energy reserves and therefore body mass in the present study may have been an artifact. Robins near buildings may have been in better energetic condition because of access to bird tables, and it is just such situations that domestic cats occur. However the individuals predated by cats in this study all came from isolated houses, where the availability of supplementary food was limited. Robins that are heavier than average will experience a higher wing loading than average birds, with an associated reduction in flight performance. Their ability to avoid predators will therefore be compromised.

### 2.2.5.3. The effects of radio-tags on the robin.

Of the 13 field studies of small birds using radio-tracking listed in Table 2.21. nine (69%) considered the effects of the devices. Of those that did, five (56 %) recorded modified behaviour, ranging from initial discomfort to desertion of nests and three (33 %) recorded increased predation. Only one study (11 %) attempted to assess change in energetic condition, as indicated by body mass change, but found no effect. The most detailed assessment of the effects of radio-tags on small birds has been carried out on captive individuals (Sykes *et al* 1990). Using the common yellowthroat to evaluate harness and two glue-on techniques for attaching radio-tags, they found significant differences between treatment and control groups behaviour, flying ability and physical condition. Differences between treatment groups however, suggested that glue-on techniques were to be preferred over harnesses, although retention times were shorter (Sykes *et al* 1990).

In the present study robins equipped with glue-on devices rapidly lost mass compared to controls during winter. The mean midpoint temperature over the period of observation was 4.3°C (range -1.2-9.5 n=84 for 3 yrs) compared to 15 °C for Maryland. U.S.A. in October (from climate tables) where Sykes *et al* (1990) carried out their evaluation. This indicates considerably higher thermoregulatory costs in the robin at this time, resulting in a greatly magnified heat loss through the thermal window in the birds plumage caused by the glue-on package. There was no mass change in moulting robins fitted with glue-on radio-tags in August, when the mean midpoint temperature over the period was 15.7 °C (range 11.7-20.7 n=62 for 2 yrs), suggesting the heat loss through the thermal window was normally unimportant in late summer.

Although there was no significant effect on body mass or total fat scores during the period robins carried tail-mounted radio-tags in autumn and winter, they may have modified their time activity budgets to increase energy intake to compensate for increased costs of particular activities. It was not possible to record time budgets from treatment and control individuals in the dense shrub layer of the study site however, without bias towards when birds were visible. Consequently the energy expenditure was measured relative to an un-tagged control bird using the doubly labelled water technique. The difference between experimental and control birds was however within the error of the technique indicating no significant increase in energy expenditure by radio-tagged robins. Similar studies on larger wild birds are inconclusive. Pennycuick *et al* (1990) found energy expenditure was higher in radio-marked white-tailed tropic birds, while Klaassen *et al* (1992) found no such effect on the common tern.

There was no significant tendency for robins carrying loads in the form of radio-tags, to suffer higher mortality than their un-tagged conspecifics. This was in spite of the fact that birds of greater body mass appeared more susceptible to predation. It is possible that the relationship between $P_a$ and flight muscle mass follows an inverted U-shape, with reduced power output from both emaciated and obese individuals. Robins of average flight muscle mass and equipped with radio-tags would need to use more $P_s$ to fly, but would not suffer the handicap of the decreased $P_a$ of obese birds of the same total mass and its associated effect on their ability to avoid predators.

The causes of mortality of the robins which died while radio-tagged, and could therefore be recovered, were different from the causes of mortality suggested by carcass recoveries and ringing recoveries (Table 2.26.). Carcass and ringing recoveries are biased towards the causes of death that allow bodies to be found, such as road and window casualties. These seen likely to form a minority of deaths, while predated and starved birds are very difficult or impossible to locate. The data from Harper (1984), who used the same categories, are intermediate between the starvation and predation biased mortality of radio-tagged birds and the mortality of ringing and carcass recoveries which are biased towards accidental deaths. This probably represents high effort in finding carcasses supplemented with ringing recoveries. It is interesting that no birds in the present study were killed by other robins compared to 18 % found by Harper (1984).

**Table 2.26.** Comparison of the causes of mortality in the robin estimated from radio-tagged birds which died, recovered carcasses and ringing recoveries.

| | Radio-tagged birds | | Carcass recoveries | | | | Ringing recoveries | |
|---|---|---|---|---|---|---|---|---|
| | | | This study * | | Harper (1986) | | Mead (1984) | |
| | No. | % | No. | % | No. | % | No. | % |
| Starvation | 5 | 50 | 1 | 6 | 11 | 16 | 48 | 2 |
| Aerial predator | 2 | 20 | 0 | 0 | 8 | 12 | 86 | 4 |
| Ground predator | 2 | 20 | 0 | 0 | 0 | 0 | 0 | 0 |
| Domestic cat | 0 | 0 | 8 | 47 | 12 | 18 | 1195 | 51 |
| Killed by other robins | 0 | 0 | 0 | 0 | 12 | 18 | 0 | 0 |
| Drowned | 1 | 10 | 0 | 0 | 0 | 0 | 67 | 3 |
| Road casualty | 0 | 0 | 4 | 23 | 6 | 9 | 524 | 22 |
| Window casualty | 0 | 0 | 2 | 12 | | | 280 | 12 |
| Trap | 0 | 0 | 0 | 0 | 0 | 0 | 138 | 6 |
| Unknown | 0 | 0 | 2 | 12 | 19 | 28 | 0 | 0 |
| Total | 10 | | 17 | | 68 | | 2338 | |

* Excluding those only recovered because they could be located by their radio-tags.

To conclude, although it would be premature to assume from the present results that the additional loads had no effect, it appeared that the attachment of 1.8 g tail-mounted radio-tags had no significant effect on the behaviour, body condition, energy expenditure or survival of the robin in winter.

## 2.3. The dipper.

### 2.3.1. Methods.

2.3.1.1. The study sites.

The study sites selected to radio-track territorial dippers are shown in Fig.2.14. The three sites encompassed a range of different watercourse widths and flow rates to ensure that the birds studied occupied territories of potentially varying of quality (Table 2.27.). More importantly, however, sites were chosen for their easy access along their whole length from a road or track, so that the length of water course could be rapidly searched for birds which had moved out of range.

2.3.1.2. The study population.

The population from which dippers were selected for radio-tracking was monitored regularly as part of a long term study of dipper behavioral ecology and population dynamics. Most individuals were already marked with B.T.O. rings and individual combinations of colour rings.

Dippers were captured at nocturnal roost sites with hand nets, or on their daytime territories using mist nets placed across the river or stream. Prior to attaching radio-tags, individuals were subjected to a standard examination and a set of measurements was taken. This is described fully along with measures of structural size and energetic condition by Newton (1989) and Ward (1992). In the present study however, body size and composition was not considered further.

2.3.1.3. Radio-tag attachment.

Newton (1989) used radio-tags on dippers to monitor the dispersal distances of juvenile dippers as they achieved independence and searched for a suitable location to establish non-breeding territories. Radio-tags were attached using tail-clips. The same design of tail-clip was used to attach Biotrack SS-1 transmitters powered by silver cells to dippers

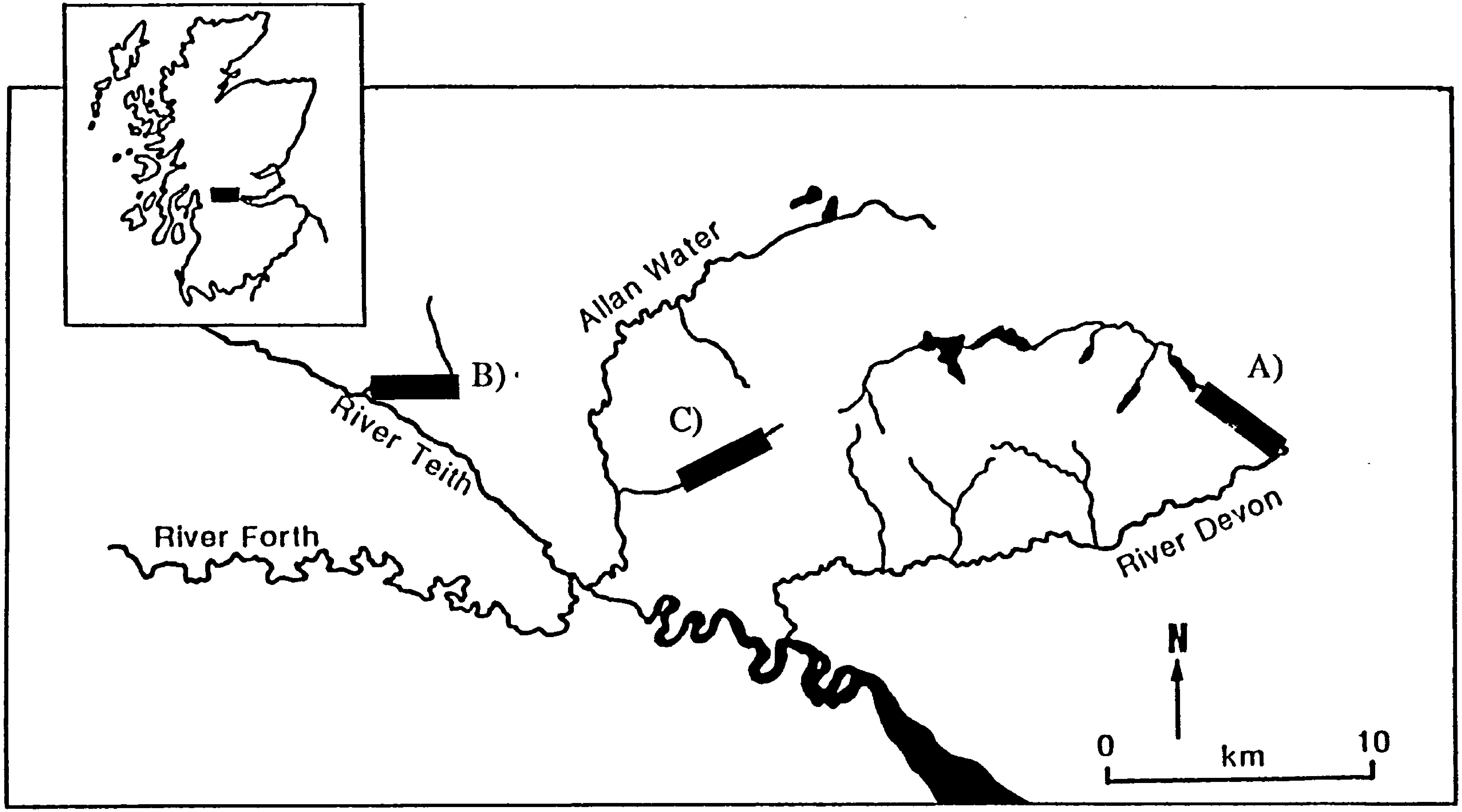


**Fig.2.14.** The dipper study sites in relation to local river catchments. A) Lower River Devon, B) Ardoch Burn, C) Whary Burn.

**Table 2.27.** Width, altitude and length of the study water courses on which dippers were radio-tracked.

| Water course | Width (m) | | Altitude (m) | Length of study area (m) |
|---|---|---|---|---|
| | Mean | Range | | |
| Lower River Devon | 15 | 12-20 | 150-200 | 2500 |
| Ardoch Burn | 8 | 4-11 | 50 | 3500 |
| Whary Burn | 2 | 1-3 | 230 | 3500 |

in the present study. Tail-clips consisted of two one millimetre thick perspex plates clamped together using a pair of brass bolts of one millimetre diameter. The design of the clips is shown in Appendix 3. Tail-clips weighed 3.2 g making a total radio-tag package mass of 4.0 g. This represented 7 % body mass for a 56 g female and 6 % body mass for a 69 g male.

Tail-clips were fitted to the tail rectrices in the same way as to robins, except that the bulk of the package lay dorsally and under the upper tail coverts (Plate 2.5.). This was to reduce the amount of time the transmitters would be immersed in water while birds were wading. Care was taken to ensure that the radio-tags did not obscure access to the preen gland. Because dippers were much larger than robins, radio-tags fitted dorsally in this way were normally hidden from view by feathers and had no apparent effect on the aerodynamic or hydrodynamic profile of the bird. This was particularly important considering the aquatic lifestyle of the dipper. The drag imposed by a transmitter package on a submerged dipper trying to maintain its position in fast flowing and turbulent water may have significant effects on energy expenditure or foraging success. The number of radio-tags deployed on dippers during 1990 and 1991 and details of their recovery are shown in Table 2.28.

Dippers often struggled considerably during the procedure and needed to be restrained in the corner of a bird bag. Tail-clips could however be fitted and the bird released within a few minutes.

The range of the transmitters was generally similar to that of radio-tags deployed on robins. Dippers were more likely to move out of the one kilometre maximum range but could always be relocated after a systematic search. Birds sometimes used feeding or, more often, nocturnal roost sites which were shielded from the surrounding countryside by rocky overhangs or gorges. The range of radio-signals in these situations was considerably reduced.

### 2.3.2. Results; the effect of radio-tags on the dipper.

#### 2.3.2.1. Behaviour

Radio-tagged dippers appeared to behave normally after release, following a short bout of intensive preening typical of any dipper after release. Birds caught on their territories during the day quickly recommenced foraging while those caught at roost readily returned to the ledges and holes used as roost sites.

**Plate 2.5.** A dipper equipped with a tail-mounted radio-tag photographed at roost. The roost site was on a natural riverside cliff.

**Table 2.28.** Number of radio-tags deployed on dippers in 1990 and 1991 using tail-clips, and details of their recovery.

| | No. | % |
|---|---|---|
| No. radio-tags fitted | 12 | |
| No. recovered from live birds | 3 | 25 |
| No. moulted or slipped off | 2 | 17 |
| No. in which water proofing failed | 1 | 8 |
| No. recovered from dead birds | 0 | 0 |
| No. not recovered | 6 | 50 |

Radio-tagged dippers were adept at removing antennae from transmitters, presumably during preening. This considerably reduced their range, but was overcome by reinforcing the base and first few centimetres of the antenna with silicone rubber.

#### 2.3.2.2. Energetic condition

The dipper shows very little daily or seasonal trend in body mass (Bryant & Tatner 1988). This allowed comparison between measurements of body mass at different times of day and on different days. The initial body mass of the dippers that subsequently carried tail-mounted radio-tags for a mean duration of 19 days (range 4-29) was not significantly different from their body mass when the radio-tags were removed (Wilcoxon Signed-rank Matched-pairs test Z=-1.52 ns n=9, median initial mass=59.0g range 57-74, median final mass=56.5g range 55-77). Furthermore, there was no relationship between mass change and the period of time that the package had been carried (r=-0.12 ns n=9).

#### 2.3.2.3. Energy expenditure

The cost to a dipper body mass of 69 g and flight wing span of 305 mm of carrying a tail-mounted 4.0 g radio-tag was calculated to represent an increase of 8 % in the chemical power required for level flight, using the computer program of Pennycuick (1989) with metabolic variables set at the default values and device drag assumed to be zero.

For the months in which most dippers carried radio-tags (October and November), average time budgets contained 2.9 % of time in flight and 22.4 % of time diving over the active period (Bryant *et al* 1985). Hydrodynamic drag on a body is approximately 12 times the aerodynamic drag (Wilson & Culik 1992). It was therefore a priority to minimise any increase in energy expenditure incurred by dippers carrying radio-tags during diving. When diving, dippers use their wings flexed at the wrist with the primary feathers trailing behind. The diving wing span of a dipper for which the flight wing span equals 305 mm is 130 mm, estimated from a dead bird (Fig 2.15.). Therefore when diving, dippers experience an increase in wing loading and therefore power required to produce forward motion over and above that required to overcome hydrodynamic drag. The speed of water flow over a diving bird is fastest over the interscapular region (the maximum spindle diameter; Wilson & Culik 1992). Packages mounted in this position therefore would have the most pronounced drag effects during diving. By mounting the radio-tag on the tail any turbulence produced will not act on

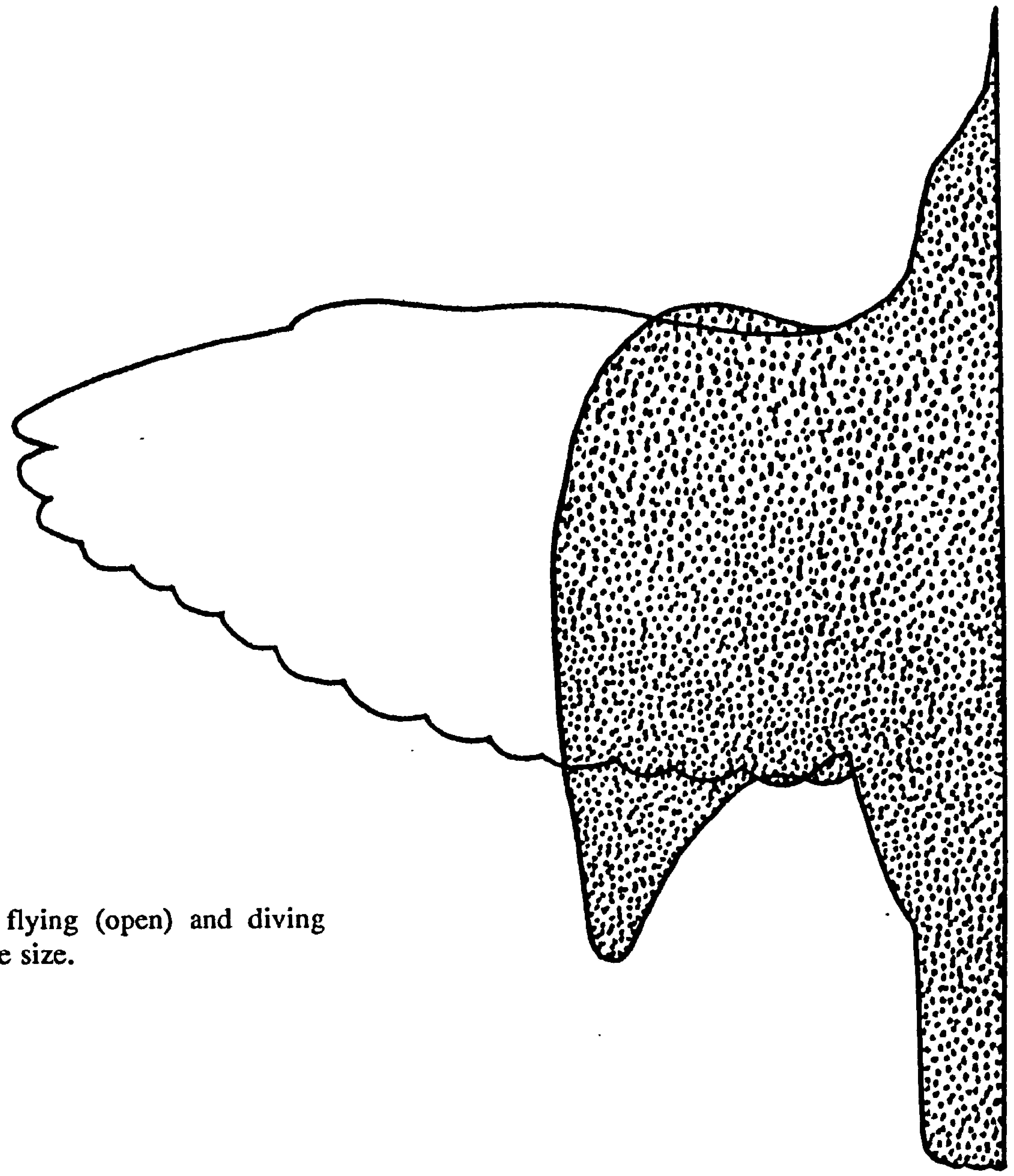


**Fig.2.15.** Wing configuration for a flying (open) and diving (stippled) dipper, shown life size.

the birds body, but rather trail out behind it (Wilson & Culik 1992), although, as with the robin, such an off axis load may have an effect on flight performance.

#### 2.3.2.4. Survival

No dippers died while carrying radio-tags. Two predation attempts were observed on tagged dippers during radio-monitoring. One bird was encountered and pursued by a female hen harrier at dusk. The dipper responded by diving into the water and swimming to safety under the overhanging stream bank. Another individual behaved similarly in response to an unsuccessful attack by a male sparrow hawk.

### 2.3.3. Discussion.

Newton (1989) found no effect on dispersing juveniles of being equipped with tail-mounted radio-tags. Similarly in the present study, the radio-tags had no significant effect on the body mass or survival of dippers during the autumn.

# Chapter 3.

# 3. Territory and neighbourhood structure: the robin.

## 3.1. Introduction.

Of the previous studies of the robin in which the location and extent of territories have been measured (Lack 1940 1965, Jackson 1956, Adriaensen & Dhondt 1983, Harper 1985, Brindley 1991), none has considered territory shape. Maps of territories from some previous studies (Lack 1965, Adriaensen & Dhondt 1983, Brindley 1991) however show that the shapes of the territories, although often irregular, are polygonal in nature (Fig 3.1.). The definitions by which the edges of territories were located often varied between studies (Table 3.1.) and were qualitative in nature. Any problems of independence between observations and sample size were not considered.

The form of a territory may be the result of the quality and activity of neighbours, as well as that of the owner. On territory maps produced by other studies, the edges of territories were invariably indicated as discrete lines. The territories of neighbours are often shown as being close packed and sharing common boundaries (Fig 3.1.).

Having determined the location and extent of territories, previous researchers have given little attention to their internal structure and pattern of use, for example the possible existence of centres of activity and the intensity with which any boundaries were visited. Also, measures of the extent of territories have been based on observations collected over months or even a whole breeding season (Table 3.1.). Any changes in location or extent of territories within seasons are described in anecdotal terms if at all (eg Adriaensen & Dhondt 1983).

So, although the territorial behaviour of the robin has received a great deal of study (above references and references therein), the territory structure has yet to be described in rigorous quantitative terms. Therefore, before a complete understanding of the economics of territorial behaviour can be obtained, the existing ideas of territory and neighbourhood outlined above must be assessed and if necessary refined.

Territories have no value for foraging after dusk. Individuals must select sites in which they can roost safely until dawn. Although observations of the nature of roost sites used by robins exist (Swann 1975, Cramp 1988), there is little information on the locations of roost sites selected by an individual in relation to its territory, and changes in the use of such sites on successive nights. For a robin in midwinter, approximately two thirds of each 24 hr period

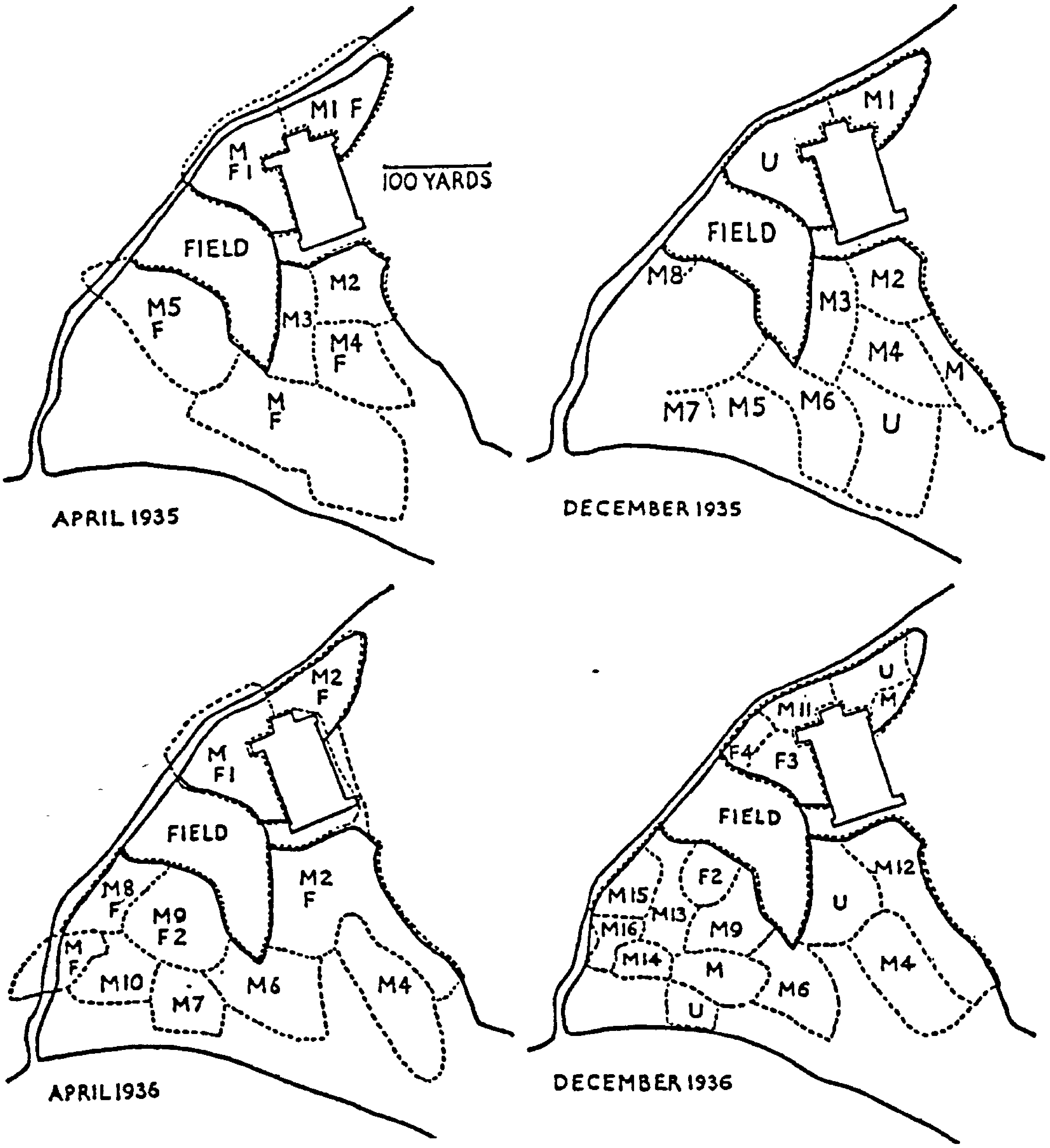


**Fig.3.1.** Maps of the individual territories of non-breeding robins, taken from Lack (1965). Note that the territorial boundaries are close-packed, such that there are no gaps between neighbours. M denotes males, F denotes females and U denotes unsexed.

**Table 3.1.** Definitions of territory used to locate territory boundaries in previous studies of the robin.

| | |
|---|---|
| **Lack (1940);** | "Continuous line drawn round all locations of boundary disputes and song posts". |
| **Harper (1984);** | "Records of boundary disputes and song posts plotted on maps". |
| **Adriaensen & Dhondt (1990);** | "Continuous line drawn round daily observations (sightings, song posts, intraspecific interactions, captures, responses to playback, dawn chorus counts), leaving out open areas". |

will be spent roosting. Consequently, in addition to providing a place safe from predators, the selection of roost sites may play an important role in the energy budget and daytime territorial behaviour of the robin.

## 3.2. Methods.

### 3.2.1. Accuracy of radio location estimates.

All radio-tracking was done using a hand-held three element Yagi antenna and RX-81 receiver. The $\theta_{0.95}$ error arc (Springer 1979, Saltz & Alkon 1985) of the antenna was taken as equal to $\pm 5°$, although trials suggested this was an overestimate. Radio-tagged birds were easy to locate, and due to their confiding nature were often observed visually. On occasions when individuals remained out of sight, bearings were taken "by eye" from about 10 m away to determine the location of the bird. Using this method, radio locations could confidently be assigned to one metre square grid cells, and were always confirmed to be correct if the bird subsequently moved into view. Radio location estimates were allocated a grid reference on an accurate map of the study area.

### 3.2.2. Sampling protocol.

Independence between successive radio locations is an implicit assumption in statistical measures of animal movement (Swinhart & Slade 1985, Worton 1987). The minimum sample interval for which it was possible to collect consistently accurate location estimates for the robin was two minutes. A sample of such continuous tracking data was analyzed to determine the $t^2/r^2$ ratio along with the $\alpha_{0.25}$ critical value (Swinhart & Slade 1985), this being the upper boundary of significance from table 1. in Swinhart & Slade (1985). The results from an individual that was particulary inactive (during very windy conditions) indicated that the minimum sample interval to produce a non-significant $t^2/r^2$ ratio followed by two successive non-significant intervals was six minutes (Fig 3.2.). Data from individuals which were more active showed a shorter time to independence. Within the 60 min time frame examined, there was no evidence for individuals following prescribed routes as indicated by a return to dependence at longer sample intervals (Swinhart & Slade 1985). The sample interval adopted for this study was however 60 min. Although much longer than required to achieve statistical independence between successive locations, it enabled up to 10 radio-tagged individuals to be monitored concurrently, and ensured radio-locations were collected over a period of several

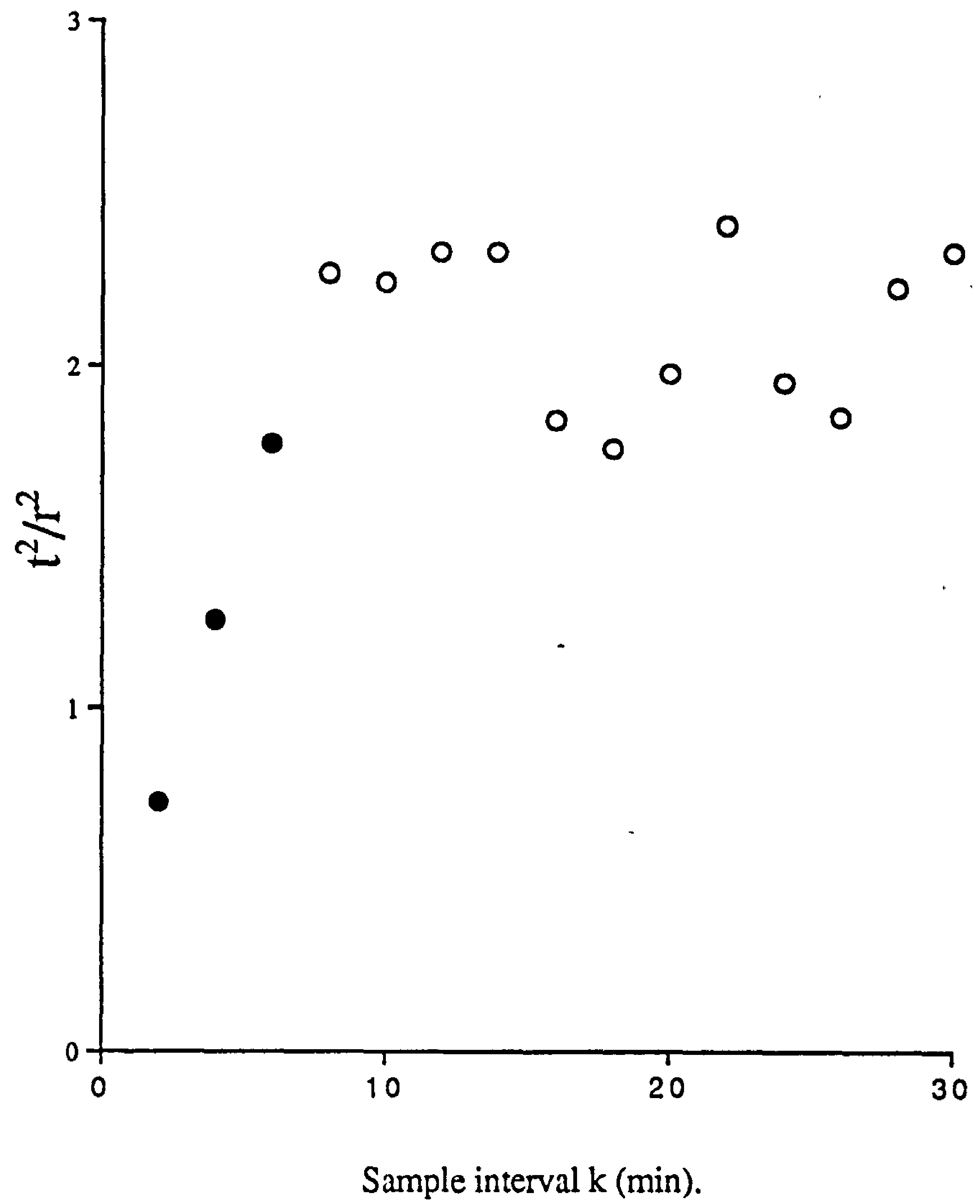


**Fig.3.2.** Values of the $t^2/r^2$ ratio (Swinhart & Slade 1985) as a function of sample interval. Data are from a single individual monitored for one hour. Solid symbols indicate $p<0.25$, open symbols indicate $p\geq0.25$. Probability levels refer to a one-tailed test of the null hypothesis that the locations were statistically dependent.

days, reducing any possible bias caused by exceptional daily variations in space use.

The number of such discontinuous location estimates required to accurately represent the space used by robins was determined by calculating observation-area asymptotes (Odum & Kuenzler 1955, Kenward 1987, Harris et al 1990) using non-statistical minimum convex polygons as the measure of the area used. The results for 10 individuals indicated that a sample size of 40 radio-locations represented in excess of 95% of the true maximum area (Fig 3.3.a.). Being an outline technique, the minimum convex polygon method of measuring space use is particularly sensitive to edge locations (White & Garrot 1990). Since it is conceivable that an individual which is actively defending a territory may spend more time near the edges of its range than near the centre, an asymptote was also constructed for five individuals using the number of 25 m$^2$ grid cells visited in place of an outline estimate of area. The results suggested that the sample size required to achieve saturated sampling of the interior of the range was also 40 locations (Fig 3.3.b.). When sample size exceeded 40, the rate at which new cells were visited dropped from an average of 0.33 to 0.08 per additional location.

Consequently a standardized sample size (Harris *et al* 1990) of 40 statistically independent location estimates was adopted to represent space use by the robin. This was termed an individuals' range. Radio locations were collected throughout the daylight hours, with exact times varying between days. The required sample size was obtained after four to five days.

Any interactions with conspecifics or behaviour associated with territorial advertisement and defense, shown by a focal robin each time it was relocated was recorded along with the position of the bird. This behaviour included evicting intruders, being evicted, mutual display, song, and tic calls (Cramp 1988).

### 3.2.3. Locating roost sites.

The locations of roost sites were recorded in the same way as daytime radio locations. The nature of the roost sites were recorded at the time or in daylight on the following day. Sites were assigned to the mutually exclusive qualitative categories shown in Table 3.2. These categories included all the possible sites birds could choose based on previous information (Cramp 1988). The advantage of such qualitative categories was that they could be quickly and consistently applied in the field. Roosting individuals were rarely visible without them being disturbed. The location and nature of sites could however be determined

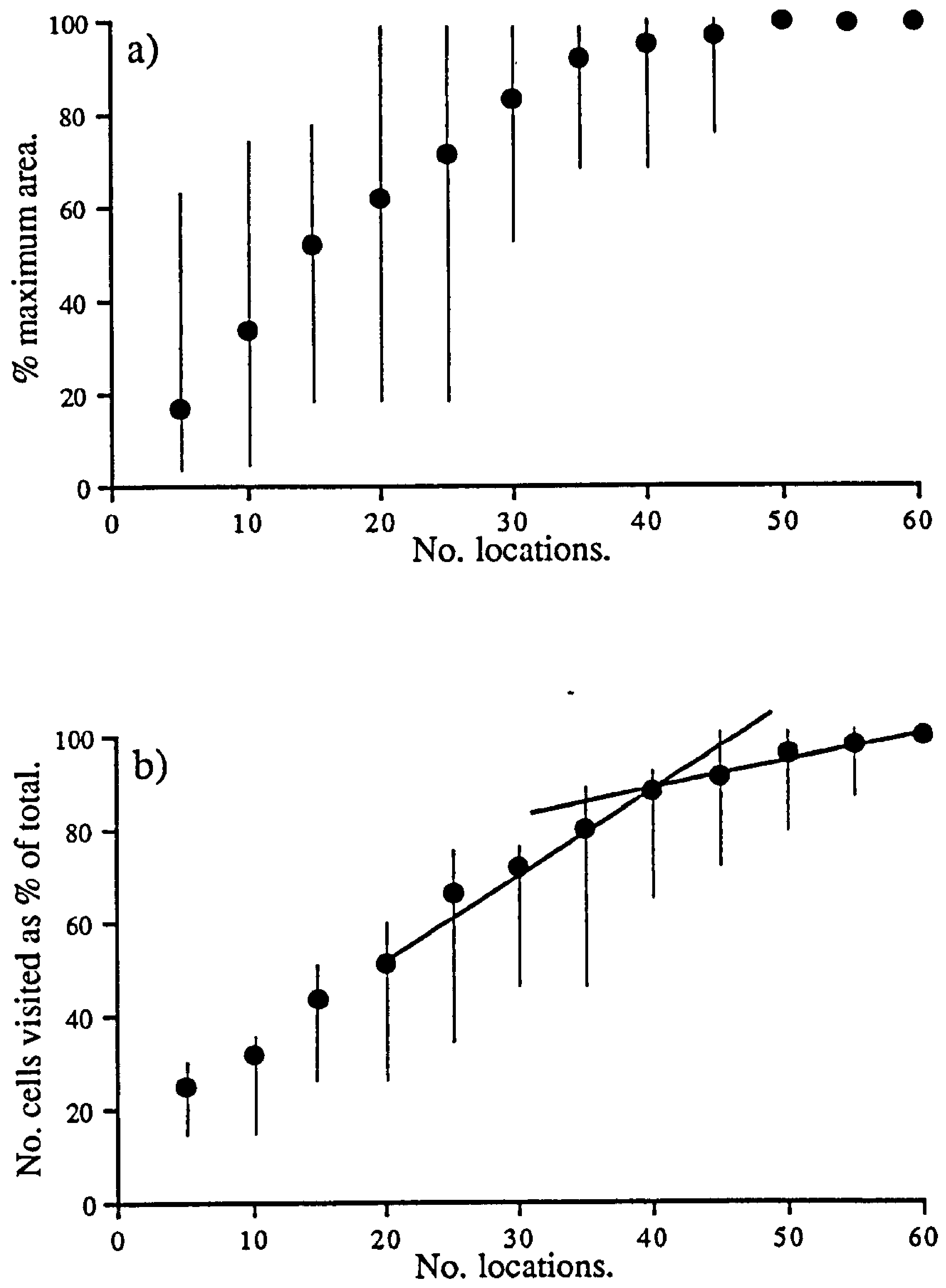


Fig.3.3. Observation-area asymptotes (Odum & Kuenzler 1955) for discontinuous radio-tracking locations from non-breeding robins. Asymptotes are constructed using two measures of range size; a) the minimum convex polygon containing all locations (mean and range for 10 individuals) and b) the number of 25m$^2$ grid-cells visited (mean and range for five individuals). In b) the best fit lines emphasise the point at which the rate at which new cell were visited dropped from 0.33 to 0.08. Sampling achieved saturation after approximately 40 location estimates for both measures of range size.

**Table 3.2.** Categories used to quantify the quality of roost sites used by robins.

| | |
|---|---|
| **i)** | On ground in open. |
| **ii)** | Below ground in hole. |
| **iii)** | Above ground in sparse vegetation. (Deciduous trees and shrubs eg young birch *Betula* and sycamore *Acer*). |
| **iv)** | Above ground in medium vegetation. (Evergreen shrubs eg *Rhododendron* and broom *Cytisus*). |
| **v)** | Above ground in dense vegetation. (thorny shrubs, gorse *Ulex*, brambles *Rubus*). |
| **vi)** | Above ground in hole. |

accurately. Roost sites were located on the night following each day that discontinuous tracking had been carried out.

### 3.2.4. Range shape.

Most studies of space use have not considered the shape of the range outlines that they produce. A simple method to quantify shape is to calculate the eccentricity ($\varepsilon$), where $\varepsilon$ equals one minus the ratio of the major and minor axes (eg Swinhart & Slade 1985). This is an unambiguous procedure when applied to ellipses since the axes always pass through the focus (Korn & Korn 1968). However, this needs to be further qualified when applied to irregular polygons since they do not have a point analogous to the focus of an ellipse. Irregular range outlines are frequently the result of applying polygon range estimators to radio-tracking data. Consequently, the method by which range shape was measured is described in Fig.3.4. $\varepsilon$ ranges from zero for a radially symmetrical polygon or circle to one for an straight line.

### 3.2.5. Defended-area.

The definition of a territory as a defended-area has been widely accepted (Kaufmann 1983). In addition, this definition is easily applied to determining the location and extent of territories in the field.

The defended-areas of robins were determined by recording the locations at which they exhibited behaviour associated with territorial advertisement and defense. This is based on the assumption that territorial individuals only communicate their territorial ownership from within their territory; the area that they defend by evicting intruders. This behaviour included song, tic calling and evicting of intruders (Cramp 1988). Behaviour in which the focal bird was subordinate or equal in status to a conspecific (being evicted or display without aggression respectively) was not included, since they will both occur outside the territory.

Behaviour was recorded during routine relocations of radio-tagged robins. Additional observations were made on a casual basis at all times of day. The interval between recording observations of the same individual was never less than 60 mins to ensure statistical independence. Over each month, different individuals were observed for similar lengths of time.

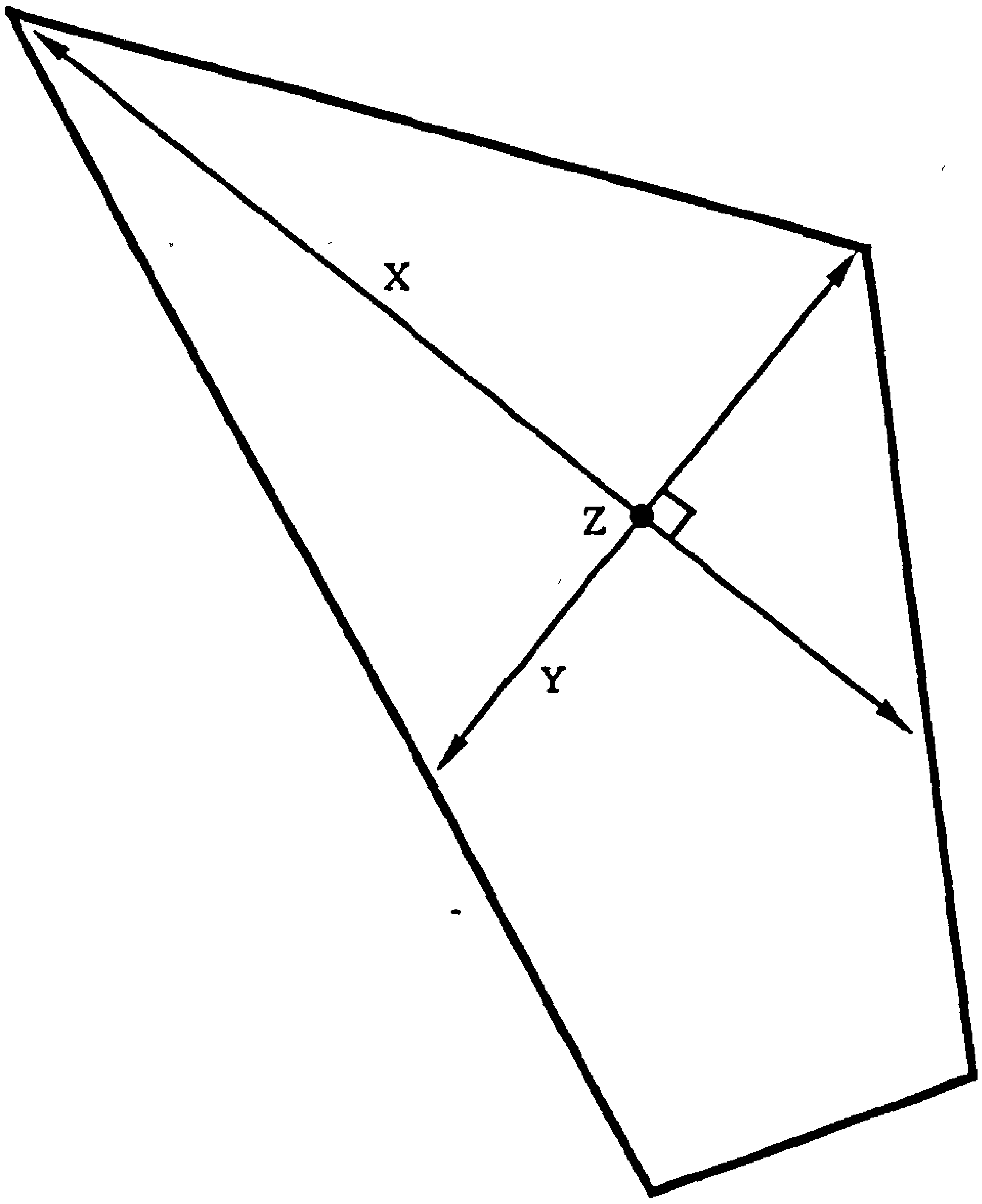


**Fig.3.4.** Calculating the eccentricity $\in$ of irregular polygons.

$$\in = 1-(Y/X)$$

*Where;*
*Z=The geometric centre of the polygon; the point furthest from all corners, determined by measurement.*
*X=The length of the longest axis which passes through the geometric centre.*
*Y=The length of the axis perpendicular to X which also passes through the geometric centre.*

Increasing values of $\in$ indicate increasing departure from radial symmetry.

The sample required to accurately represent the defended-area of individuals was determined by constructing observation-area asymptotes using minimum convex polygons containing all the locations. This technique was used since it is sensitive to edge locations, and only an outline of the area was required. An asymptotic sample size was achieved at 10 observations, based on the results from nine individuals (Fig 3.5.). Consequently a standardized defended-area was defined as the space within a minimum convex polygon applied to 10 locations of behaviour.

The observations contributing to the defended-area that was associated with a particular range were always made during the same month, and usually during collection of discontinuous tracking data. Observations supplementary to this were used to produce estimates of the location and extent of defended-areas for individuals that were not radio-tracked in a particular month.

## 3.3. Results.

### 3.3.1. Independence between ranges.

168 ranges of standardised sample interval and sample size were collected from 56 robins of both sexes and various ages between August 1990 and May 1992. From these, random samples of ranges were selected such that each individual contributed only one range, ensuring statistical independence. Individuals were assumed to be independent between years. Samples represented a) non-breeding individuals (the end of the annual moult in August until the spring song surge in February) and b) breeding individuals (post spring song surge until the fledging of young). In both samples, ranges were distributed uniformly over time. Unless otherwise stated the results presented here refer to the non-breeding individuals.

Because the distributions described frequently included small sample sizes with frequent outliers, non-parametric techniques were used throughout when comparing range statistics.

### 3.3.2. Selecting appropriate range estimators.

A frequently used estimator of range and territory size in previous studies of small birds has been the minimum convex polygon (eg Davies & Lundberg 1984, Hanski & Haila 1988, Hanski & Laurila 1993). This range estimator is non statistical and so allows direct comparisons to be made between studies, although it provides no information on the intensity

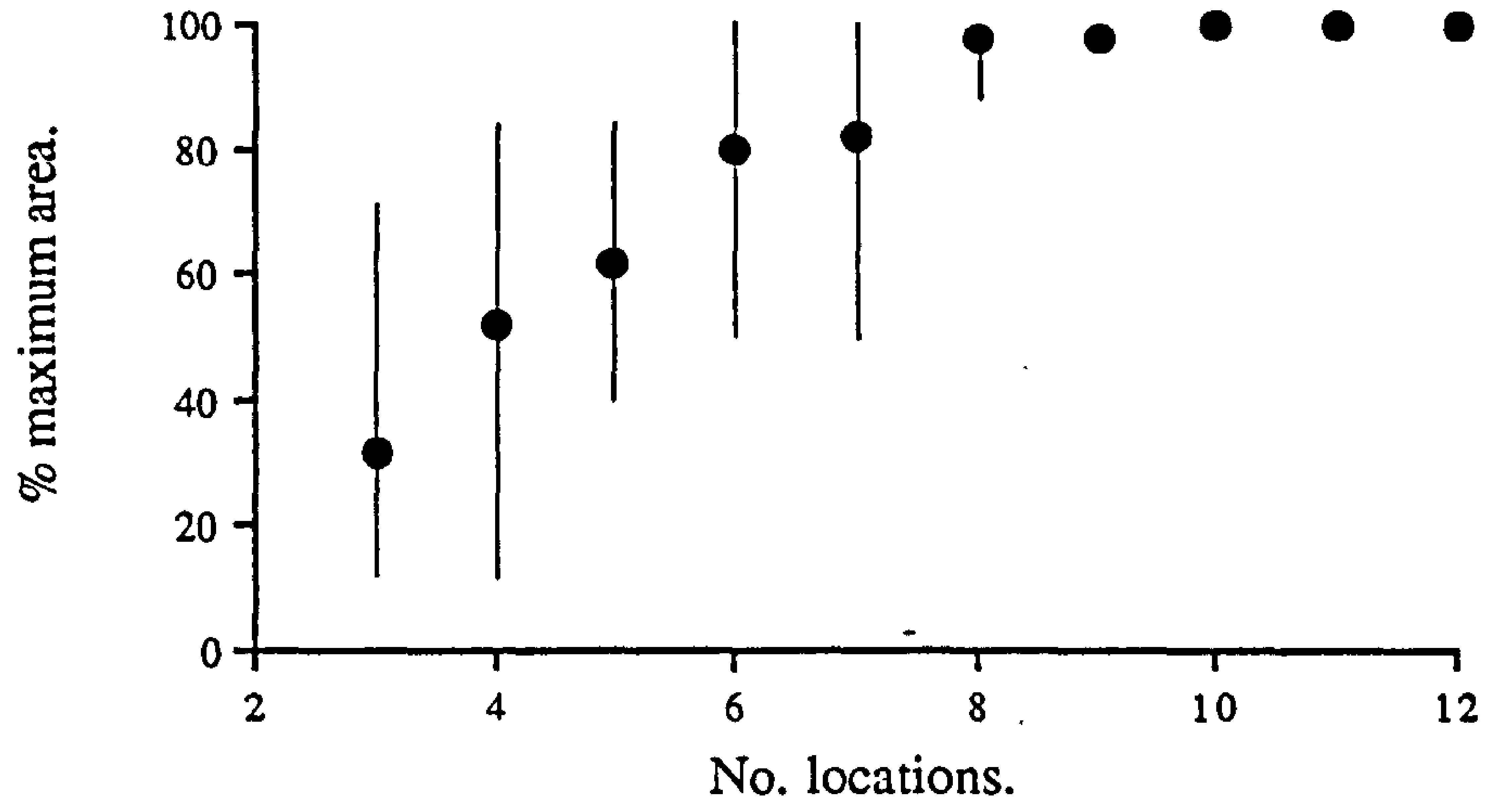


**Fig.3.5.** Observation-area asymptote (Odum & Kuenzler 1955) for discontinuous locations at which robins exhibited territorial advertisement and defense behaviour. This included song, tic-calls and the eviction of intruders (Cramp 1988). Data are means and ranges for nine individuals. An asymptotic sample was achieved at approximately 10 observations.

of range use and may be strongly affected by peripheral locations (White & Garrot 1990). However, to provide meaningful comparisons with other studies of territoriality in small birds, the sizes of ranges were determined by applying this technique to the standardised sample of location estimates from each robin. This represented the simplest estimate of range size, and was termed the maximum-area. Median and quartiles of the maximum-area for the sample of radio-tracked robins are shown in Table 3.3. The measures of range use for all individuals developed in this and subsequent chapters are presented in Appendix 4. During analysis using outline range estimators, a boundary strip of width equal to half a resolution cell (in this case half a metre), was added to each location. This ensured that any estimates of range area allowed for the level of accuracy of the locations estimates (Kenward 1990).

When three dimensional histograms of the radio-locations contributing to each range were examined, it was clear that the distributions of locations from the majority of individuals were non-uniform and multinuclear (Fig 3.6.). This imposed a limitation on the choice of range estimator which could be used to quantify the dispersion of the location estimates in each range. Parametric ellipse models (Jennrich & Turner 1969) were excluded because of their assumption of normality. Mono-nuclear range polygons (Kenward 1987) were also inadequate for the same reason. It was considered that contour models such as kernel and harmonic mean estimators (Worton 1989, Dixon & Chapman 1980), although non-parametric and applicable to multinuclear distributions, did not realistically represent the true range. This was because the probability of an animal occurring in each position within the range are calculated from all the locations in the sample, causing the isolines to veer round and include unused areas in very patchy distributions (Kenward 1987). Consequently the most appropriate technique for estimating the structure of ranges used by robins was sequential cluster analysis (Kenward 1987, 1990, 1992).

### 3.3.3. Defining core regions.

Sequential cluster analysis was carried out on each range, using a joining rule that initiated clusters with a minimum of three locations (Kenward 1992). The addition of a boundary strip, of width equal to half a resolution cell, to each location ensured that cores containing three or more locations at the same grid reference had an area of one resolution cell (one square metre) (Kenward 1990). Plots of percentage area against percentage of locations assigned to clusters were then produced (utilization distribution plots: Ford &

**Table 3.3.** Median values of the different measures of range use for non-breeding robins. Statistics refer to Mann Whitney U-tests between territorial and non-territorial individuals. Figures in parentheses show interquartile range. The data for all individuals are shown in Appendix 4.

| Class of individual and sample size | Maximum-area ($m^2$) | No. core-nuclei | Core-area ($m^2$) | Usual-area ($m^2$) |
|---|---|---|---|---|
| All<br>(n=51) | 3340<br>(1414-10310) | 4<br>(3-5) | 60<br>(43-126) | 543<br>(277-1228) |
| Territorial<br>(n=43) | 2399<br>(1315-8361) | 4<br>(3-5) | 54<br>(39-84) | 468<br>(255-803) |
| Non-territorial<br>(n=8) | 19970<br>(10343-26140) | 5<br>(4-6) | 146<br>(129-213) | 2887<br>(5424-10754) |
| W | 351 * | 268 | 350 * | -# |

* $p<0.005$

\# The size of the usual-area is the basis for the definition of territorial and non-territorial space use. The difference between the usual-areas of robins in each category, therefore, will be significant by definition.

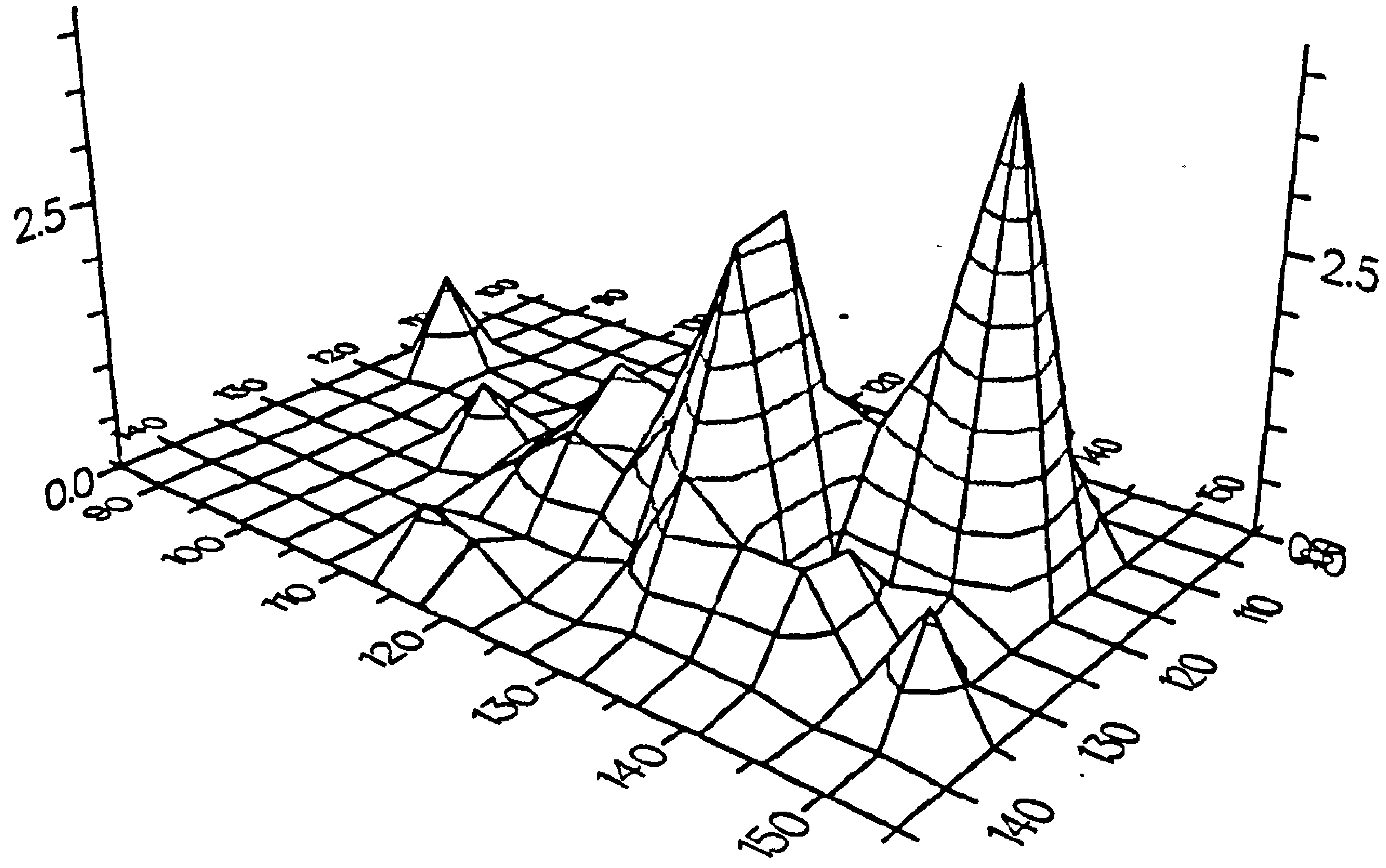


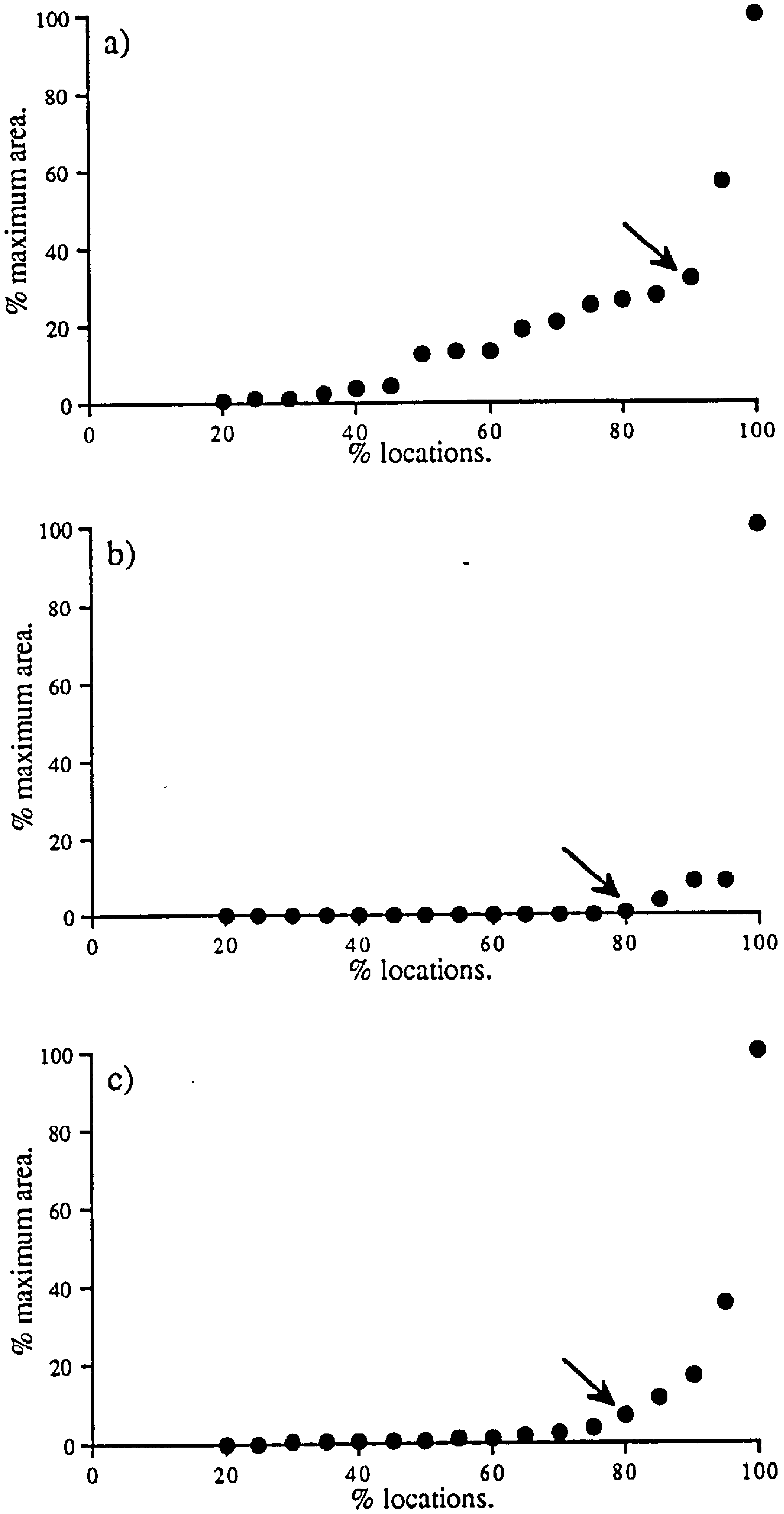
**Fig.3.6.** Histogram in three dimensions showing an standardised sample of radio-locations from robin F636519 during November (n=40). Locations were assigned to 25m$^2$ grid-cells. Horizontal axes indicate map reference, the vertical axis indicates the frequency of locations in each cell.

Krumme 1979). The inflexion point, beyond which additional locations were more widely scattered, was used to determine the percentage of locations contributing to any core areas (Kenward 1987, Harris *et al* 1990)(Fig 3.7.). Each plot was examined individually so as to detect any differences between individuals. Birds which visited widely separated locations more frequently will show an inflexion point at a lower percentage. In the majority of cases the core percentage was easy to define (Fig.3.7.a.), however also illustrated are some of the less straight forward cases. When maximum-areas were very large, the true inflexion point was sometimes less obvious (Fig.3.7.b.)(there was a two orders of magnitude difference between the smallest and the largest maximum-range). This could be overcome simply by expanding the Y axis. Occasionally the utilization distribution plots followed the form of a smooth exponential function (Fig.3.7.c.). If all the locations contributed to the core areas, the utilization distribution plot would approach a straight line with no inflexion point (Kenward 1990). The reason why some utilization plots resembled an exponential function is possibly that several different core areas within the range showed different exclusion values, masking any inflexion point (Wray *et al* 1992). In the few cases that this occurred, the percentage of locations contributing to core areas was taken as the percentage at which the slope of the utilization distribution plot was equal to one. On average core areas contained 77 % of the location estimates (range 55-90 n=51).

### 3.3.4. Core areas and range patchiness.

Of the core areas defined by cluster analysis, 98 % produced more than one centre of activity (n=51). The degree to which an animal concentrates its activity in such centres can be assessed by calculating the partial area ($A_p$) of its range. This is the total area of the convex polygons surrounding the locations assigned to each core area divided by the area of a convex polygon containing all core locations (Kenward 1990). Values of $A_p$ can range from one (locations distributed evenly) to zero (locations concentrated several single points). $A_p$ was calculated for each of the ranges (Fig 3.8.). The median value of $A_p$ was 0.11 (range 0.01-1.00, n=51). The locations making up ranges therefore generally exhibited very patchy distributions. A range of mean $A_p$ (0.22) was characterised by 77% of the locations being contained within only 1.8 % of the maximum-range area. The individual core regions defined by sequential cluster analysis were termed core-nuclei. Values of the median and quartiles for the number of core-nuclei occupied by the sample of robins that were radio-tracked are shown

**Fig.3.7.** Utilization distribution plots (Ford & Krumme 1979) from the results of sequential cluster analysis for three non-breeding robins. In a) is shown a typical plot, the arrow marks the inflexion point beyond which locations no longer contribute to core regions. When maximum-areas were very large the true inflexion point was less obvious (b). This could be overcome by expanding the vertical axis. Occasionally the plots followed the form of a smooth exponential function (c). The percentage of locations contributing to core regions was taken as the point at which the slope was equal to one.


a)
b)
c)
% maximum area.
% locations.
0
20
40
60
80
100

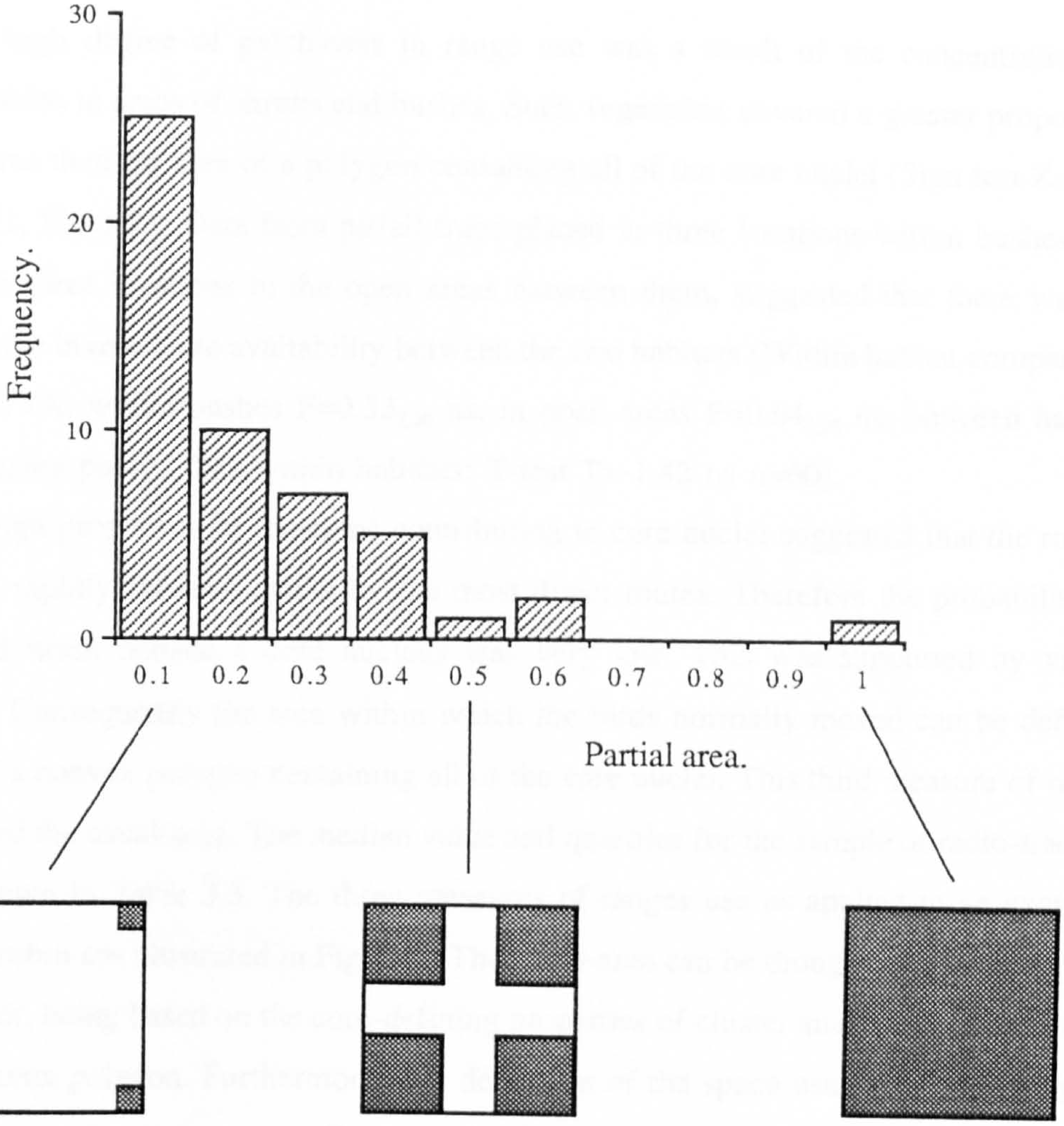


**Fig.3.8.** Frequency histogram of partial area $A_p$ for the ranges of non-breeding robins (n=51). Also shown are hypothetical ranges of three different values of $A_p$, illustrating how decreasing $A_p$ reflects the increasing fragmentation of core regions.

in Table 3.3.

This high degree of patchiness in range use was a result of the concentration of activity by robins in areas of shrubs and bushes. Such vegetation covered a greater proportion of the core area than the area of a polygon containing all of the core nuclei (Sign test $Z=5.92$ $p<0.005$ $n=51$, Fig 3.9.). Data from pitfall traps placed in three locations within bushes and shrubs and in three locations in the open areas between them, suggested that there was no difference in the invertebrate availability between the two habitats (Within habitat comparison oneway ANOVA; within bushes $F=0.33_{2,20}$ ns, in open areas $F=0.64_{2,20}$ ns, between habitat comparison using pooled data within habitats; T-test $T=-1.42$ ns $n=60$).

The high proportion of locations contributing to core nuclei suggested that the robins were moving rapidly between nuclei by the most direct routes. Therefore the probability of being located when outside a core nucleus was very low. This was supported by visual observations. Consequently the area within which the birds normally moved can be defined as the area of a convex polygon containing all of the core nuclei. This third measure of range use was termed the usual-area. The median value and quartiles for the sample of radio-tracked robins are shown in Table 3.3. The three measures of ranges use as applied to an example range from a robin are illustrated in Fig.3.10. The usual-area can be thought of as a composite range estimator, being based on the core-defining properties of cluster analysis and the simple minimum convex polygon. Furthermore, this definition of the space usually occupied by an individual has an advantage over isoline models of multinuclear ranges in that it is based on the actual pattern of movement of the robin, rather than a generalized mathematical algorithm. On average, the usual-area contained 79 % of locations, 77 % of which lay in the core-nuclei.

### 3.3.5. Defended-area and range use.

The summary statistics for the different measures of range use and number of core-nuclei are presented in Table 3.3. By definition core-area ≤ usual-area ≤ maximum-area. In order to assess the relationship between these and the defended-area it was necessary to compare a) the degree of overlap of the polygon outlines and b) the similarity in size of the standardised defended-areas and the different measures of range use for each individual.

Of the 51 ranges making up the independent sample of non-breeding individuals, only 25 showed enough territorial advertisement behaviour to constitute standardised defended areas. The median percentage polygon overlap between the defended-area and the different

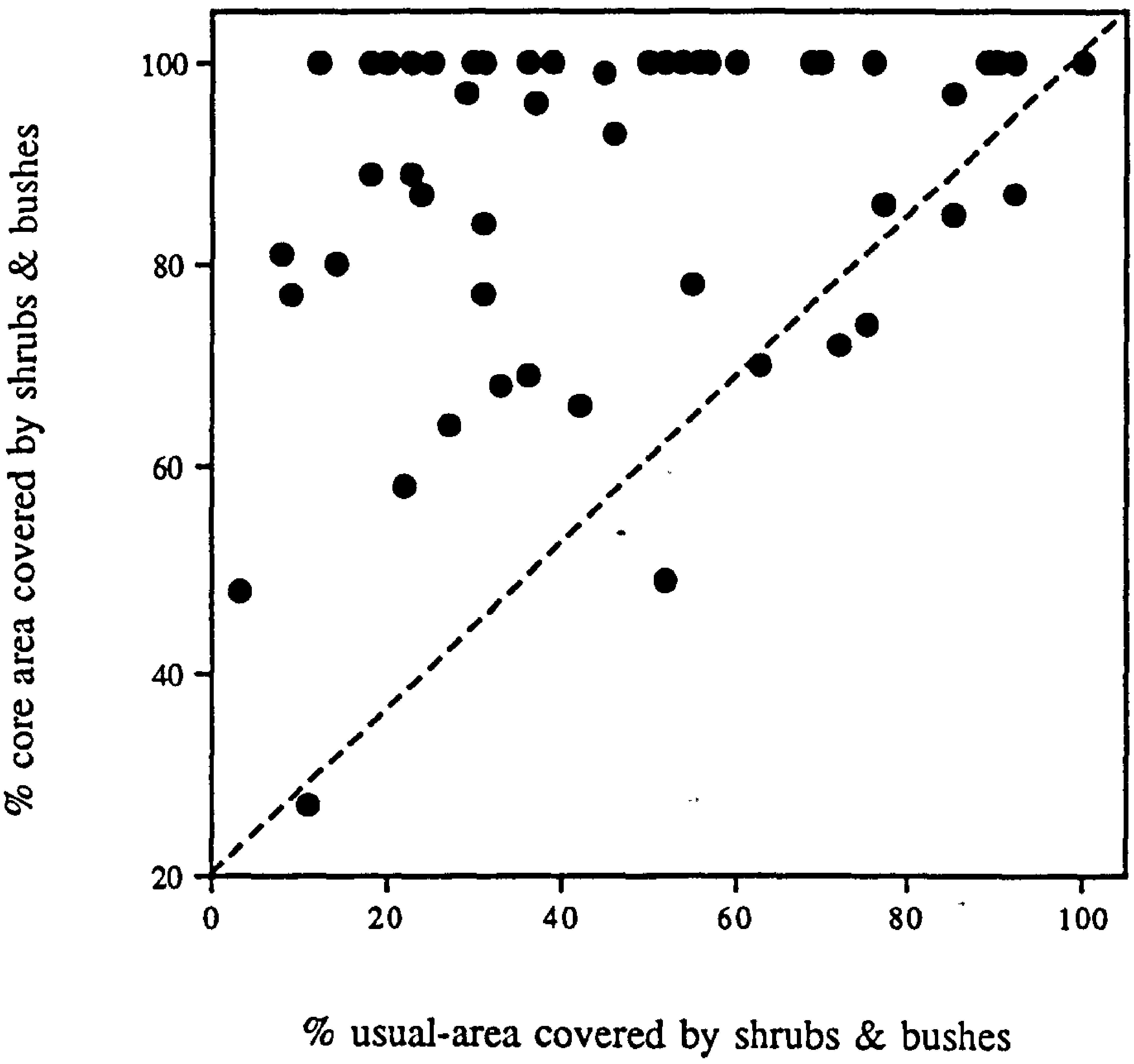


**Fig.3.9.** Plot of percentage core area covered by shrubs and bushes with percentage usual-area covered by shrubs and bushes. Clearly there was a strong preference for robins to site their core-areas in shrubs and bushes (Sign test Z=5.92 p<0.005 n=51). The dashed line indicates no preference.

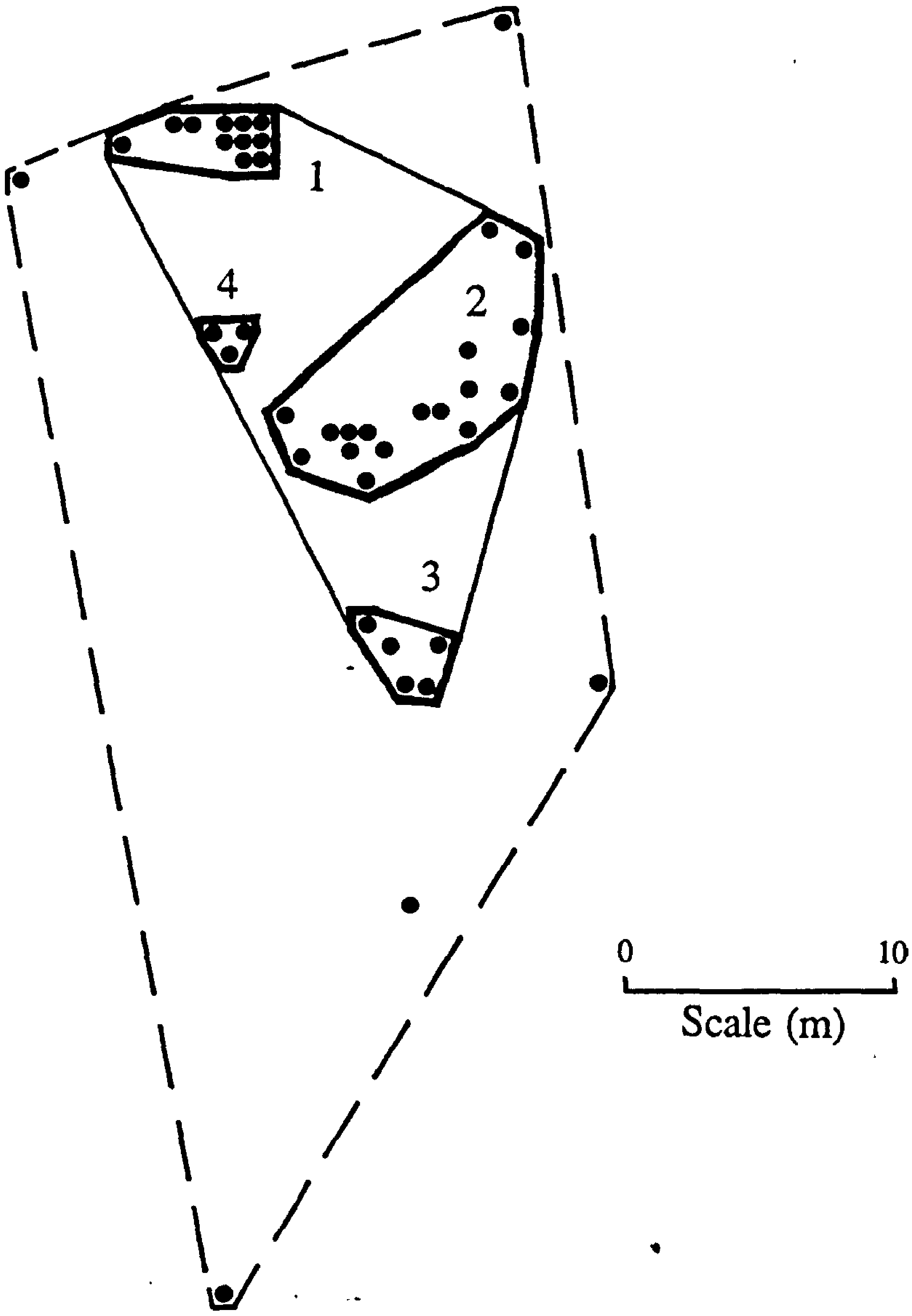


**Fig.3.10.** An example of a range occupied by a non-breeding male robin. The standardised sample of 40 location estimates was recorded over five days from 18th September, north is towards the top of the figure. Also shown are the different measures of range use as applied to this individual. Thick solid lines indicate the convex polygons containing the locations assigned to the core area, as determined by the examination of utilization plots from sequential cluster analysis. In this example the robin used four core-nuclei, here numbered clockwise from the most northerly. The thin solid line indicates the usual-area; the convex polygon which contains all the locations assigned to the core-nuclei. The dashed line shows the maximum-area; the convex polygon which contains all of the location estimates in the sample.

measures of range use within individuals is shown in Table 3.4. Polygon overlap is the area of one polygon which is overlapped by another. The defended-area lay almost entirely within the maximum-area and both defended-area and usual-area showed high mutual polygon overlap. In addition, the defended-area contained part or all of 80 % of the core nuclei of each range.

There was no significant difference between the size of the usual-area and defended-area for each individual (Wilcoxon Matched-pairs Signed-ranks test $Z=-0.23$ ns $n=25$). However the differences in size between defended-areas and core-areas, and defended-areas and maximum-ranges were both significant (Wilcoxon Matched-pairs Signed-ranks tests $Z=-4.37$ $p<0.005$ $n=25$, $Z=-4.37$ $p<0.005$ $n=25$ respectively). The usual-area therefore was the best candidate for an estimate of the location and extent of the territory, since it showed similar size to and high overlap with the defended-area. An example of a range occupied by a robin showing core-nuclei and defended area in relation to local habitat features is presented in Fig 3.11.

### 3.3.6. Characteristics of the usual-area.

For the ranges of both territorial and non-territorial individuals, there was a strong negative relationship between usual-area and core area as a percentage of usual-area ($r_s=-0.78$ $p<0.005$ $n=51$, Fig.3.12.). The curve shows the expected distribution if all usual-areas contained the same core area (the mean core area of all birds tracked). In general the observed data closely approached this.

Only 25 of the 51 ranges from non-breeding individuals had associated asymptotic defended-areas. Of the usual-areas that did not have such defended-areas, some were unusually large (Fig 3.13.a.). Furthermore such ranges were much larger than those which did have associated defended-areas (Fig 3.13.b.). This suggests the existence of widely ranging non-territorial individuals within the population.

Harper (1984) recorded the presence of non-territorial individuals in a population of robins at Cambridge. They were categorised as non-territorial simply by their widely ranging behaviour (Harper 1984). Since in this study the space use of such otherwise elusive and difficult to observe individuals could be measured, it was possible to derive a more rigorous definition enabling individuals to be assigned to territorial or non-territorial categories.

**Table 3.4.** Median polygon overlap of the different measures of range use within individuals. (n=25).

| Nature and direction of overlap | % polygon overlap [#] | |
|---|---|---|
| | Median | Range |
| Maximum-area on usual-area | 100 * | - |
| Usual-area on maximum-area | 22 | 2-62 |
| Maximum-area on defended-area | 100 | 65-100 |
| Defended-area on maximum-area | 20 | 2-54 |
| Usual-area on defended-area | 73 | 28-100 |
| Defended-area on usual-area | 66 | 25-100 |
| % of core-nuclei within defended-area | 75 | 33-100 |

\# The % area of the second named polygon which is overlapped by the first named polygon.

* By definition.

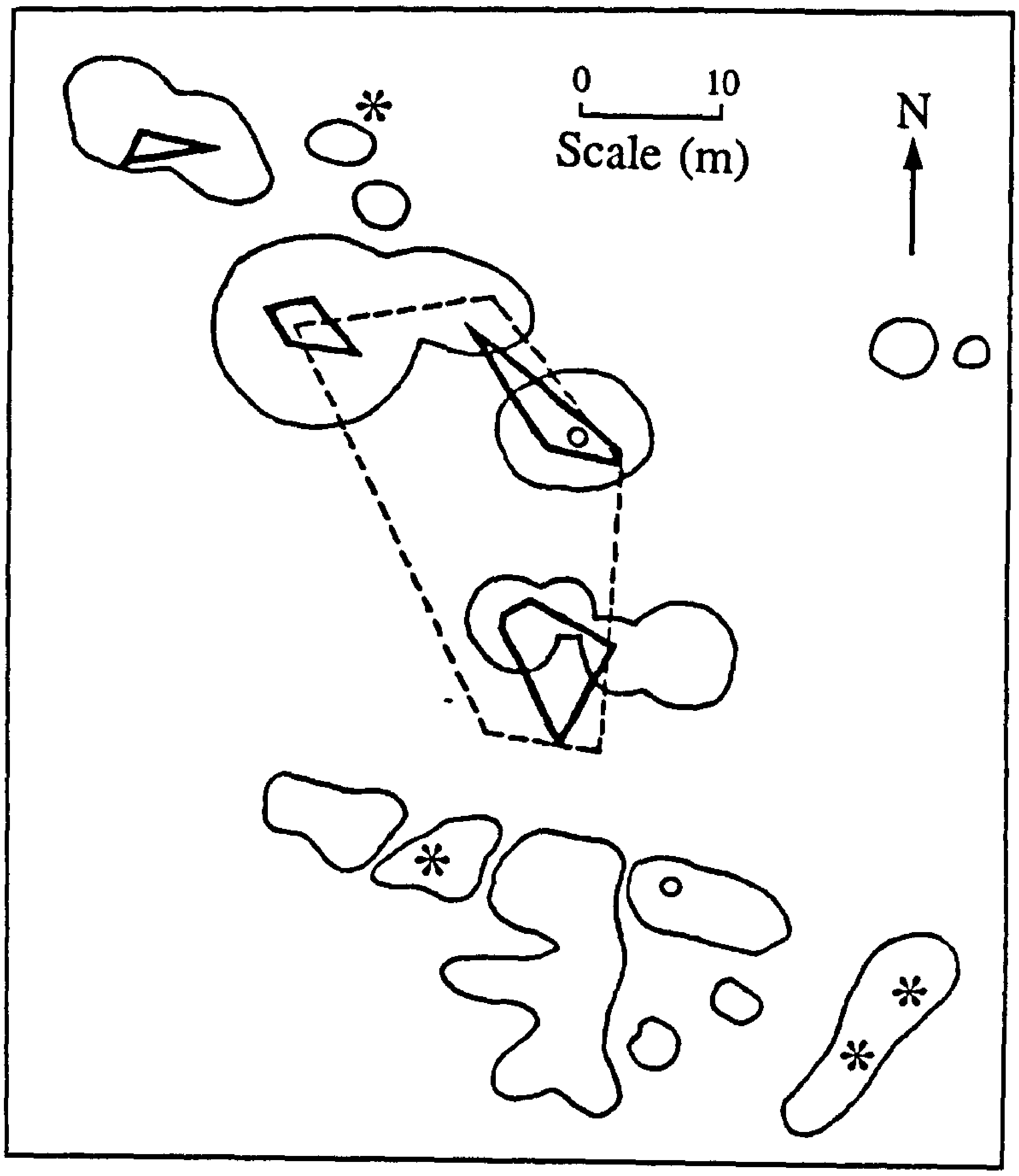


**Fig.3.11.** An example of the standardised range and defended-area of a first year male robin radio-tracked during september. The thick solid lines outline the four core-nuclei while the dashed line outlines the defended-area. Thin solid lines show the local habitat features (shrubs and bushes). Four excursive locations are marked by asterisks and the two roost sites used during the period are shown by open symbols.

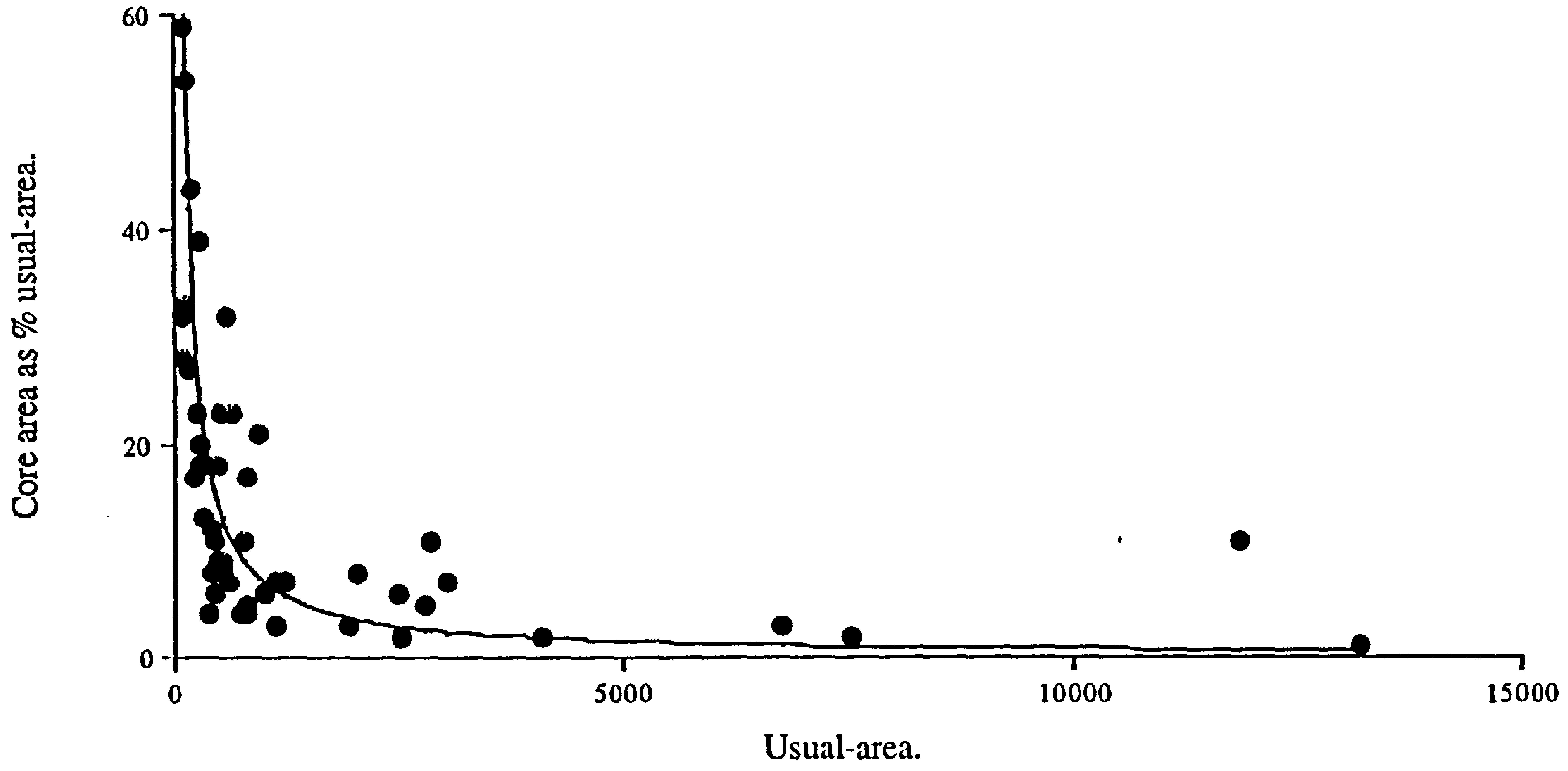
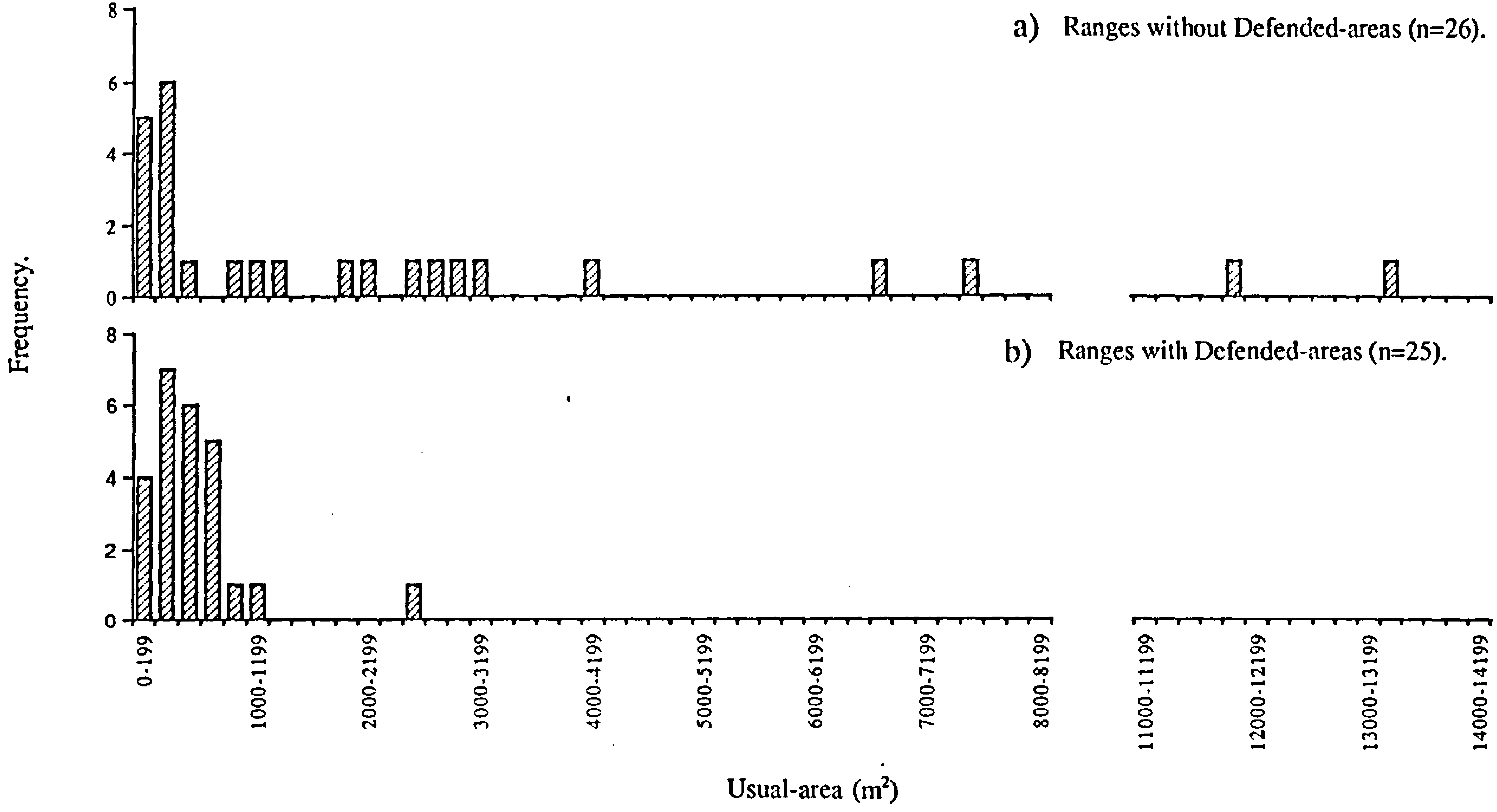


**Fig.3.12.** Plot of core area as a percentage of usual-area, against usual-area for non-breeding robins (rs=-0.78 p<0.005 n=51). The curve shows the expected distribution if all ranges contained the same core area; the mean core area of all birds tracked. One range was is not shown on the plot since it was mono-nuclear. In this individual therefore, the core area as a percentage of the usual-area equalled 100.


a) Ranges without Defended-areas (n=26).

b) Ranges with Defended-areas (n=25).

**Fig.3.13.** Frequency histograms of usual-area for ranges which did not have an associated defended-area (n=26)(a) and ranges which did have an associated defended-area (n=25)(b). Ranges were occupied by non-breeding robins. Note the break in the horizontal axis.

On examining the frequency distributions, it was clear that there was no obvious cut-off point for assigning individuals to such categories on the basis of usual-area alone. Of the individuals which did not have an associated standardised defended-area, those that were territorial may still have shown more advertisement behaviour than those that were non-territorial. The usual-area of each individual plotted against the percentage of locations at which territorial advertisement and defense behaviour was recorded during tracking is shown in Fig 3.14. This is an estimate of the frequency of territorial advertisement behaviour that is comparable between individuals. Using this estimate there was no significant tendency for robins to invest in these activities differently over the course of the Autumn and Winter (correlation between proportion of locations with advertisement and defense behaviour and day of year with day one set to 1st August; $r_s$=-0.07 ns n=43). This was largely due to the fact that some individuals very rarely vocalised even in the early Autumn. Of the ranges with associated defended-areas, none showed a usual-area greater than 2500 $m^2$. Although some individuals with defended-areas showed little or no advertisement behaviour, no individuals of usual-range size greater than 2500 $m^2$ were observed to engage in advertisement and defense behaviour at more than 8 % of locations (Fig.3.14.). Although rarely engaging in activity associated with the communication of territorial status, the remaining birds which lacked standardised defended-areas were categorised as territorial. This is because an individual may still maintain a territory even if it never needs to communicate its territorial status or evict any intruders. Consequently a cut-off point between territorial and non-territorial individuals of 2500 $m^2$ was adopted. Therefore by definition, the usual-areas of non-territorial individuals were considerably larger than those that were territorial (Fig 3.14.). Maximum-areas and core areas were also significantly larger (Table 3.3.), but the difference between the number of core-nuclei was not significant (Table 3.3). In territorial individuals, the usual-area contained on average 79 % of locations, 78 % of these being in the core-nuclei. The corresponding values for the usual-areas of individuals that were categorised as non-territorial were 77 % and 74 % respectively, indicating a slightly greater dispersion of locations.

The usual-area polygons of individuals that were classed as territorial showed high eccentricity, indicating a high degree of departure from the shape of a regular polygon (Fig 3.15.). Examples of the usual-areas of territorial individuals which showed low and high eccentricities are presented in Fig 3.16.

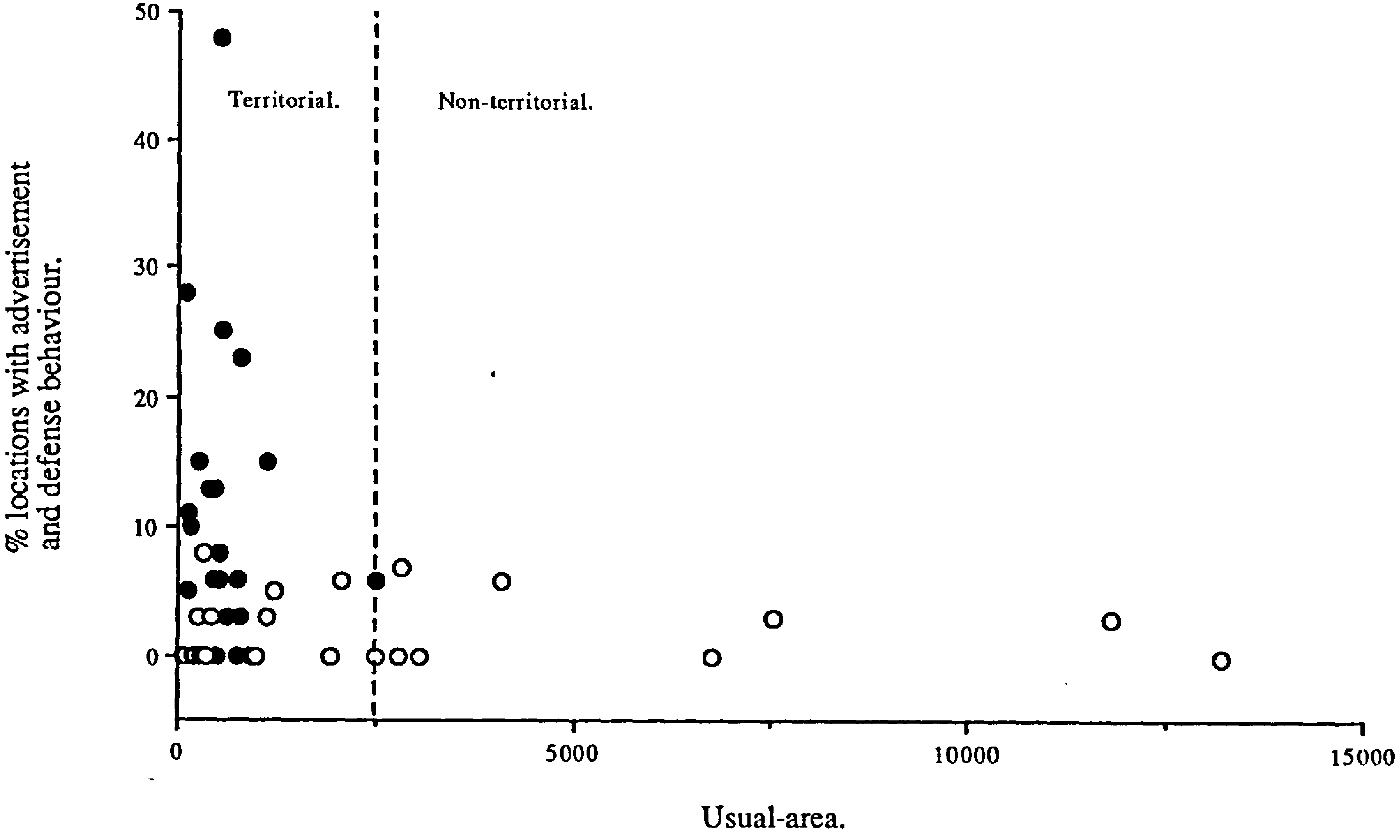


**Fig.3.14.** The relationship between usual-area and the percentage of locations at which territorial advertisement and defense behaviour occurred (song, tic-calls and evicting intruders) for non-breeding robins (n=51). Solid symbols indicate ranges with associated defended-areas, open symbols indicate ranges without associated defended-areas. The dashed line indicates the cut-off point between the ranges of individuals that were territorial and non-territorial, see text.

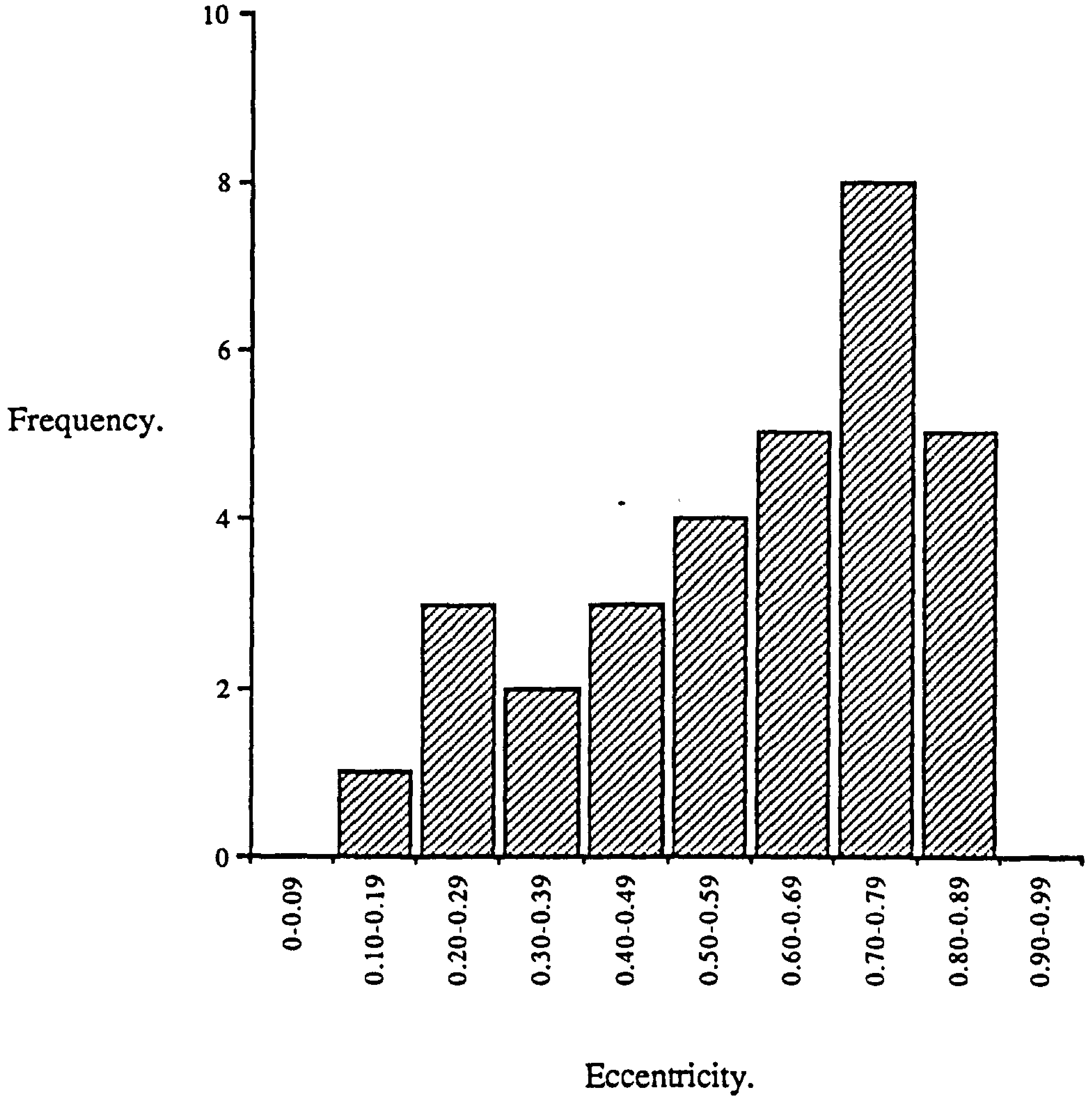


**Fig.3.15.** Frequency distribution of eccentricity Є for non-breeding territorial robins (n=43). Increasing values Є indicate increasing departure from radial symmetry.

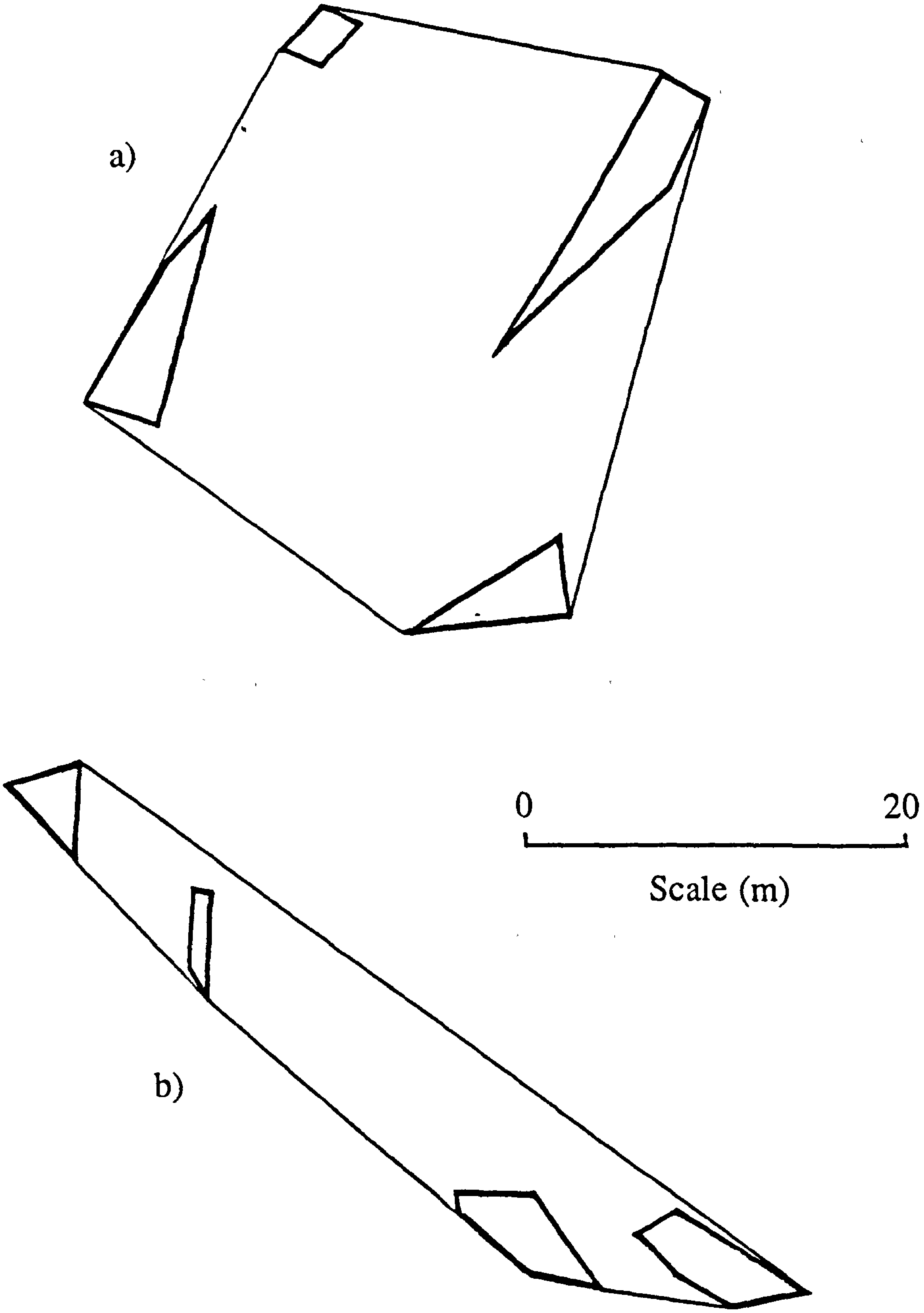


Fig.3.16. Examples of standardised ranges from non-breeding territorial robins showing low and high values of $\epsilon$, shown to the same scale.

a) F646516; $\epsilon$=0.22 Highly polygonal.
b) H227556; $\epsilon$=0.85 Highly linear.

Thick lines indicate core-nuclei, thin lines usual-areas.

There were no significant differences in the size or eccentricity of the usual-areas of territorial robins between age and sex classes (Mann-Whitney all ns $p<0.05$ level $n=43$). For age comparisons, birds were classed as adult or first year. There was no difference in the age structure of the groups of robins that were territorial and non-territorial (comparing first years with adults $\chi^2=0.02$ ns df=1, 53 % of territorial birds ($n=43$) and 50 % of non-territorial birds ($n=8$) were in their first year of life). Because most robins disappeared before they could be sexed in the breeding season the cell frequencies were too small to compare the sex ratios of the territorial and non-territorial portions of the populations. The available data however show that 35 % of the territorial birds were female ($n=20$) while 80 % of the non-territorial birds were female ($n=5$).

### 3.3.7. Range fidelity.

The assumption that the use of space is unchanging during the period of monitoring is inherent in all statistical ranges estimators (White & Garrot 1990). However ranges may change in a) size and b) location. These may be measured over the short term (days) or the long term (months), and may be gradual or abrupt. Ranges which do change in size and/or location indicate low fidelity.

The degree to which this assumption was correct was investigated using the grid-cell approach of Doncaster (1990). This technique is based on the utilization of grid-cells rather than the size and location of polygons. This allowed all of the locations in each sample to be used without losing any details of the range anatomy. All locations were assigned to 25 $m^2$ cells. This increased the number of cells that contained several locations without obscuring the overall configuration of the range (Doncaster 1990).

The grid cells occupied by an asymptotic sample of location estimates can be thought of as a cohort in a population. Between successive cohorts, new cells may be recruited and old cells "die" as they are abandoned. A range showing high fidelity to size but weak fidelity to location will leave a trail of "dead" cells across the habitat, while maintaining a constant area of live occupied cells (prevailing area), and a steadily increasing cumulative area. The number of cells surviving from the initial cohort (initial area) will eventually decrease to extinction.

No other data are currently available on range fidelity in small birds, so absolute values produced in this way as yet have little value. It was possible however to compare the relative degrees of range fidelity over the short term between individuals categorised as territorial and non-territorial using the definition described above.

The results for territorial and non-territorial ranges separated by a mean inter-cohort interval of 6.4 and 6.2 days respectively are shown in Fig 3.17. Ranges of both territorial and non-territorial individuals showed no change in their prevailing areas (Mann-Whitney U=14.5 ns, territorial n=10 non-territorial n=5). The non-territorial individuals, however, occupied new grid-cells and abandoned previously used cells approximately three times faster then territorial individuals (cumulative area Mann-Whitney U=0.0 $p<0.005$ territorial n=10 non-territorial n=5, initial area Mann-Whitney U=1.0 $p<0.005$ territorial n=10 non-territorial n=5). The ranges from territorial individuals showed high fidelity to both location and extent. Although size also remained relatively constant for the ranges of non-territorial individuals, their ranges showed low fidelity to location over the same time interval, indicating range drift (Doncaster 1990). An example of the relative range fidelity for concurrently tracked territorial and non-territorial individuals is shown in Fig 3.18., displayed using usual-area outlines.

Change in range fidelity is seen at its most dramatic during territory takeovers. Both range size and location can change drastically over just a few days. Since this is a rare, unpredictable and abrupt phenomenon, it is very difficult to record the changes in range use. One such takeover was recorded by radio-tracking however, and is illustrated in Fig.3.19.

For non-breeding territorial robins, usual-area was not correlated with day of year (day one set at 1st August)($r_s$=0.11 ns n=43), indicating high fidelity to range size. Ranges frequently revealed low fidelity to location however when viewed over several months. In some individuals this appeared to be highly directional territory drift. An example of such behaviour is shown in Fig 3.20.

Previous studies have described three periods of change in the space use of the robin over the course of the year; a) adult moult and juvenile dispersal; b) the establishment of non-breeding territories by adults and juveniles and c) the establishment of breeding territories by males and mate selection by females (Lack 1965, Cramp 1988). There are few data in this study with which to examine changes in the location and extent of ranges over the first two periods, however more information was available on the third stage; the change from non-breeding individual territories to breeding pair territories.

There was no significant difference between the usual-area of non-breeding and breeding individuals (Mann-Whitney W=116 ns non-breeding n=43, breeding n=6, non-

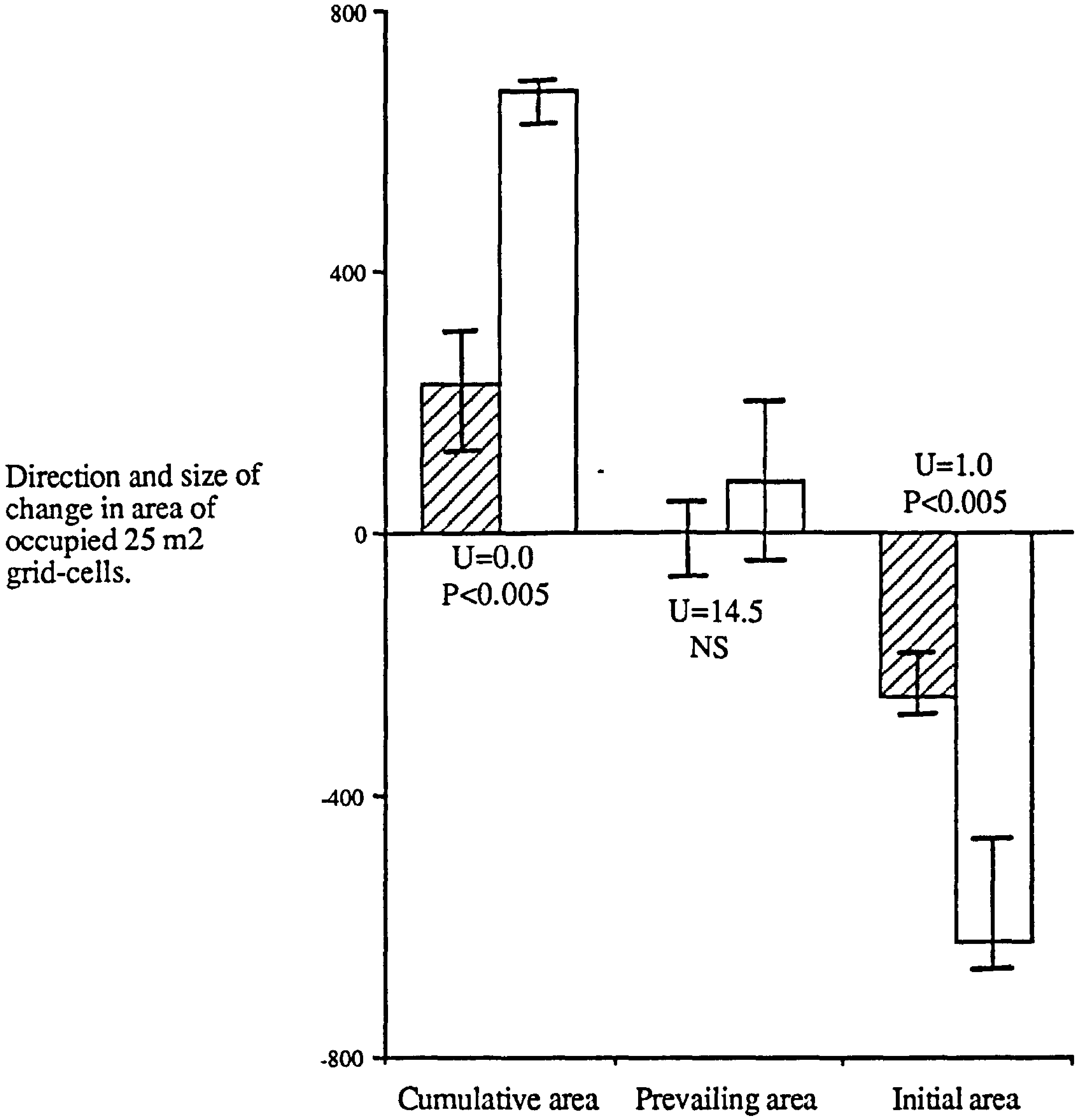


**Fig.3.17.** Comparison between the median short term change in area of 25m$^2$ grid-cells occupied by territorial (hatched)(n=10) and non-territorial (open)(n=5) non-breeding robins. Statistics and probability levels refer to one-tailed Mann-Whitney U tests, error bars indicate interquartile range. Mean inter-cohort interval (the interval between the completion of data collection for the first standardised range and the beginning of the second) was 6.4 days (territorial) and 6.2 days (non-territorial). Taking the decrease in area of the initial cohort as an estimate of range fidelity, territorial ranges changed by 39 m$^2$ day$^{-1}$ while non-territorial ranges changed by 108 m$^2$ day$^{-1}$.

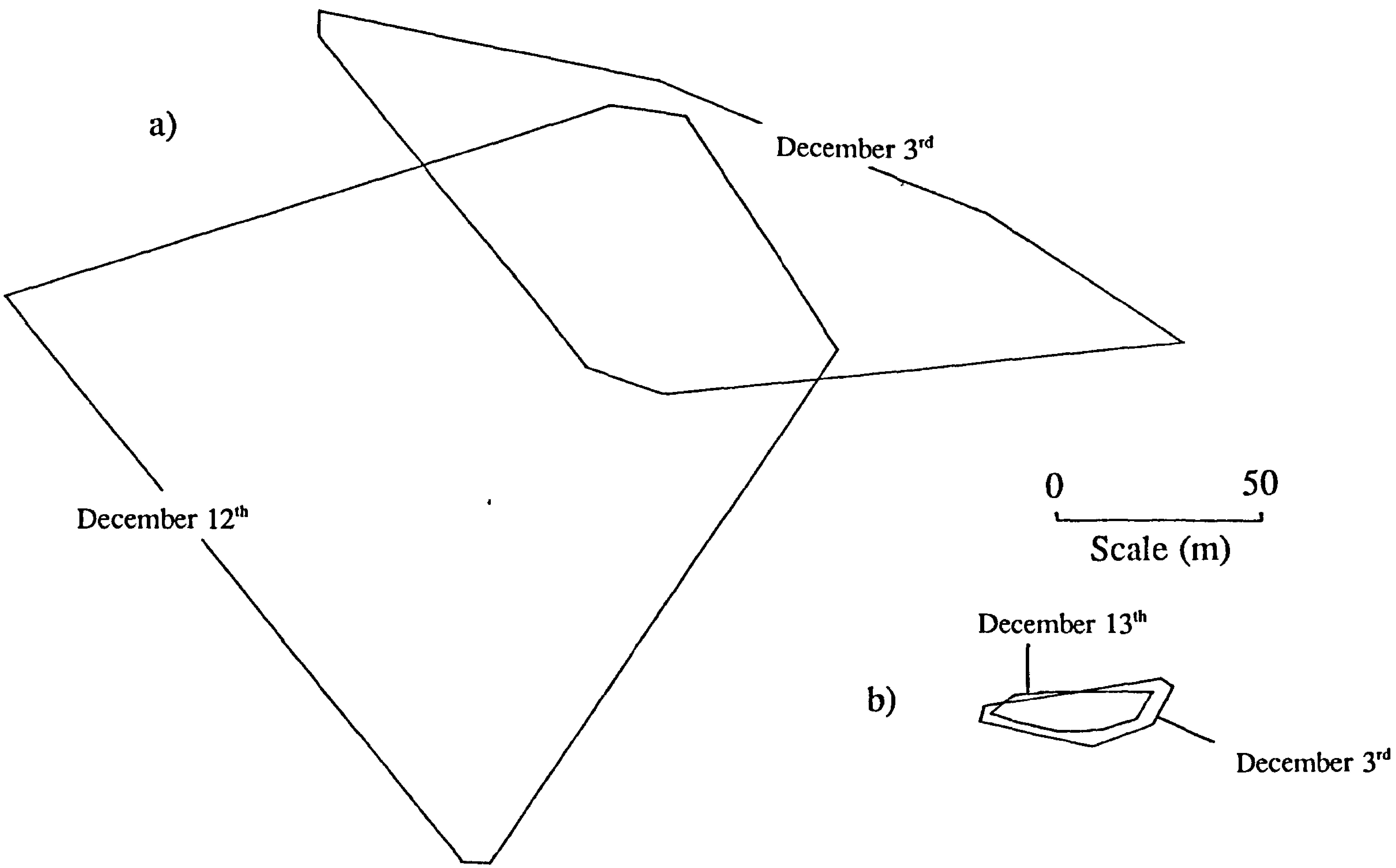


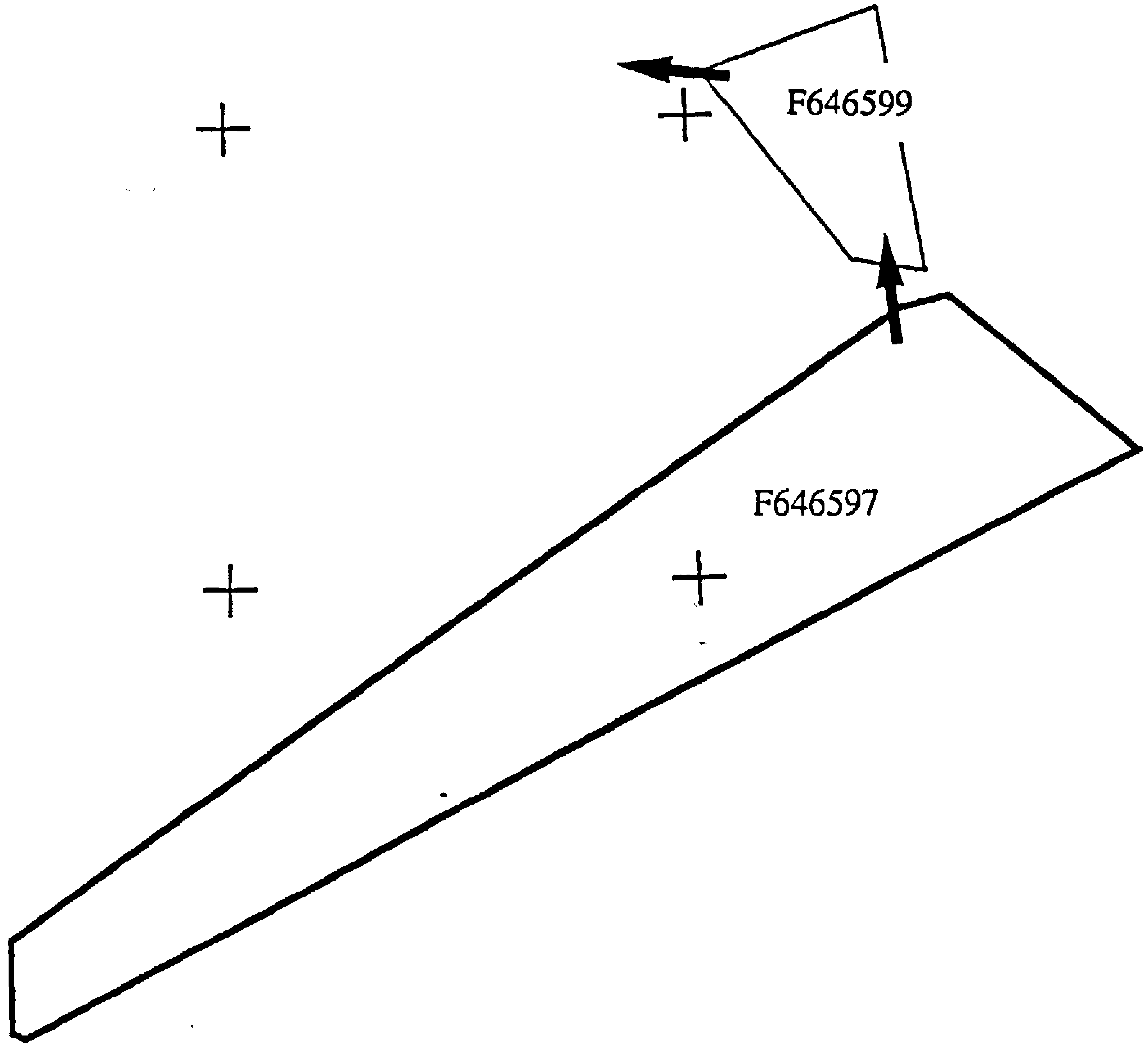
**Fig.3.18.** Examples of short term range fidelity in non-breeding robins, shown to the same scale. Dates indicate the first day of data collection for each range.

a) H227558; non-territorial, intercohort interval equals three days.
b) F646594; territorial, intercohort interval equals five days.

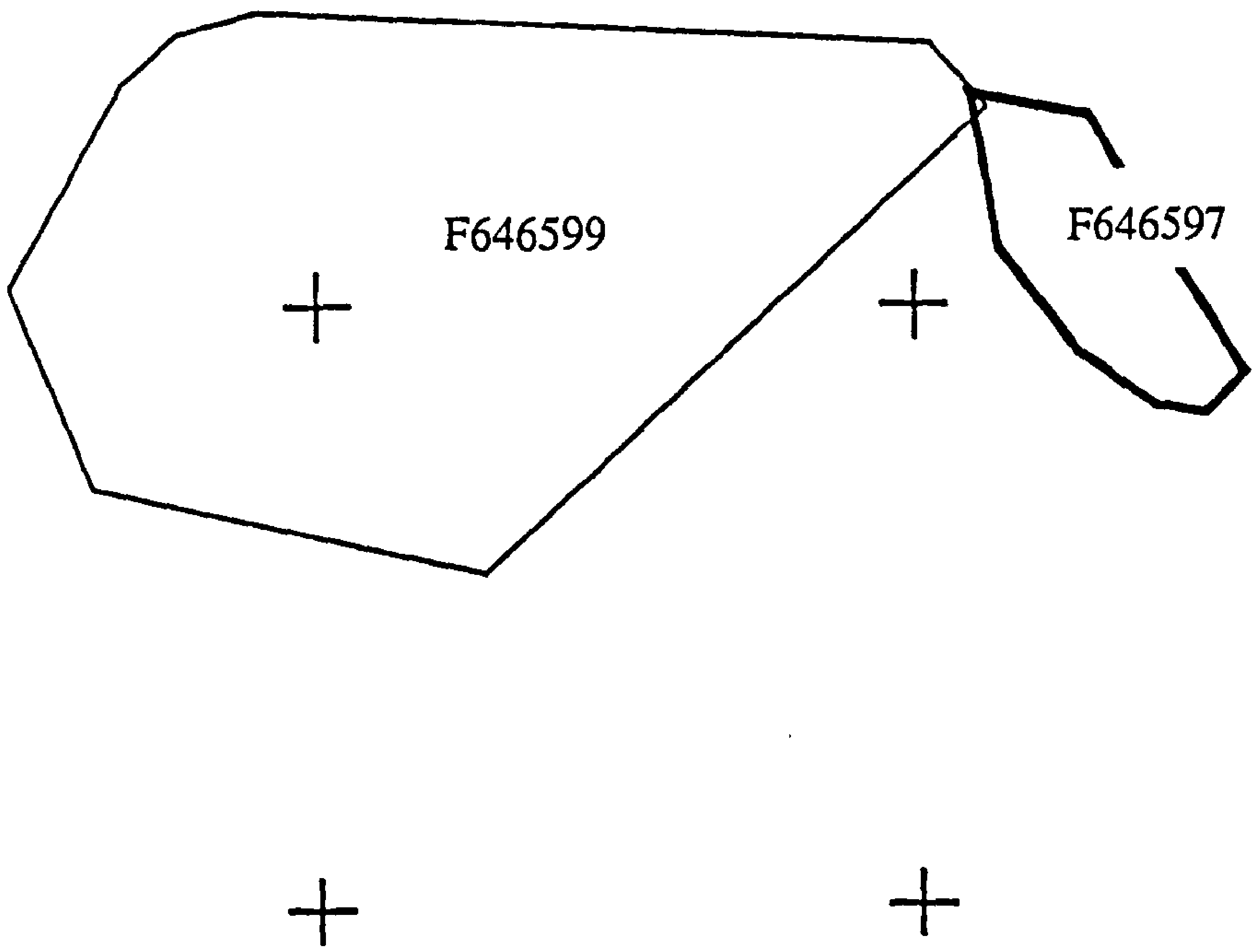
Outlines indicate usual-areas to emphasise consistent or inconsistent locations of the core-nuclei they enclose.

**Fig.3.19.** An example of a territorial takeover in non-breeding robins, recorded by radio-tracking. Between the 18th October (a) and the 24th October (b), non-territorial robin F646597 (thick outline) moved onto the area occupied by robin F646599 (thin outline) and became territorial. F646599 consequently became non-territorial, as indicated by the changes in usual-area. Arrows indicate the directions of range drift. The crosses mark the corners of a reference hectare on the map grid.

a) 18th October



b) 24th October



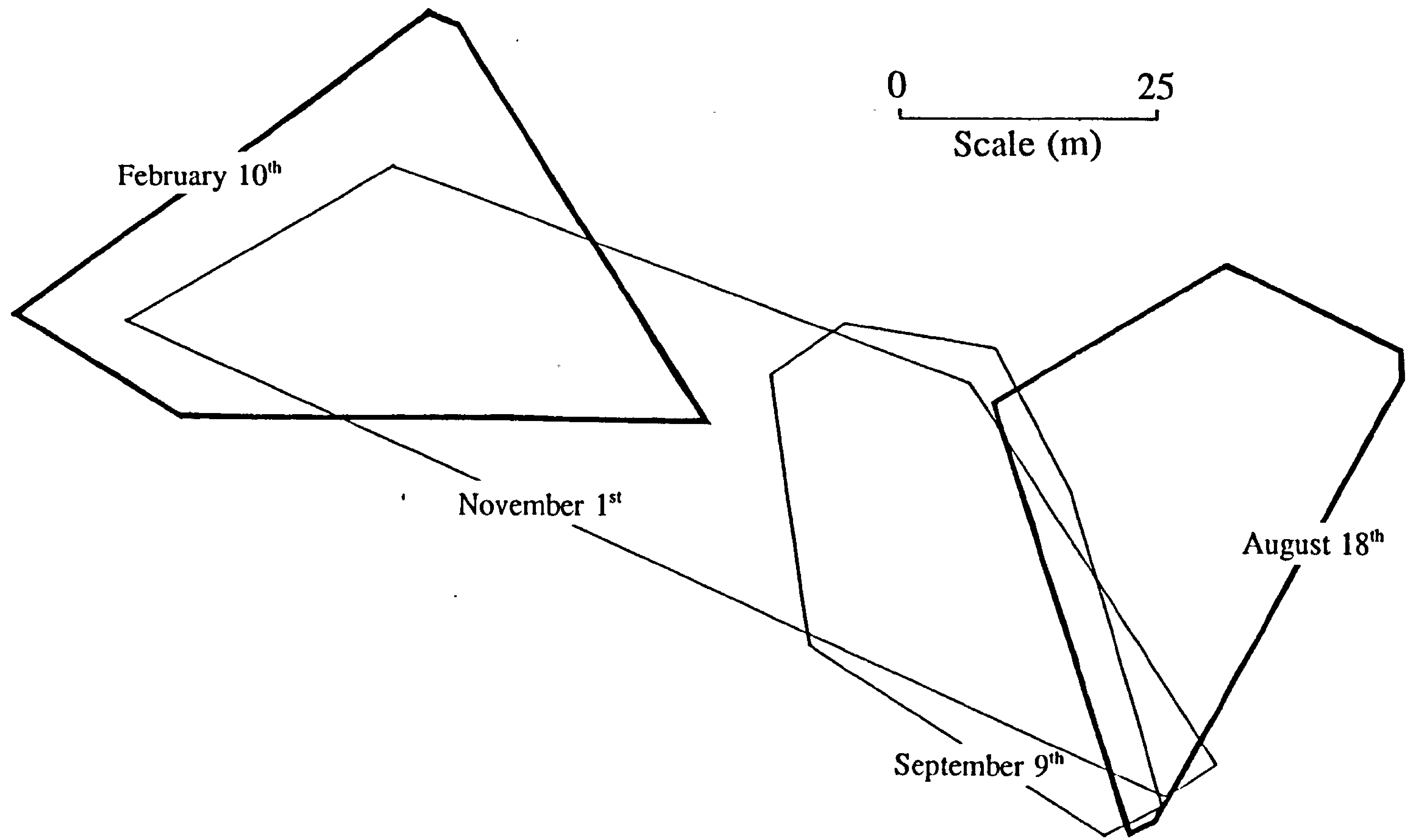


**Fig.3.20.** Example of long term directional range drift by a 2nd year male robin between August 1991 and February 1992. Outlines indicate the usual-areas. The first range was occupied during late primary moult and the last during the breeding season.

breeding median=468 $m^2$ range 60-2495, breeding median 485 $m^2$ range 327-2138). The beginning of the breeding season was characterised by an abrupt and synchronised surge in territorial advertisement behaviour (Fig 3.21.). One male which had moved onto the territory of and paired with a neighbouring female began singing on 28th January, approximately 20 days before the majority of the population. This individual was predated by a sparrowhawk on the second day, and illustrates the potential cost of advertisement by song. Over this period most territorial males showed no change in the extent of their usual-area (Fig.3.22.a.). A few males however showed a short lived phase during which their usual-areas were typical of those occupied by non-territorial birds (Fig 3.22.a.). An example of such "pre-territorial" male behaviour is shown in Fig 3.23. Migrant males which arrived in the study area at around this time initially appeared to go through a similar pre-territorial phase before settling on a breeding territory (Fig 3.22.a.).

All resident females abandoned their territories and occupied non-territorial drifting ranges (Fig 3.22.b.), before pairing with a male and sharing its territory. Examples of the changes in location and extent of the usual-areas during the preceding Autumn and Winter of a male and female which subsequently paired are shown in Fig 3.24.

### 3.3.8. The individual within the neighbourhood.

The understanding of neighbourhoods requires neighbours to be identified. Previous studies have used qualitative definitions such as looking for common boundaries between the territories of different individuals. Because radio-tracking can provide a rigorous definition of a territory however, a similarly rigorous definition can be constructed for the categorisation of neighbours.

The simplest model of a neighbourhood of polygonal territories consists of close packed regular polygons of similar size (Fig 3.25.a.). Each territory has a diameter d, the diameter of a circle of equivalent area. Near neighbours are those territories that are accessible within a distance 1.5d from the centre of the focal territory, excluding those that are separated by an intervening territory. Far neighbours may be defined as those other than near neighbours. This definition, however, is inadequate when some territories show high eccentricity. The number of near neighbours will be underestimated near the poles of an eccentric focal territory (Fig 3.25.b.). In addition, large territories will have a greater region of influence within which neighbours may occur, than small territories. This will lead to an

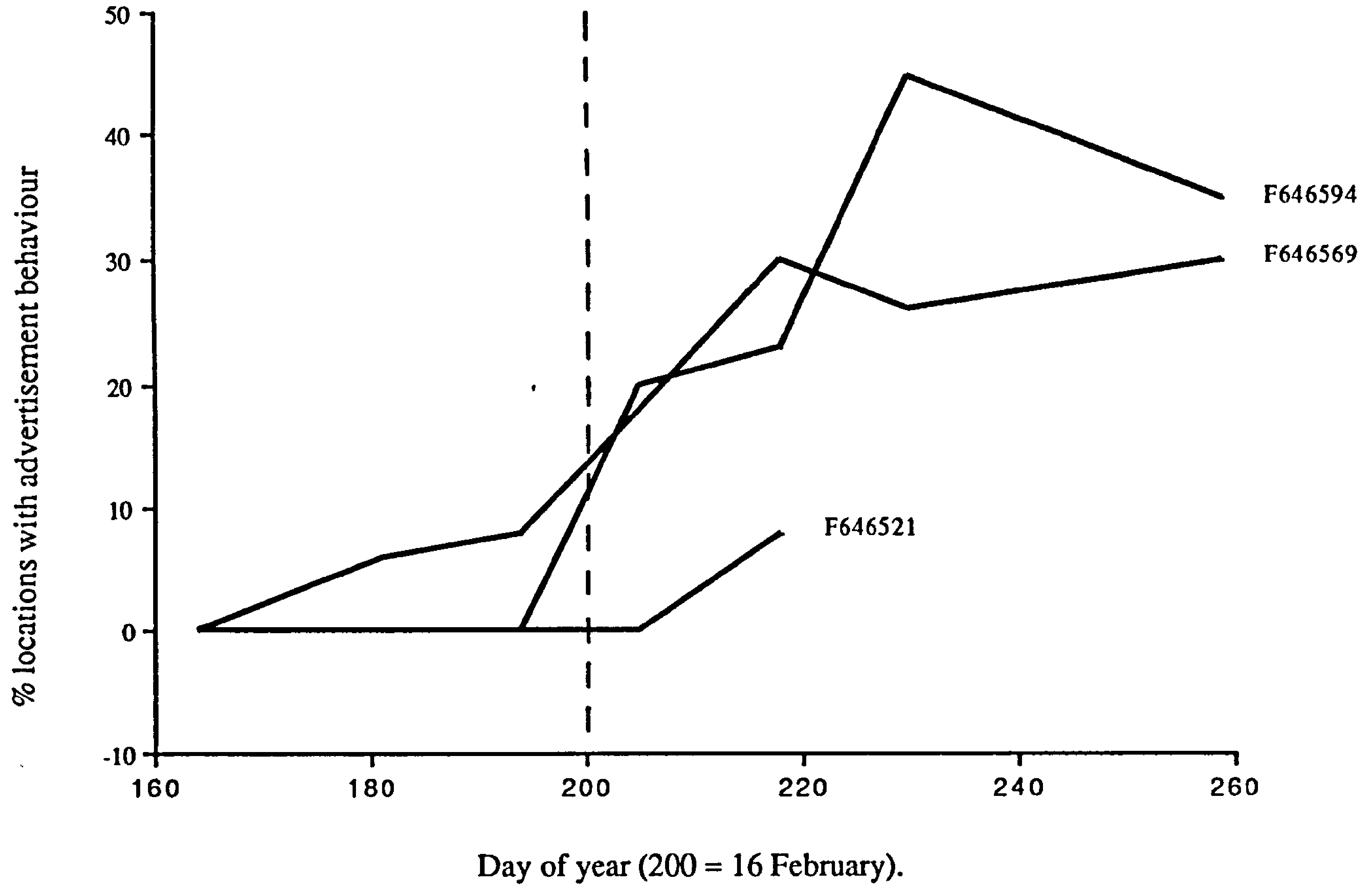


**Fig.3.21.** The surge in territorial advertisement and defense behaviour in male robins associated with the onset of the breeding season in the spring. The lines show data from three resident individuals.

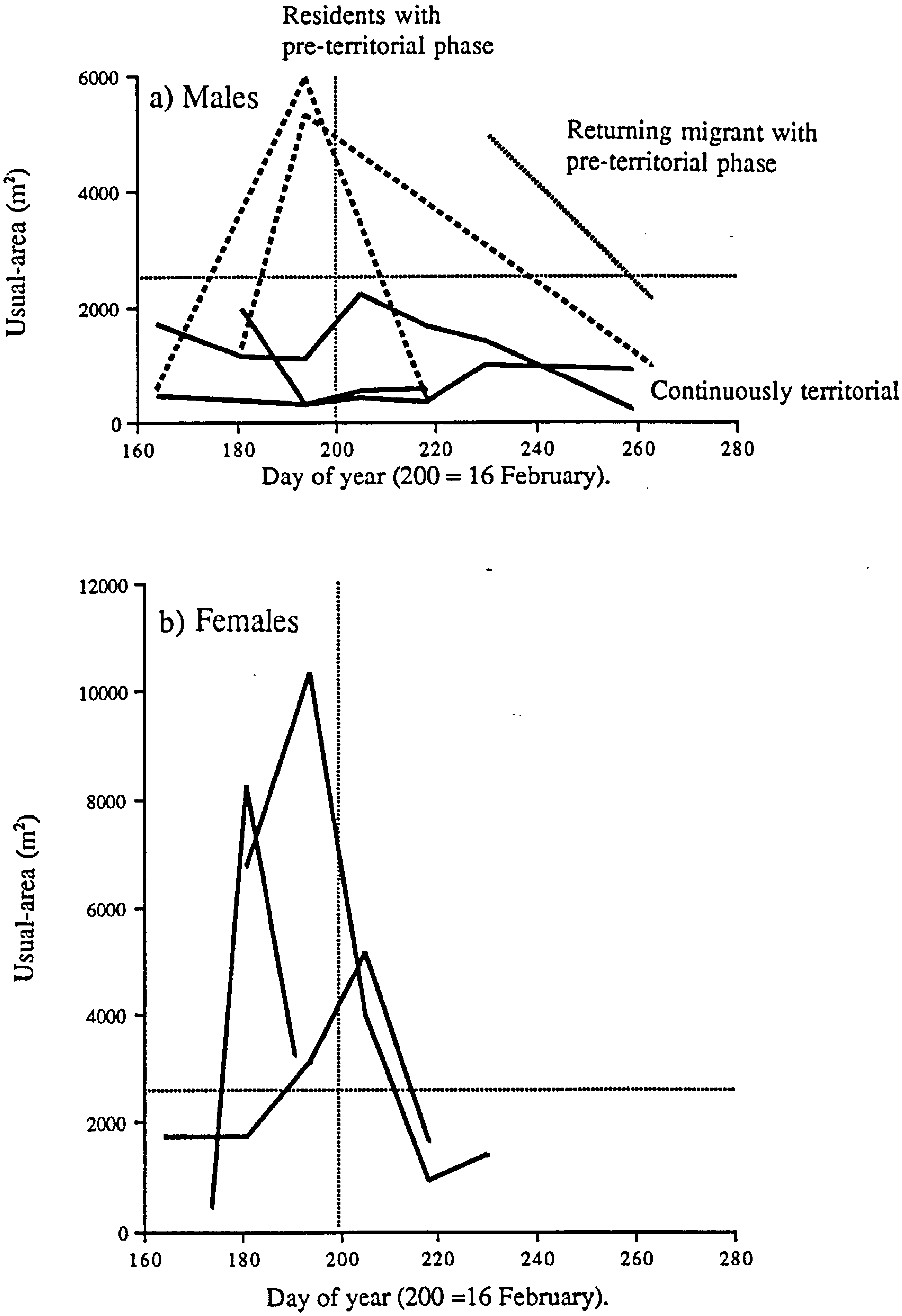


**Fig.3.22.** Changes in the usual-area of individual robins over the period in which the spring song surge occurs. The males can be divided into three categories on the basis of changes in fidelity to the usual-area they occupy (a). All females undergo a non-territorial phase during this period as they search for mates (b). The horizontal line indicates the cut-off between territorial and non-territorial range size while the vertical line indicates the onset of spring song in males. Other lines indicate range use histories for different individuals.

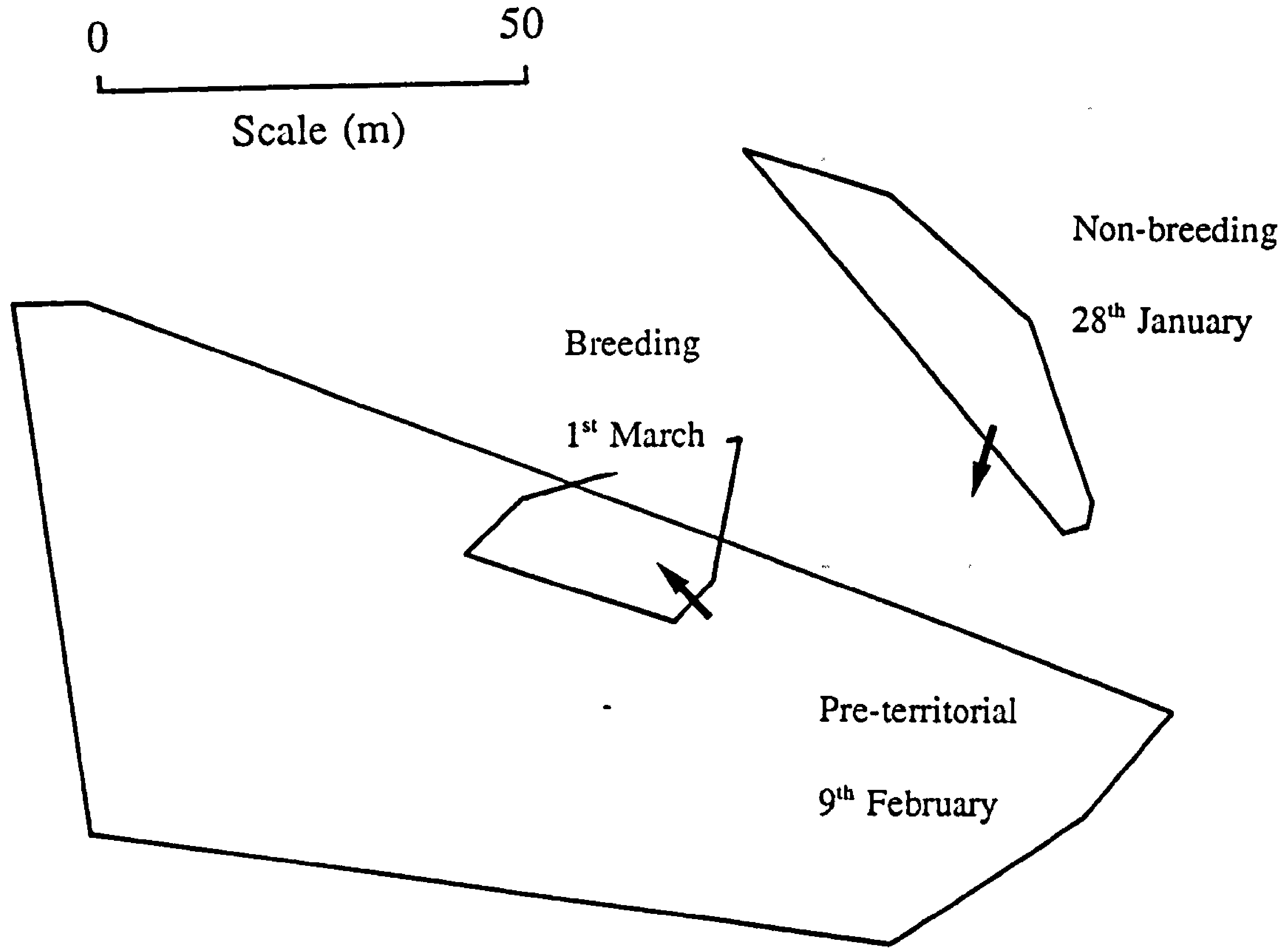
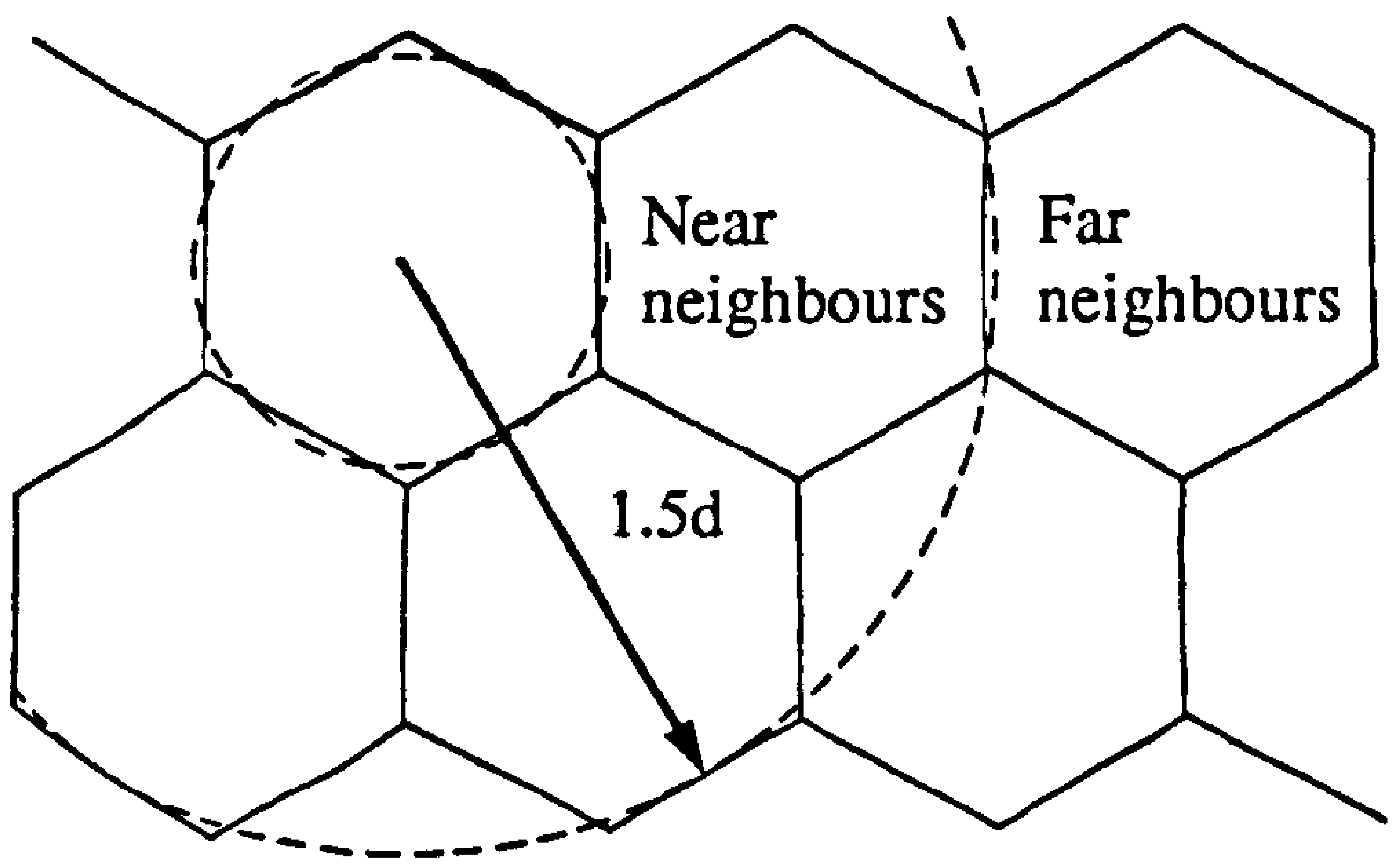


**Fig.3.23.** Example of the range drift associated with the spring song surge shown by a resident male robin that exhibited a pre-territorial phase between non-breeding and breeding territoriality.

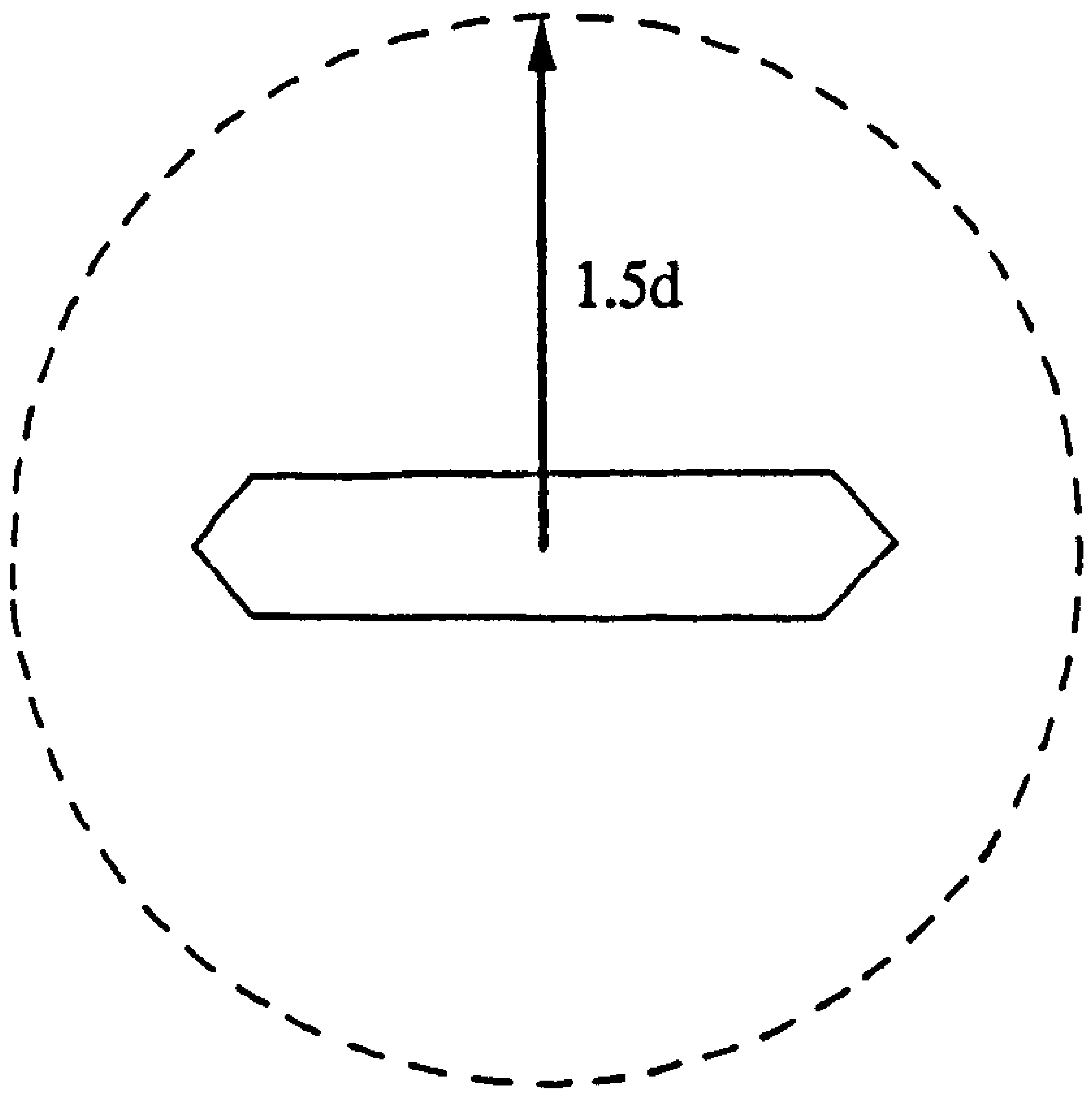
**Fig.3.24.** Range use histories for a male and female robin during the Autumn preceding their pairing in spring. Both birds were initially territorial. Thin lines indicate the usual-areas of continuously territorial male F646594. The thick line indicates the usual-areas occupied during the nomadic wandering of female F646582. These ranges lay largely outside the cluster of territories containing F646594. Arrows indicate the direction of range drift.

**Fig.3.25.** The development of a definition that enables neighbours to be classified according to the spacing of local territories.

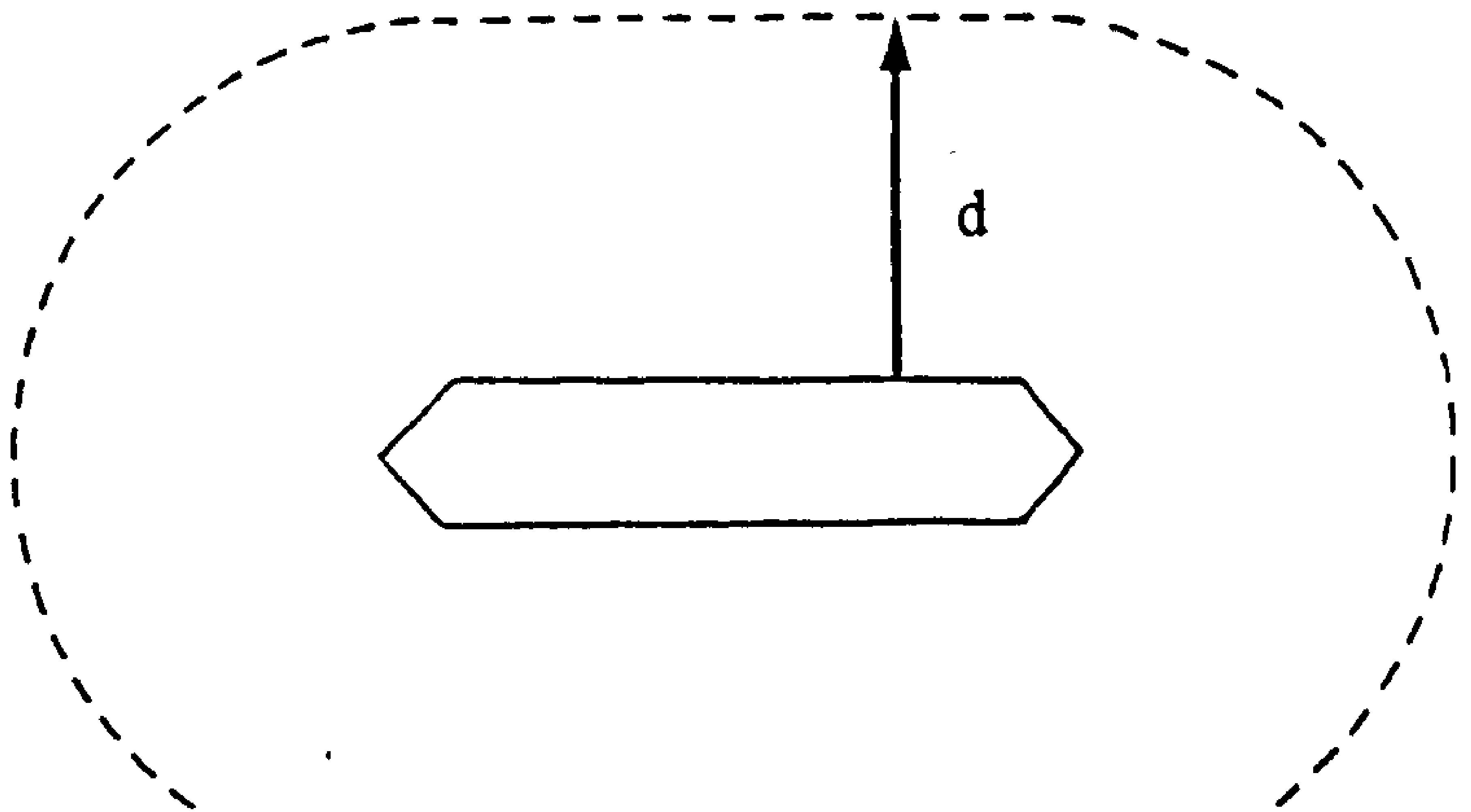
a) The simplest model of a neighbourhood of polygonal territories consists of close packed regular polygons of similar size. The near neighbours of a focal territory will lay within 1.5 territory diameters (d) of the centre of the territory and will not be separated from it by any intermediate territories. Each territory here has six near neighbours.



b) However this definition is insufficient when territories show high eccentricity, the number of near neighbours being underestimated near the poles of the focal territory.



c) Modification of the definition such that near neighbours lay within one "standard" territory diameter of the edge of the focal territory will overcome this problem, and will allow consistent estimation of the number of near neighbours for any configuration and size of territory.



overestimation of the number of near neighbours. Modification of the definition such that the near neighbours lay within one standard territory diameter from the edge of the focal territory will overcome this problem, and allow consistent identification of near neighbours and far neighbours for any size and shape of territory (Fig.3.25.c.). In this study a standard territory was a regular hexagon of area equal to the median usual-range area of a territorial individual, which corresponded to a circle of diameter 25 m. This value has biological meaning, representing the maximum movement distance that a robin can make within a radially symmetrical usual-area of median size.

The number of near neighbours was determined by estimating the number of usual-areas in which all or some of their edges lay within 25 m of the edge of each focal territory. Territories further than this distance were classed as far neighbours even if there were no intervening territories. The usual-areas of non-territorial individuals were not considered to have neighbours nor be a neighbour of a territorial individual. This is because they were characterised by rapid range drift, leading to an overestimate of the number of near neighbours they had at any one time. Not all of the territorial birds in the study area could be tracked concurrently. Since territorial individuals showed high fidelity to the location they occupied however, estimates of the location and extent of territories based on usual-areas from the previous month, or defended-areas alone, were used when assessing the number of near neighbours. In practice, the precise locations of the territory edges were only needed for the minority of cases which fell close to the 25m cutoff distance from the edge of a focal territory. Because tracking was often carried out on clusters of territories and the advertisement behaviour of birds that were not tracked was also recorded, all neighbours could be categorised.

There was no pattern to the number of near neighbours each individual experienced, except than none had the six near neighbours that would be expected if territories were close packed regular hexagons (Fig 3.26.).

The percentage polygon overlap of the different measures of utilization distribution between dyads of concurrently tracked near neighbours are shown in Table 3.5. The term dyad is used to refer to two individuals, to avoid confusion with the term pair used to describe birds during breeding. As described above, polygon overlap is the area of one polygon which lays within the edges of another. When measuring the overlap between near neighbours, each dyad only contributed one overlap value to the sample to ensure statistical

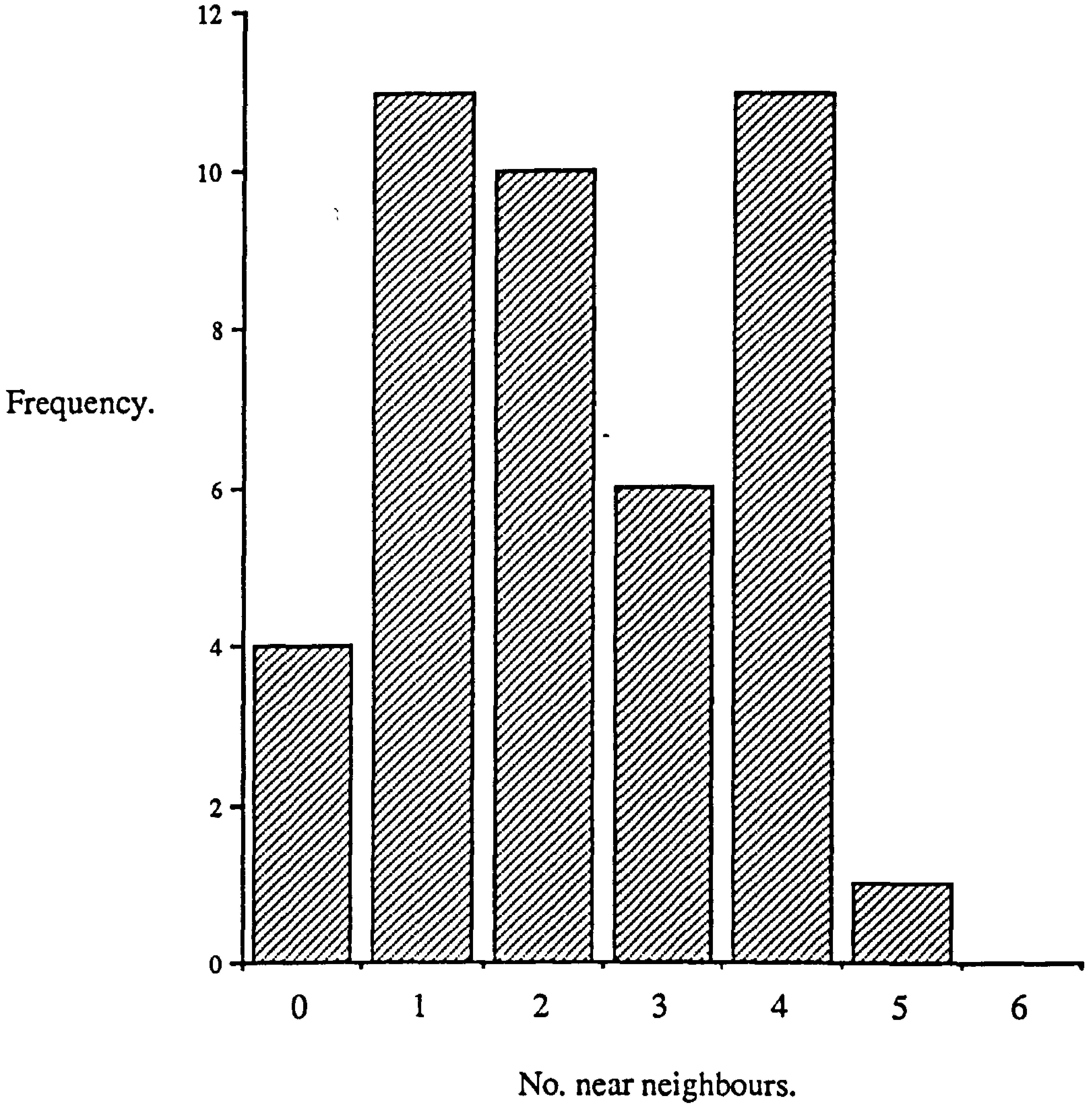


**Fig.3.26.** Frequency distribution of the number of near neighbours experienced by each non-breeding territorial robin (n=43).

**Table 3.5.** Median polygon overlap of the different measures of range use between dyads of near neighbours.

| Types of polygon in dyad and direction of overlap | % polygon overlap* | | No. dyads in sample |
|---|---|---|---|
| | Median | Range | |
| Maximum-area on maximum-area | 32 | 0-83 | 16 |
| Maximum-area on usual-area | 0 | 0-68 | 16 |
| Usual-area on usual-area | 0 | 0-4 | 16 |
| Defended-area on defended-area | 0 | 0 | 7 |

* The % area of the second named polygon which is overlapped by the first.

independence. The degrees of overlap of the different measures of range use on near neighbours were different. The maximum-areas of near neighbours showed considerable polygon overlap. The usual-areas and defended-areas, however, never overlapped. The maximum-areas showed no median overlap with the usual-areas of near neighbours. The median distance between the usual-areas of near neighbours was 12 m (range 1-23 n=16), nearly half the diameter of a standard territory. The interstices between the usual-areas of near neighbours were considered to be undefended neutral ground. This contained habitat features that were apparently indistinguishable from those in which core-nuclei were sited. The usual-areas of a group of territorial robins over a 12 day period is illustrated in Fig 3.27. During this period minimal range drift will have occurred, and so the usual-area outlines are comparable. Note the unoccupied habitat features located in the interstices between the usual-areas.

A second analysis of the degree of overlap between near neighbours was carried out using the measure of static interaction developed by Doncaster (1990). This can provide information on the degree to which the occupied grid-cells of two ranges overlap, and also whether the shared area contains the most or least utilized cells of each range. Since the technique is based on the positions of the grid-cells occupied by the locations, it can reveal more detail about how the internal structure of the ranges interact than can polygon outline techniques with their associated assumptions.

Locations were assigned to 25 $m^2$ grid-cells to increase the number of observations per cell. The number of cells visited by both birds gives a simple estimate of the grid-cell overlap between the members of the dyad. Spearmans' correlation coefficient was then calculated from the pairs of cell frequencies for all the cells visited by one or both birds. This tests for correlation between the two ranges. The value of the correlation in part depends on the degree of grid-cell overlap between the members of the dyad. It was clear that most dyads shared very few grid-cells (Table 3.6.). The interpretation of the values of $r_s$ for such small degrees of overlap is difficult, however the following values from Doncaster (1990) can be used as a guide. If for two ranges of the same size, the shared area contained the most utilized cells of each range, $r_s$ would be approximately -0.4. If the shared area contained the least utilized cells of one or both ranges, $r_s$ would be approximately -0.8. $r_s$ equals -0.86 if no cells are shared. The observed values of -0.7 to -0.8 indicated heavily utilized cells are never shared by neighbours. For comparison the value for a dyad during mate-guarding of a female by its

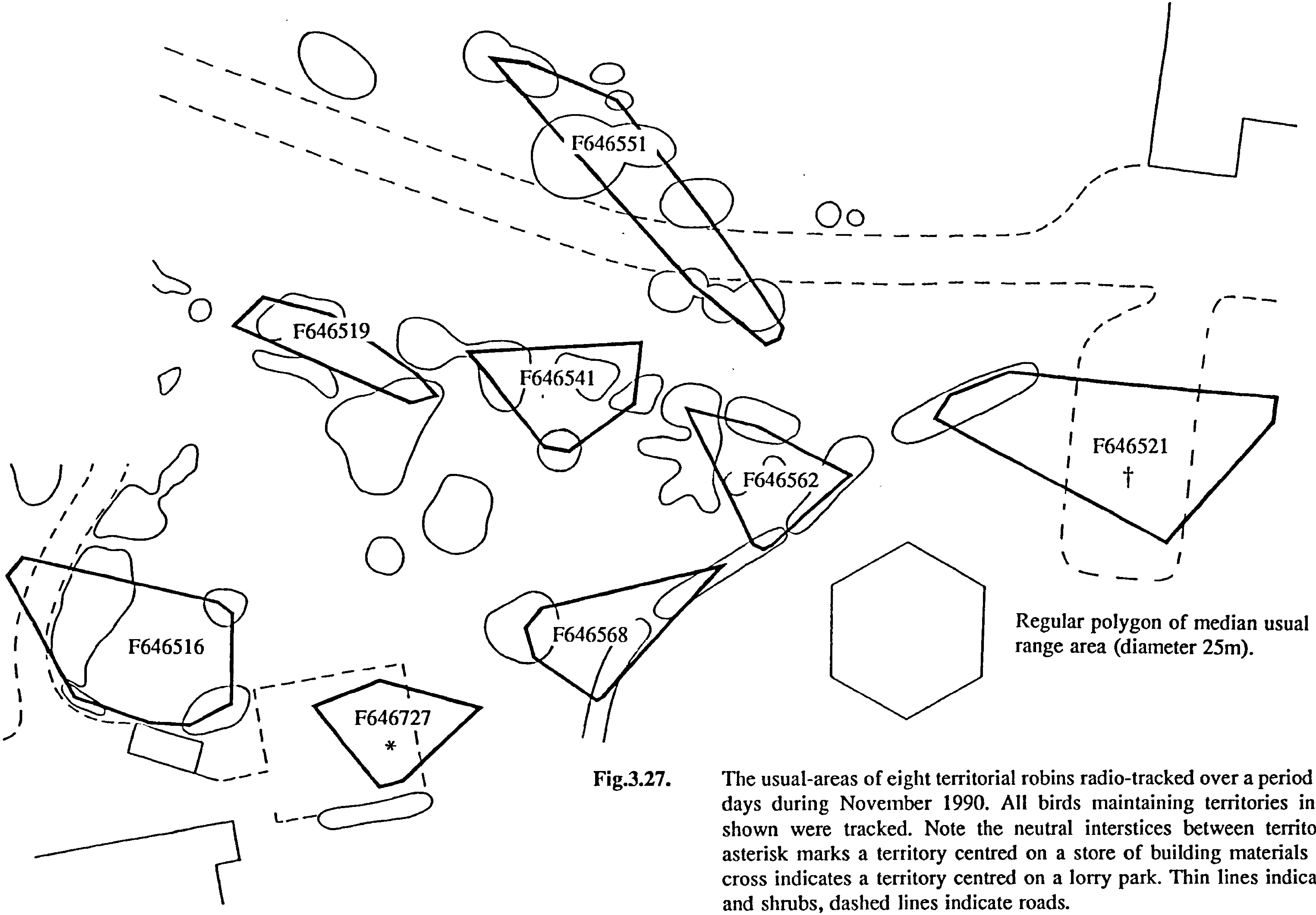


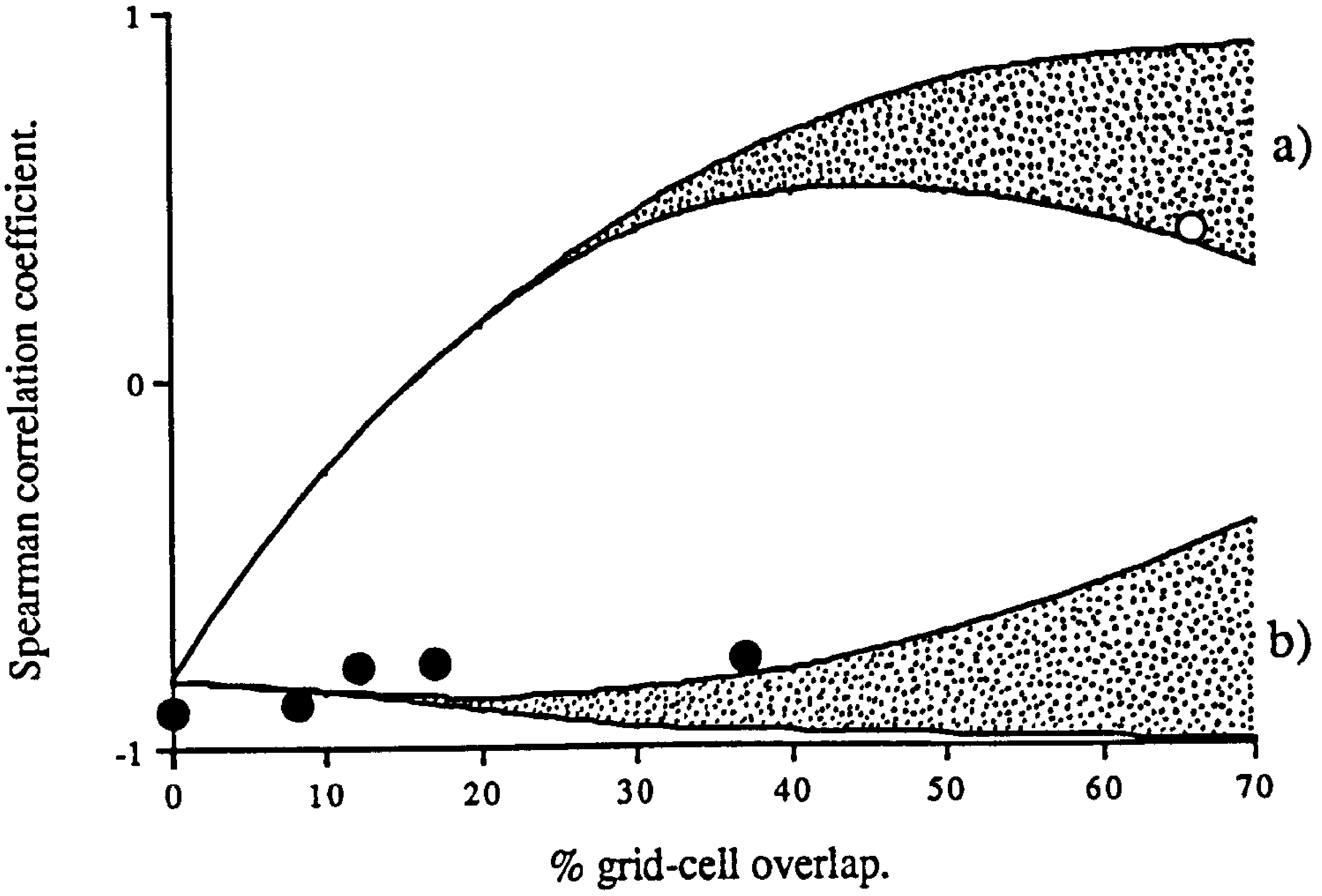
**Fig.3.27.** The usual-areas of eight territorial robins radio-tracked over a period of twelve days during November 1990. All birds maintaining territories in the area shown were tracked. Note the neutral interstices between territories. The asterisk marks a territory centred on a store of building materials while the cross indicates a territory centred on a lorry park. Thin lines indicate bushes and shrubs, dashed lines indicate roads.

**Table 3.6.** Static interaction between dyads of territorial robins measured using Spearman correlation and measures of range overlap using occupied grid-cells and minimum convex polygons.

| Stage of annual cycle<br>Members of dyad# | $r_s$ * | % overlap | |
|---|---|---|---|
| | | Occupied grid-cells | Maximum-area polygon |
| **Non-breeding** | | | |
| F646583/F646579 | -0.76 | 37 (35-39) | 65 (56-73) |
| F646540/F646551 | -0.77 | 17 (15-18) | 60 (52-68) |
| F646551/F646581 | -0.78 | 12 (11-13) | 56 (45-67) |
| F646590/F646587 | -0.88 | 8 (7-8) | 63 (42-83) |
| F646727/F646568 | -0.90 | 0 | 52 (45-59) |
| **Mate-guarding** | | | |
| F646581/H227560 | 0.40 | 66 (57-75) | 93 (89-97) |

\# Individuals included twice came from different years.

* Probability levels not important.



**Appendix to Table 3.6.** Graphical presentation of the data in Table 3.6. Spearman's correlation coefficient between the intensity with which dyads of territorial robins used areas of grid-cell overlap in their ranges plotted against the % grid-cell overlap. Closed symbols represent non-breeding near neighbours and the open symbol represents a pair during mate-guarding. The two shaded areas show the theoretical distributions of $r_s$ based on Doncaster (1990) and adapted from Tew & Macdonald (1994), that would correspond to sharing of the most utilized (a) and the least utilized (b) grid-cells within ranges.

Tew T.E. & Macdonald D.W. (1994). Dynamics of space use and male vigour amongst wood mice *Apodemus sylvaticus*, in the cereal ecosystem. **Behav. Ecol. Sociobiol.** 34 337-345.

mate indicates the sharing of heavily utilized cells. On comparing the results of polygon overlap and static interaction, it was found that in one dyad, although the maximum-areas showed substantial overlap, the two birds visited none of the same 25 $m^2$ grid-cells.

Individuals classed as non-territorial used very large usual-areas relative to those that were territorial, and frequently ranged outside the main study area. In addition, because of the rapid range drift typical of non-territorial individuals it was not possible to identify dyads of near neighbours with any degree of confidence. Therefore a quantitative assessment of polygon overlap or static interaction was not possible. On plotting all the usual-areas of non-territorial and territorial robins using the same general area over a two month period, however, it was apparent that although the usual-areas of non-territorial birds often overlapped those of some territorial birds, they never ranged over the area most densely populated by territorial birds (Fig 3.28.).

From measuring short term fidelity, it was clear that the usual-areas of territorial robins maintained a constant size. This was also found to be true over the whole non-breeding season ($r_s$=0.11 n=43). The number of near neighbours and therefore local population density, however, decreased with day of year over the course of the Autumn and Winter ($r_s$=-0.40 p<0.01 n=43). This reflected the decline in population size during this period due to natural mortality.

### 3.3.9. Excursive activity.

For territorial birds, locations which occurred outside the usual-area were considered to be excursive. The excursive area therefore was the maximum-area minus the usual-area. On average 21 % of locations were excursive (range 7-45 n=43). The positions of excursive locations in relation to the neighbourhood could be allocated to a number of different categories; a) neutral interstices between territories and b) the usual-areas of neighbours; which included i) the usual-areas of near neighbours and ii) the usual-areas of far neighbours. A mean of 6 % of locations were in the usual-ranges of neighbours (min 0 max 35 n=43). The strengths of the relationships between the different measures of excursive activity and number of near neighbours (an estimate of local population density) are shown in Table 3.7. As excursive area increased with decreasing local population density, the percentage of locations that were excursive remained constant. Of the excursive locations, three quarters were in the neutral interstices between territories and only one quarter inside neighbouring

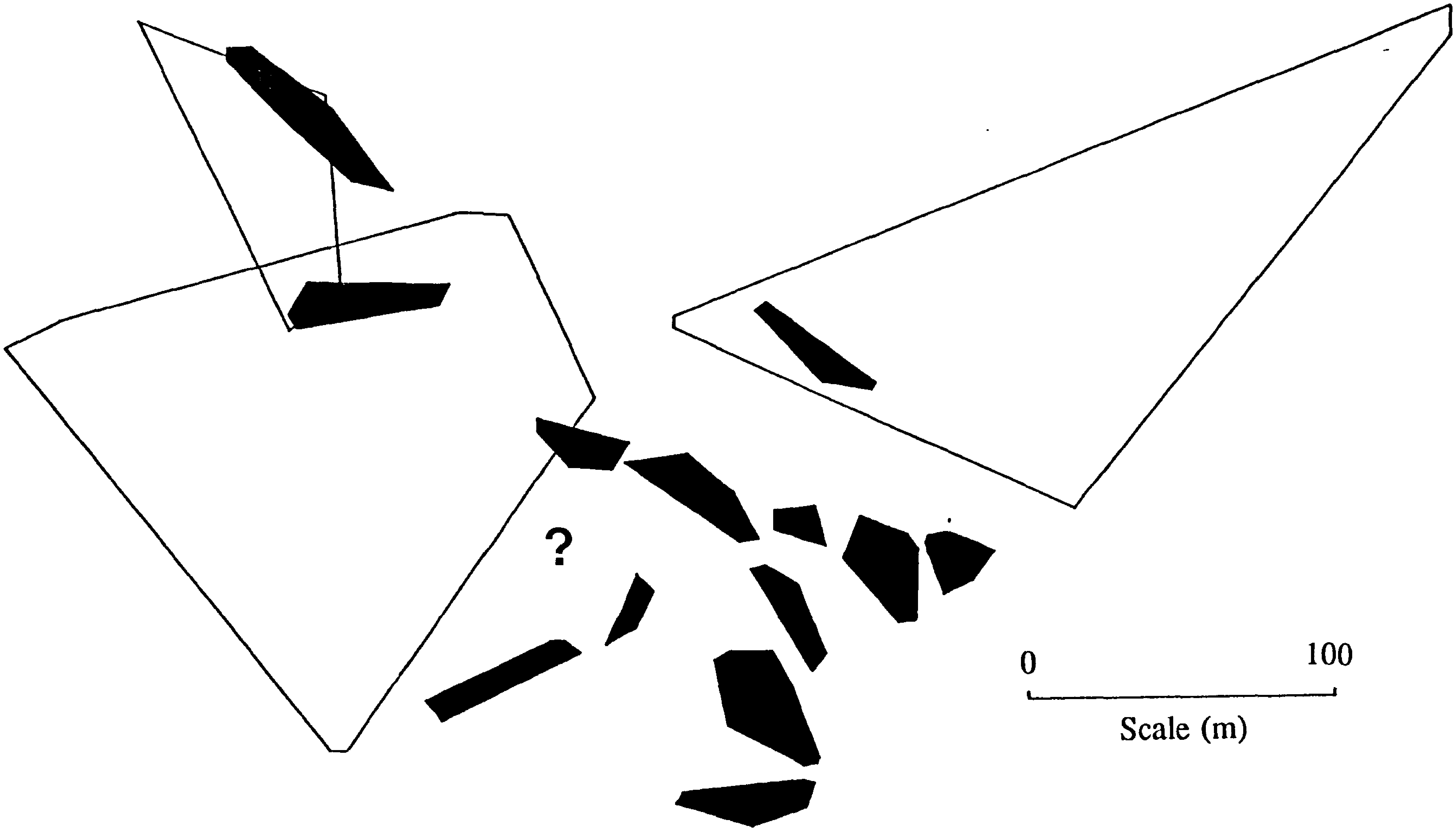


**Fig.3.28.** Usual-areas observed by radio-tracking during November and December 1991. All robins except one territorial individual, indicated by a question mark, were monitored. Solid ranges denote territorial individuals, open ranges denote non-territorial individuals. The territories are clustered in the block of woodland in the Biolerhouse Wood study area (Fig.2.1.).

**Table 3.7.** Correlations between number of near neighbours, an estimate of local population density, and different measures of excursive activity (n=43). The value in parentheses excludes an obvious outlying point.

| Measure of excursive activity | $r_s$ |
|---|---|
| Usual-area ($m^2$) | -0.16 |
| Excursive area ($m^2$) | -0.51 *** |
| % locations that were excursive | -0.01 |
| % locations that were in neutral interstices | -0.08 |
| % locations that were in neighbours | -0.08 |
| % locations that were in near neighbours | 0.27 *<br>(0.32 **) |
| % locations that were in far neighbours | -0.33 ** |

* $p<0.1$ ** $p<0.05$ *** $p<0.005$

territories. Furthermore, as local population density decreased, the robins showed the same probability of being located during intrusive activity. This came about by the shifting of intrusive activity into the territories of far neighbours.

### 3.3.10 Roost selection.

The robins were never active dusk despite some of the study area being continually illuminated by security lights. The vast majority of territorial birds preferred roost sites in habitat features similar to those which contained core-nuclei. Of 43 individuals, each contributing one randomly selected roost night to the sample, 98 % of sites were in bushes and shrubs and only 2 % in sites away from such vegetation (chi-square goodness-of-fit test $\chi^2=44.08$ 1df $p<0.005$ n=43). When roosting in vegetation, sites were nearly always from one to three metres above ground, only occasionally selecting sites low in the canopy of larger trees. On the rare occasions when birds were located visually, they were perched on thin branches away from the foliage of the bushes. Most sites were however thought to be among dense clusters of leaves (Fig.3.29.a.). Sites away from shrubs and bushes were in holes on the ground. These included rabbit burrows (Fig.3.29.b.) and abandoned mouse holes in drifts of dead leaves (Fig.3.29.c.). Similar behaviour was shown by the non-territorial birds although the sample size was too small for statistical analysis. Non-territorial birds were excluded from analysis of roost selection in relation to the usual-area because of their low fidelity to range location and the small number of individuals monitored.

There was no marked tendency for territorial birds to prefer sites in their own usual-ranges (51 %) over excursive sites (49 %) (Chi-square Goodness-of-fit test $\chi^2=0.33$ 1df ns n=43). The quality of sites used by robins which roosted on their own usual-area and in excursive locations is shown in Table 3.8. The cell frequencies were too low for statistical comparison, however it was apparent that birds which roosted excursively were more likely to obtain sites in medium density vegetation such as *Rhododendron* and broom suggesting that these may represent the sites of highest quality. Of those sites that were outside the usual-area however, there was a significant tendency for birds to select sites in neutral interstices (77 %) rather than sites in the usual-areas of neighbours (23 %), (chi square goodness-of-fit test $\chi^2=6.55$ 1df $p<0.05$ n=22). This sometimes resulted in the formation of communal roosts containing two to three robins within a few metres of each other in the same bush. Robins may therefore leave their daytime territories at dusk to congregate in roost sites of high

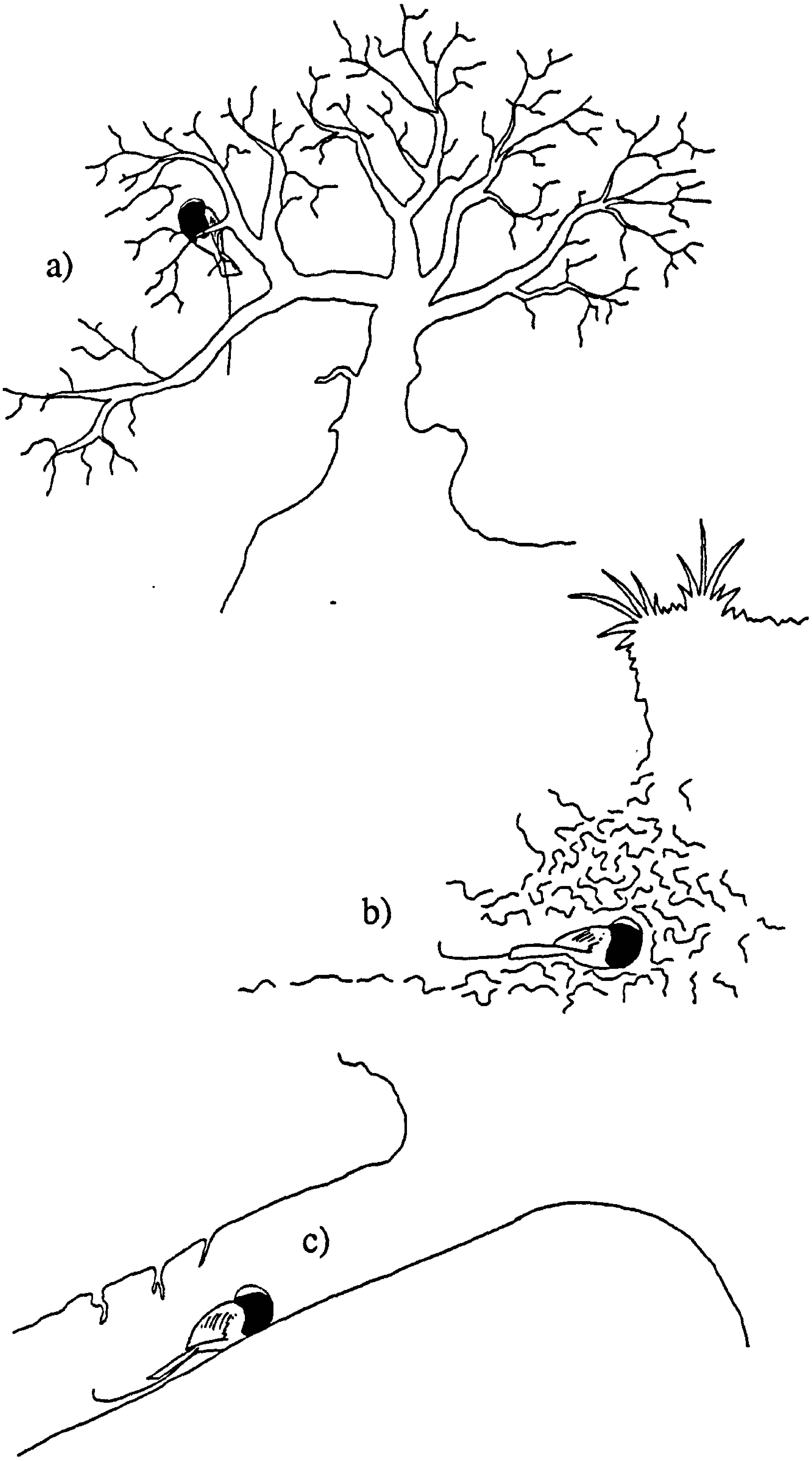


**Fig.3.29.** A diagrammatic summary of the types of roost site used by robins during the non-breeding season. Most frequently used were sites in bushes and shrubs (a). During very cold weather robins were located roosting in drifts of dead leaves (b) and in rabbit burrows (c).

**Table 3.8.** The quality of sites selected by territorial robins which roosted within their own usual-area or excursively. Only one randomly selected roost night was included from each individual.

| Category of site * | In own usual-area | | Excursive | |
|---|---|---|---|---|
| | No. | % | No. | % |
| i) On ground in open | 0 | 0 | 0 | 0 |
| ii) On ground in hole | 3 | 5 | 0 | 0 |
| iii)In sparse vegetation | 12 | 21 | 4 | 18 |
| iv) In medium vegetation | 39 | 67 | 18 | 82 |
| v) In dense vegetation | 4 | 7 | 0 | 0 |
| vi) Above ground in hole | 0 | 0 | 0 | 0 |
| Total | 58 | | 22 | |

* See Table 3.2. for full details.

quality in the neutral interstices between territories.

There was no difference in the distance from the edge of their usual-area, over which birds travelled to sites in the usual-areas of neighbours or in neutral interstices (Mann-Whitney U=16.5 ns, in neighbours n=5, in neutral interstices n=11). Furthermore, there was no relationship between the distance to the roost site and local population density estimated from the number of near neighbours ($r_s$=-0.11 ns n=22).

Roost sites were always discrete locations with little variation, so it was easy to determine when birds were using a different site to that used on the previous night. Different territorial individuals used different numbers of roost sites over a period of five consecutive nights. The number of sites used differed significantly from the expected number if no preference was expressed (chi-square goodness-of-fit test $\chi^2$=14.8 4df $p<0.01$ n=34); more individuals using fewer sites. The total number of sites used provides little information on the degree to which birds re-selected the same site to that used on a previous night (roost fidelity). A bird which alternated between two sites was considered to show greater fidelity than a bird which visited five sites once each, but lower fidelity than a bird which used the same site on each night. The degree of infidelity to both numbers of sites used and number of changes in site can be quantified by an index of roost infidelity ($R_{inf}$; Fig.3.30.). $R_{inf}$ equals zero for total roost fidelity. $R_{inf}$ shows strong positive correlation with both number of sites used and number of changes in site ($r_s$=0.98 and 0.99 respectively n=43). Increasing infidelity therefore results in a linear increase in $R_{inf}$. There was, however, no relationship between $R_{inf}$ and usual-area, day of year or local population density ($r_s$ all ns at the $p<0.05$ level n=43).

## 3.4. Discussion.

### 3.4.1. Territory definition and structure.

Robins showed a marked preference for concentrating their activity in areas of bushes and shrubs. These occupied only a small proportion of their usual-area. Such a preference by the robin has been recorded previously by Hoelzel (1989) and Adriaensen & Dhondt (1990), who suggested the advantages of occupying such sites could include protection from predators and severe weather. Results from the present study indicate that prey availability was unlikely to be a factor (section 3.3.4.). These habitat features were therefore considered to be resources of high quality. Analyses of radio-tracking data from great tits has shown that within ranges individuals concentrated their activity in small localised patches, spending little time between

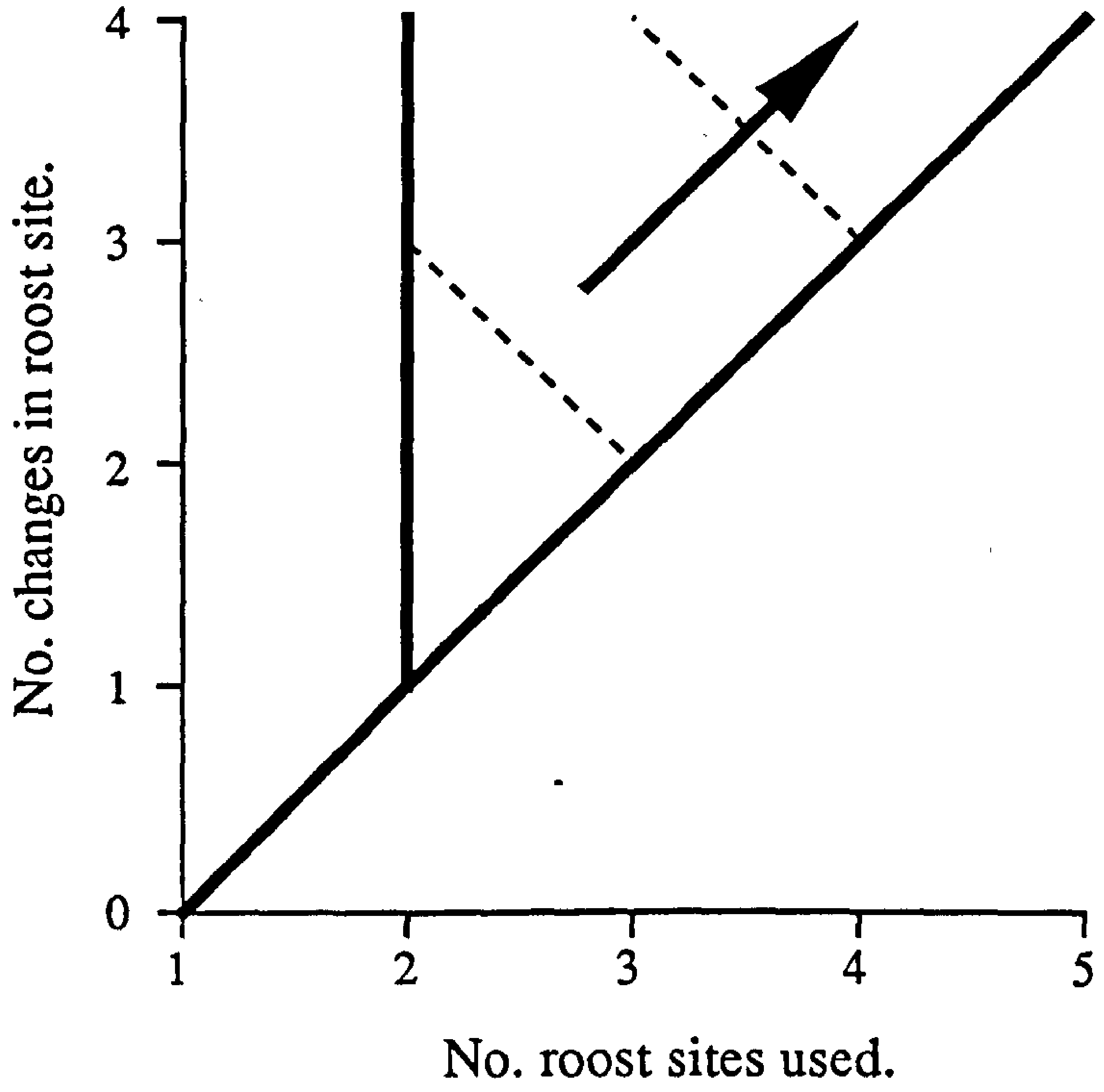


**Fig.3.30.** The behaviour of the index of roost infidelity $R_{inf}$ in relation to the number of roost sites used and number of changes in roost site over a five night period. Where;

$$R_{inf} = \sqrt{\text{No. sites used} \times \text{No. changes in site}}$$

Dashed lines join equal values of $R_{inf}$ and the arrow indicates the direction of increasing $R_{inf}$.

these areas (East & Hoffer 1986). This pattern of space use is identical to that shown by the robins in this study, and may be typical of small birds occupying heterogeneous habitats.

Although the extent of the usual-areas varied, all contained similar areas of high quality resources, as suggested by the area of their core-nuclei. This phenomenon has been observed in a number of other studies (eg Davies & Lundberg 1984, Kenward 1982b), and possibly represents the amount of high quality resource that each individual requires access to in order to survive.

Not all ranges had associated standardised defended-areas. Of those that did, the high degree of polygon overlap and similarity in size between the usual-area and defended-area for each individual suggested that the robins were only spending time and energy in the defense of their core-nuclei and the area between them. This represented the areas within which individuals concentrated their activity, and the area over which they travelled during apparently rapid commuting flights between nuclei.

The territorial status of the robins in the study population could only be determined by measuring their space use. This was because the absence of high levels of advertisement behaviour (song and tic-calls) could not be assumed to reflect a lack of willingness to exhibit territory defense. Of the individuals for which defended-areas were not available, the widely ranging behaviour of some suggested that they were non-territorial. By definition, they occupied usual-ranges that were considerably larger than those occupied by territorial birds. Although objective and quantitative, the use of a discrete cut-off point for assigning individuals to territorial or non-territorial categories does have an associated difficulty. Individual robins differed in morphology and energetic condition. This may result in some birds being able to use their range in a territorial manner while for others, a range of the same size may not be economically defendable. Because of this some individuals may have been wrongly categorised by such a discrete cut-off. Because few ranges fell close to the cut-off point, however, this was considered unlikely.

Because the absence of territorial defense or advertisement behaviour does not necessarily mean that the usual-area of a particular individual would not be strongly defended if the need arose, the usual-area of those individuals classed as territorial represents a good estimate of the location and extent of the territory.

The high eccentricity of the majority of the usual-areas of territorial individuals was inconsistent with what would be expected from the simple economic view of territorial exploitation and defense discussed in chapter 1. Because the shapes of territories occupied by other animals inhabiting two dimensional habitats have not been generally reported, it is not possible to determine the prevalence of highly eccentric ranges among other species.

In many radio-tracking studies, the assumption is made that the probabilities of locating an animal at different locations within its range will take the form of a smooth "probability landscape". This concept is reinforced by the use of isoline models, with their inherent smoothing characteristics, when estimating range use from a sample of location estimates. The results from this study of the robin suggest a more appropriate topographical analogy for describing range use may be a series of cliff-bound peaks on an almost flat plain.

### 3.4.2. Change in the location and extent of territories over time.

The range use of an animal must be defined in spatial and temporal terms (Kaufmann 1983). When applying range estimators to a sample of animal locations, an inherent assumption is that the pattern of space use is unchanging over the period of observation (White & Garrot 1990).

Over the short term (days), although both showed high fidelity to range area, the ranges of territorial robins showed very high fidelity to the habitat features they occupied compared to the ranges of non-territorial birds. The small changes that were shown can be explained in the following way. The distribution of one standardised sample of location estimates cannot be expected to be identical to the true distribution of probabilities of being located over the same period. Furthermore, subtle changes in the size and location of the centres of activity in response to short term variation in the internal state of the owner or external conditions (eg wind direction), will produce a degree of "noise" when comparing ranges which otherwise showed high fidelity. This suggests that the edges or boundaries of a territory may be better thought of highly dynamic and essentially indefinable in space. The use of the defended-area or usual-area outline can only be viewed as an estimate of the location and extent of a territory over a particular measurement period.

The ranges of non-territorial individuals drifted relatively rapidly across the habitat. Because non-territorial individuals showed such low fidelity to particular habitat features, the ranges of these individuals would not have reached an asymptote after 40 relocations. However the use of a standardised sampling protocol for the whole population ensured that representative "snap shots" of space use could be obtained that were comparable between all individuals. The total core area used by individuals which were non-territorial was significantly larger than those of territorial birds. This was considered to be an artifact of the high rate of range drift they exhibited. New core nuclei were established and old ones abandoned within the four to five day period over which standardised samples were collected. Hence although all were included in the range analysis, only some of them may have been being utilised at any particular time. The usual-area of non-territorial robins will therefore also be overestimated. Because of this pattern of space use, non-territorial individuals may be thought of as nomadic, with no particular preferred "home range". Because the assumption of range stability (White & Garrot 1990) is untrue for non-territorial robins, estimates of the location and extent of ranges are therefore of limited quantitative value. The space use of such individuals is perhaps better measured using data from continuous tracking techniques, which have no associated assumptions about sampling protocol.

Radio-tracking results show that the robin can change the pattern of its ranging behaviour most dramatically during territory takeovers. During such takeovers, non-territorial birds evict and replace an owner on its territory, forcing the latter to adopt a nomadic non-territorial existence. Fidelity to both range extent and location show massive change over just a few days.

Although usual-range size remained constant over the course of the Autumn, some individuals showed considerable directional territory drift. This supports the concept of a territory as a consequence of the activities of its owner, rather that the owner making the decision to occupy vacant a territory that is both discrete and fixed in the habitat.

### 3.4.3. Neighbourhood structure during day and night.

By deriving a robust and quantitative definition by which neighbours may be categorised, this study is the first in which the structure of neighbourhoods can be rigorously measured. There were gaps between the edges of the usual-areas of near neighbours. These neutral interstices consisted of undefended neutral ground, and were rarely or never visited even though they often contained patches of vegetation indistinguishable from those occupied by core nuclei.

Verner (1977) suggested that individuals should defend territories much larger than is necessary for their own survival. It was suggested that since selection acts on the performance of an animal relative to all others in the population, an individual could increase its fitness by inhibiting the fitness of conspecifics. One way of achieving this would be to defend large "super territories" which contain more resources than are necessary for survival. The existence of neutral interstices between territories containing superfluous high quality habitat features suggests that this form of "spiteful" (Hamilton 1970) behaviour does not occur in the robin.

Usual-areas, defended-areas and therefore territories never overlapped. The maximum-areas showed only a small degree of overlap on the usual-areas of near neighbours. This value is misleadingly small, since the maximum-areas usually overlapped the usual-area of only one of several near neighbours during the sampling period. This reduced the probability of it being recorded in randomly assigned dyads. Although the maximum-areas of dyads of near neighbours often showed considerable overlap, care has to be taken in interpreting the values, since the maximum-area polygons will be strongly influenced by a few outlying locations. Two polygons may overlap without any of the locations from which the polygons are constructed being included in the shared area. In these situations the results from static interaction using a grid-cell range estimator give a better measure of the degree of concordance between two ranges.

The degree of polygon overlap or static interaction between the ranges of territorial and nomadic non-territorial individuals would be meaningless due to the rapid range drift of non-territorial birds. It was very clear however, that although the core-nuclei and usual-ranges were much more likely to overlap with those of territorial individuals, the majority of locations were in neutral interstices. Furthermore, non-territorial birds appeared to avoid the dense clusters of territories that occurred in areas with large numbers of high quality habitat features. Many other studies have recorded the presence of non-territorial "floaters" in populations of territorial birds. These are thought to arise when habitat suitable for the economic defense of territories becomes saturated (Brown 1969, Krebs 1977, Desrochers 1988). In some populations a dominance hierarchy of floaters within territories has been observed (Smith 1978). When the owner dies its place is taken by the most dominant floater. Territory holders could benefit from this arrangement if floaters participate in territorial defense (Smith 1978). Krebs (1971) found that if pairs of great tits were removed from their woodland territories, the spaces were rapidly filled by pairs moving in from the surrounding hedgerows, which were considered habitats of lower quality. The neighbourhood structure of the robin appears to resemble this system, with nomadic non-territorial individuals surrounding patches of habitat densely populated by birds defending territories. Beletsky (1992) has presented evidence for non-territorial floaters in a population of red-winged blackbirds being attracted to regions of social instability, where they were more likely to subsequently establish territories. In the present study non-territorial robins were observed to gain territories. It is possible that they were able to monitor the behaviour of territory owners within the clusters of territories from a distance, eliminating the need for information gathering intrusions with their associated risks. Robins are able to distinguish between individuals by their song (Brindley 1991), therefore this could allow such long-range monitoring to occur.

The local population density, estimated by number of near neighbours, declined over the course of the Autumn. Yet there was no relationship with usual-area. Territorial behaviour has frequently been suggested as a mechanism to limit population density (Brown 1969, Krebs 1971, Knapton & Krebs 1974). In this study, as local population density declined (mainly through birds starving and being predated), there was no evidence for non-territorial individuals moving in and defending areas which became vacant. Therefore, it is possible that the habitat features that were defended as territories fell vacant because they were no longer economically defendable. Reasons for this could include the changing energetic requirements of owners, and changes in the quality of the habitat features that were previously defended.

Although there is some information on the nature of the sites selected by robins for roosting (Cramp 1988), the difficulties of observing individuals in low light levels at dusk means that the only way to record roost selection in a truly representative way is to use radio-tracking. Cramp (1988) describe non-breeding robins as usually roosting on the territory in dense cover. The results from this study reveal a rather different picture.

Mead (1984) describes observations of robins singing and even foraging under street lights long into the night. The robins in the present study areas never did this despite the presence of flood lights. Qualitative observations of robins under street lights away from the study area indicates that the trigger for such nocturnal activity is disturbance rather than light. Such disturbance to roosting birds is more likely to occur in areas with street lighting. Although roost sites were in habitat features indistinguishable from those which contained core-nuclei, there was no tendency for birds to select sites within their usual-area more often than excursive sites. When excursive sites were used however, they tended to be in medium density vegetation more often than when birds remained on their usual-areas. Medium density vegetation may therefore represent sites of the highest quality, perhaps in terms of rates of heat exchange. When selecting excursive sites however, there was a strong preference for sites in the neutral interstices between territories rather than in usual-areas of neighbours. The number of such sites were limited, resulting in the formation of small communal roosts. The daytime neighbourhood structure of non-overlapping territories separated by neutral interstices ceases to exist after dusk. It is replaced by territorial individuals roosting in favourable sites scattered across the habitat with their distribution bearing little resemblance to their daytime range use. Nevertheless, robins face a trade off between the potential energy savings of roosting in high quality sites away from their territory, and the possible cost of evicting any intruders on return to their territory at dawn when most challenges for territory ownership occur (Harper 1984).

### 3.4.5. A probabilistic model of territory and neighbourhood structure.

From these results, a model of territory and neighbourhood structure during daytime may be produced, based on the probabilistic use of its range by an average non-breeding territorial robin (Fig 3.31.). The range is divided into a series of utilization compartments, each with an associated probability of containing the territory owner.

The excursive activity of the robin varied with local population density. As the number of near neighbours decreased, the territorial individuals maintained the same probability of being located in excursive utilization compartments (Fig 3.32.), but increased the extent of the excursive area. Thus, when the number of near neighbours was low, territorial robins had to travel further if they were to visit the territories of the nearest conspecifics (Fig 3.33.). Because intrusions into the territories of far neighbours requires movements over larger distances, the associated energy costs would be higher. For territorial robins with different numbers of near neighbours to maintain the same probability of intruding, therefore, the intrusive behaviour must have a compensatory high value. It may be important for a robin to acquire knowledge about the quality of owners and their territories to assess the costs and benefits of changing the locations of the core-nuclei it uses. Nevertheless, the same probability of being located while engaged in intrusions does not reveal any information on the number or duration of each intrusion. Such information is only available from continuous tracking data.

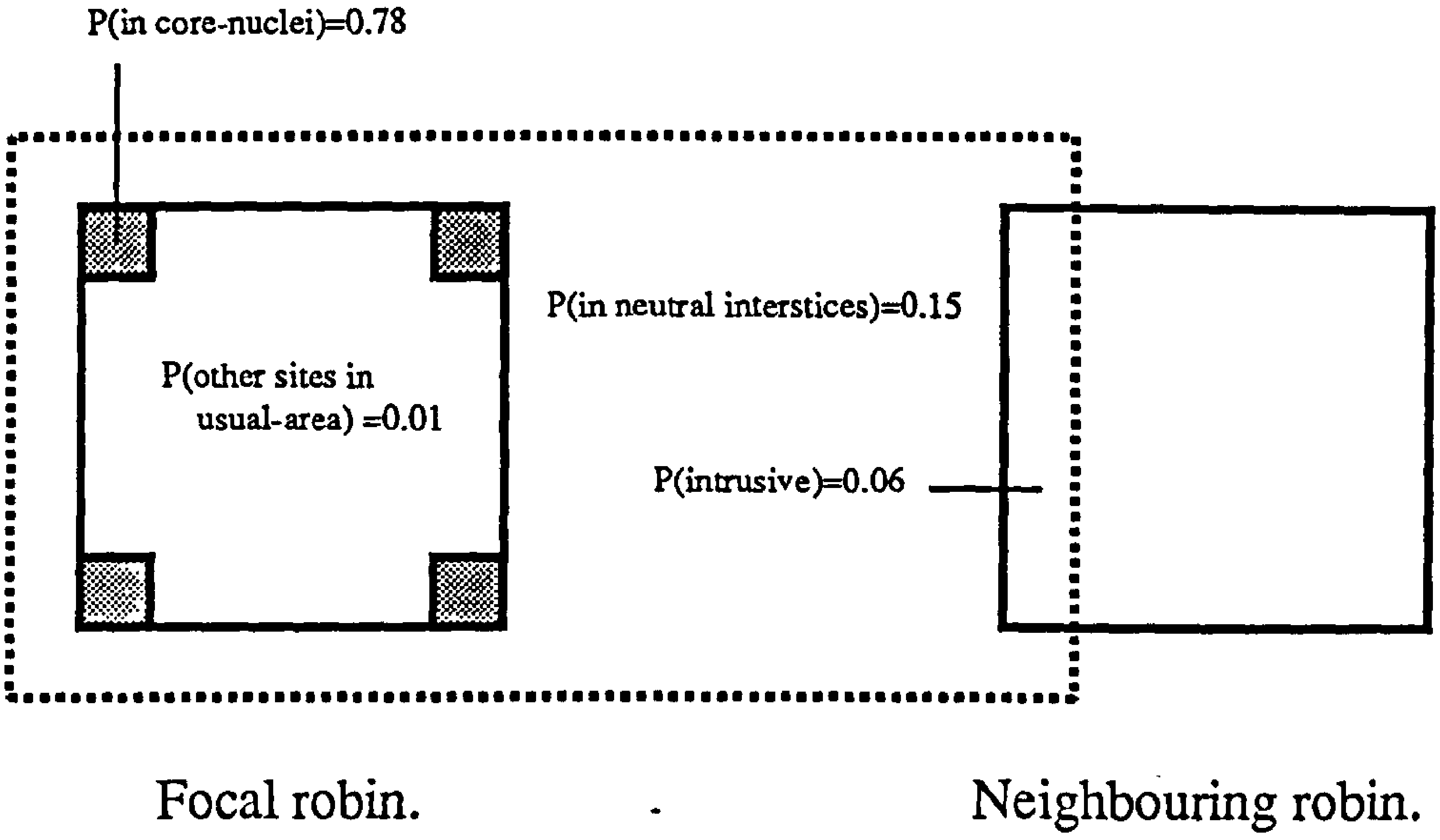


**Fig.3.31.** The model of territory and neighbourhood structure based on the probabilistic use of its' range by an average non-breeding territorial robin, based on data from 43 radio-tracked individuals. Shading indicates core-nuclei, the solid line indicates the usual-area of focal bird and neighbour and the dashed line indicates the maximum-area, part of which overlaps with the usual-area of the neighbour. The values indicate the probability of the focal bird being recorded in the different utilization compartments.

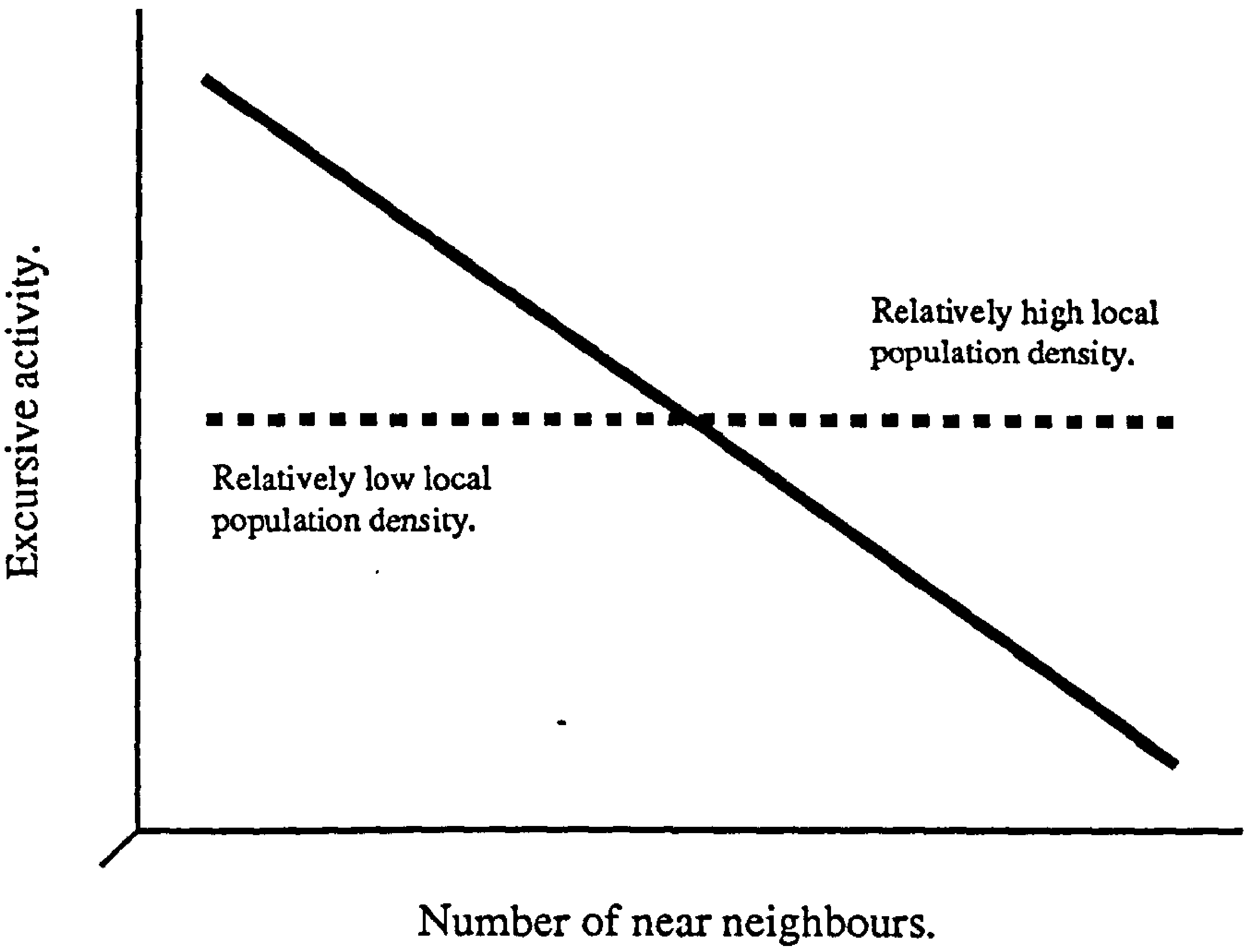


**Fig.3.32.** Diagrammatic representation of relationships between the two measures of excursive activity and the number of near neighbours, based on the correlations presented in Table 3.7. Excursive activity was measured in two ways; the excursive area (the difference between the maximum-area and the usual-area; Fig.3.10.) and the proportion of locations that were excursive. Here, the excursive area is indicated by a solid line and the proportion of locations that are excursive by a dashed line.

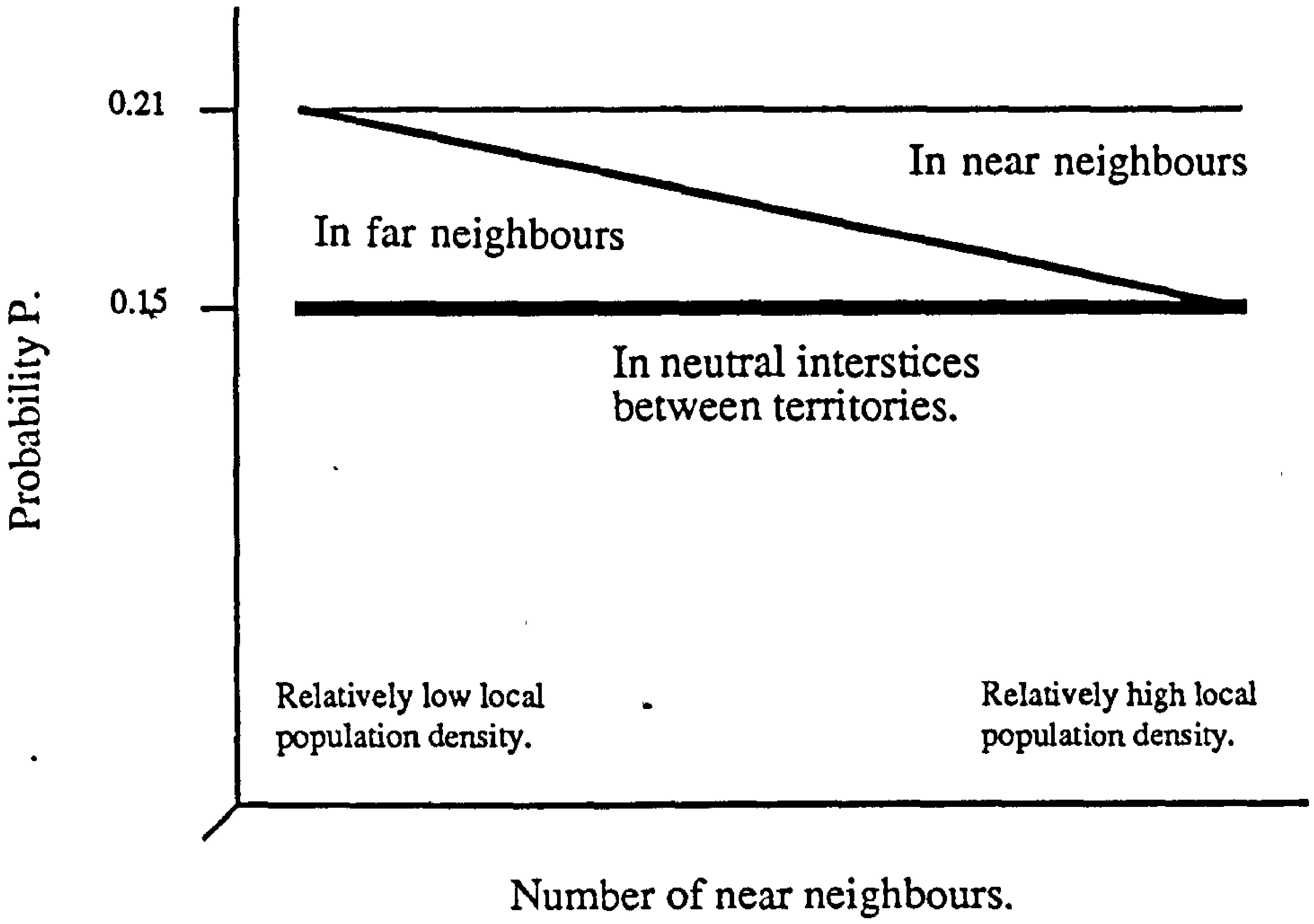


**Fig.3.33.** Diagrammatic representation of the relationships between the probability of robins being located in different excursive utilization compartments and the number of near neighbours. The probability values are based on the data from 43 non-breeding territorial robins.

### 3.4.6. Previous studies of territory of the robin in the light of radio-tracking results.

The values of territory size in the non-breeding robin that were obtained by previous studies are shown in Table 3.9. The overall median was 3800 $m^2$. The median value of territory size in the present study, estimated by the usual-area, was nearly one seventh of this (Table 3.9.). This was considered primarily due to the ambiguous and qualitative nature of the definitions used earlier to specify the location and extent of territories. This resulted in the inclusion within boundaries of the neutral interstices between territories, and the failure to take into account the effects of long term territory drift.

The effect of including neutral interstices can be illustrated by examining the differences in non-breeding territory size recorded for robins occupying different types of habitat in Belgium (Adriaensen & Dhondt 1990). Individuals apparently occupied larger territories in habitat with few bushes and shrubs and lower population density. The definition of territory used by Adriaensen & Dhondt (1990) included all sightings of each individual. Therefore these values of territory size are more comparable with the values of maximum-area recorded in the present study. The maximum-area is the sum of the usual-area (an estimate of territory) and the excursive area. When an individual occupies a territory with few near neighbours it ranges over a larger excursive area enabling it to still achieve intrusions into the territories of conspecifics. The values of territory size presented by the Belgian study and others, therefore, may not represent values of the size of territory size in the robin at all.

An even more marked difference is seen between this and previous studies when changes in territorial behaviour over the course of the year are examined. The ratio of non-breeding to breeding territory size range from 0.25 to 0.5. The ratio recorded in this study was 0.96. Once again this is probably due to the inappropriate definition of territory used by previous studies, which results in the inclusion of areas outside the extent of the true territory.

Quantitative estimates of the proportion of time spent away from the territory by robins are few. Harper (1984) reports that territorial robins spent only 7 % of their time away from their territory. The equivalent value obtained from discontinuous radio-tracking in the present study was 21 %. The discrepancy may again be explained in terms of the different approach to defining the extent of territories. The majority of the excursive locations recorded in the present study were in the neutral interstices between neighbours. Some of these would have been classed as within the territory by less rigorous definitions. Of the excursive locations recorded in the present study, an average of only 6 % were intrusive. This agrees

**Table 3.9.** Estimates of territory size given by previous studies of the robin, compared to values of the usual-area, which represents territory size in the present study.

| Reference | Study area. | Nonbreeding territory size ($m^2$) | |
|---|---|---|---|
| | | Median | Range |
| Lack (1965) | South Devon | 3000<br>(n=33) | 700-5300 |
| Jackson (1956) | Dublin | 4000<br>- | 3000-6000 |
| Harper (1986) | Cambridge | 2700<br>(n=108) | 800-6500 |
| Cramp (1988) | Oxfordshire | 4100<br>(n=62) | 1100-10900 |
| | Sussex | 7300<br>(n=18) | 3200-13400 |
| Adriaensen & Dhondt (1990) | Belgium | | |
| | Woodland | 5300 *<br>(n=15) | - |
| | Parkland | 2100 *<br>(n=46) | - |
| | Total | 3600 *<br>(n=98) | 800-11800 |
| Present study | Central Scotland | 468<br>(n=43) | 255-803 |

* Indicates mean, median not being available.

well with the value of 7 % from time/activity budgets reported by Harper (1984).

In conclusion, most studies of territoriality in mammals have used radio-tracking to monitor otherwise elusive species. Results have often indicated highly dynamic space use (eg Doncaster 1992). The results of this investigation of the space use by the robin suggest a similarly dynamic and variable territory and neighbourhood structure for a small passerine bird.

# Chapter 4.

# 4. Territory and neighbourhood structure: the dipper.

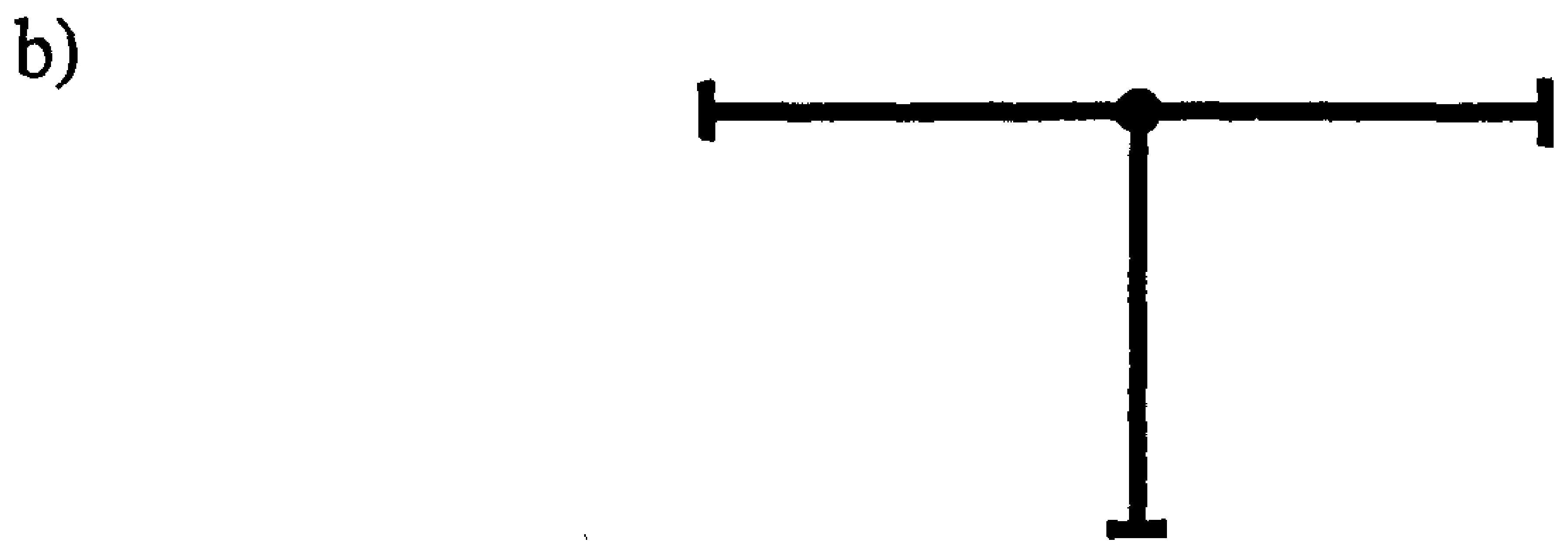
## 4.1. Introduction.

Although the biology of the dipper has been the subject of a number of studies (Bakus 1959, Price & Bock 1983, Bryant *et al* 1985, Bryant & Tatner 1988), there is little information available on the structure of territories and how this may change over time. Since the territorial behaviour shown by an individual may depend on the behaviour of its neighbours, the structure of neighbourhoods may also be important if the nature of territoriality is to be fully understood. As shown for the robin, radio-tracking provides a very powerful technique for measuring the use of space both within and between the individuals which make up neighbourhoods, and provides a common approach by which the space use of robins and dippers can be compared.

Owing to the linear nature of the riparian habitat, it is intuitively appropriate to describe the territory of the dipper in terms of length. The role of the available resource area, however, must also be considered. For example, it has been suggested that length is governed by the area of shallow water suitable for feeding (Shooter 1970). Furthermore, Robson (1956) observed territory length to be greater where the water course was narrower.

When in flight dippers closely follow the twists and turns of a water course (Cramp 1988). Territories may therefore be considered as being used only in a linear manner. Some individuals however, may exploit habitat on tributaries whose junction with the main water course is contained within the territorial boundaries. In these situations, although the movements of owners is still constrained by the riparian habitat into a linear pattern, the space use shown by such individuals can no longer be considered equal to the simplest linear territory with two boundaries. In such situations the configuration may be described as T-shaped. Since it is not possible to describe these special cases in terms of a simple outline, their shape cannot be quantified using a measure of shape analogous to the eccentricity of a polygon. It is important to note that the length within a non-linear territory is more accessible than that within an simple linear territory (Fig.4.1.). This is because, unlike in a territory of simple linear configuration (Fig.4.1.a.), it is not necessary for the owner to travel the total length of its territory when moving from one boundary to another (Fig.4.1.b.). This will result in locations along the length of such a T-shaped configurations being relatively more

Hypothetical linear dipper territory.
Length = 3x.



Hypothetical non-linear dipper territory.
Length = 3x

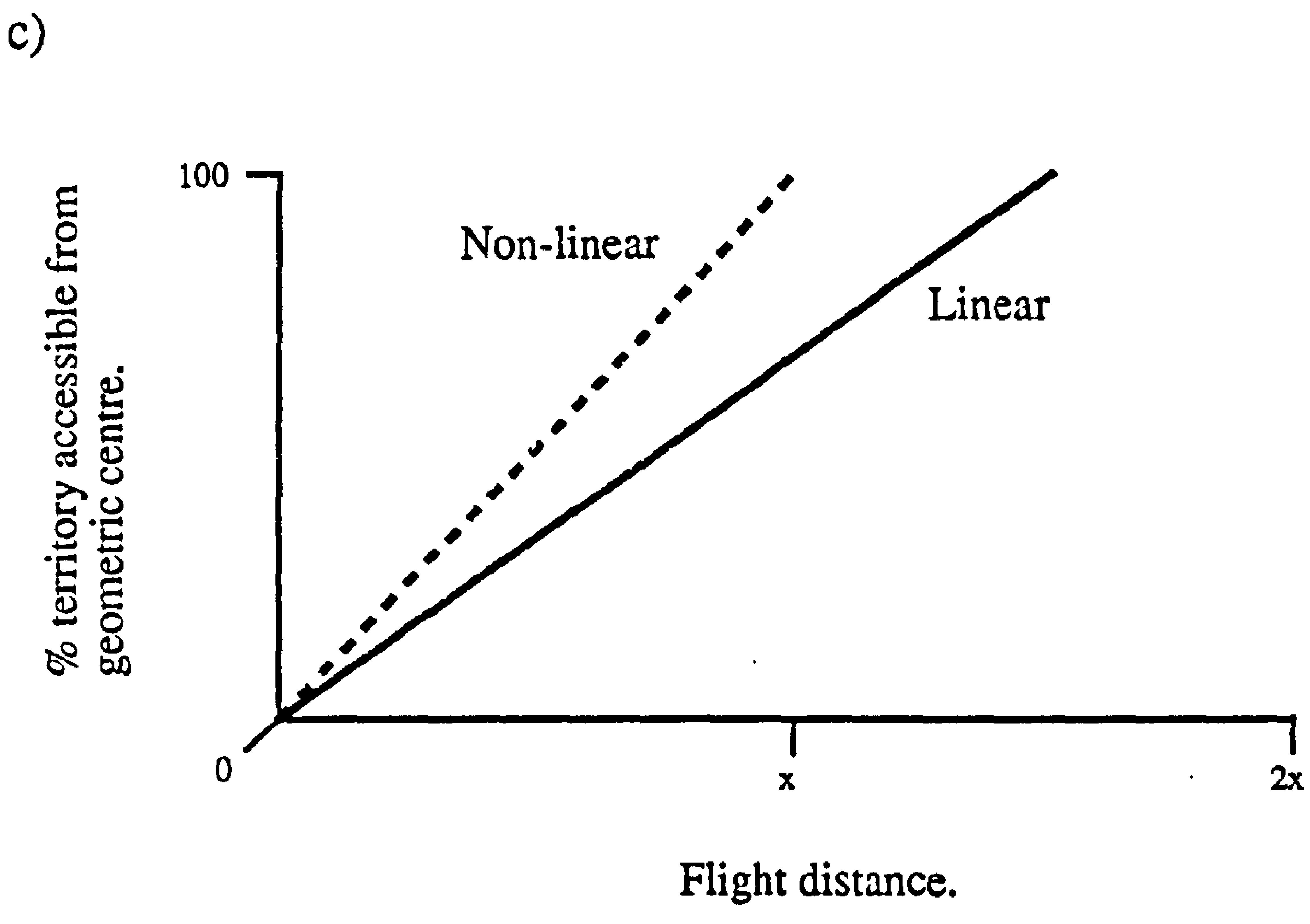


**Fig.4.1.** The accessibility of territory length in territories of different configuration; (a) simple linear, (b) non-linear T-shaped. The difference in flight distance required to reach the whole of each territory length from the geometric centre is illustrated in (c). The geometric centre of a territory is the point furthest from all of the boundaries.

accessible to occupiers than locations along a territory of simple linear configuration (Fig.4.1.c.). They must therefore be classified as being less-linear. Intermediate to these extremes is the possibility of L-shaped configurations, in which a tributary is used which joins the main water course at one end of the territory. A dipper using such a configuration may need to defend three boundaries against intruders without the benefit of the increased accessibility of boundaries conferred by a T-shaped territory. Following this, the configuration of territory that is defended by a dipper may have implications for the energy costs of exploitation and defense.

The dipper has long been known to select roost sites in artificial structures such as tunnels and bridges over water courses (Hewson 1969, Shaw 1979, Ormerod & Tyler 1990). Particularly favoured sites are often occupied by many individuals resulting in communal roosts, although most roost alone in sheltered concealed places over running water (Hewson 1969). There is little information as to the distances individuals travel to roost sites from their territories (Shaw 1979). There may be a tradeoff between the energy costs of such flights and the advantages of roosting in high quality sites. This may have consequences for the relative quality of territories occupied.

## 4.2. Methods.

### 4.2.1. Accuracy of location estimates.

For their occupants, riparian habitats generally provide high visibility both along the length of the water course and to the side into the surrounding countryside. This makes close approaches to radio-tagged dippers impossible, due to the risk of disturbance and therefore disruption of the subsequent space use. Because of this, the locations of individuals could only be recorded at some distance from the river bank and often out of sight of the bird. A directional receiver antenna records the direction from which a signal reaches it rather than the true direction of the transmitter antenna. The discrepancy between the estimated direction and the true direction of the transmitter may be termed topological error. The accuracy of location estimates of radio-tagged dippers was on some occasions further reduced by such topological error, when individuals were sheltering under overhanging banks or active in rocky gorges. It was not possible to quantify this form of error although its effects were probably small. Following this, the minimum segment of water course to which radio-tagged individuals could be assigned to locations on an accurate map was considered to be 50 m.

Although individuals frequently swam and dived while carrying radio-tags, the effect on the radio signal was minimal and birds could always be located during the daytime, although a methodical search was required for more widely ranging individuals.

### 4.2.2. Sampling protocol.

Increasing range eccentricity (departure from radial symmetry) produces a corresponding decrease in the values of $t^2/r^2$ (Swinhart & Slade 1985). Because of the linear nature of the habitat they occupy, the eccentricity of ranges used by dippers closely approached one. Using the criteria of Swinhart & Slade (1985) therefore, estimates of the time required to achieve statistical independence between successive locations estimates would be too long to be compatible with any feasible radio-tracking protocol.

Andersen & Rongstad (1989) found that, using radio-tracking data from red-tailed hawks, different sampling strategies did not significantly alter estimates or indices of range size. They went on to suggest that with highly mobile species, the time to independence (Swinhart & Slade 1985) may be an over-estimate of an appropriate sample interval when common estimators of range size, such as minimum convex polygons, are applied (Andersen & Rongstad 1989). Since the time to independence for the robin was calculated to be only a few minutes, it was therefore concluded that for the dipper, a minimum sample interval of one hour would produce location estimates that were sufficiently independent for statistical range estimators to be applied. This was often much longer when several individuals were monitored concurrently over several kilometres of water course.

The number of independent location estimates required to accurately represent the use of the dipper was determined with reference to the asymptotes of sample size with percentage of maximum length and percentage of maximum number of 50 m segments visited (Fig.4.2.). A total of 20 independent location estimates clearly represented a saturated sample. This was adopted as a standardised sample (Harris *et al* 1990) of locations estimates for the dipper. Standardised samples were collected at all times of the day over a period four days for each individual.

### 4.2.3. Locating roost sites.

The signals from radio-tagged dippers were searched for after dusk by walking along the water course. Birds roosting in their daytime range could quickly be located. Birds

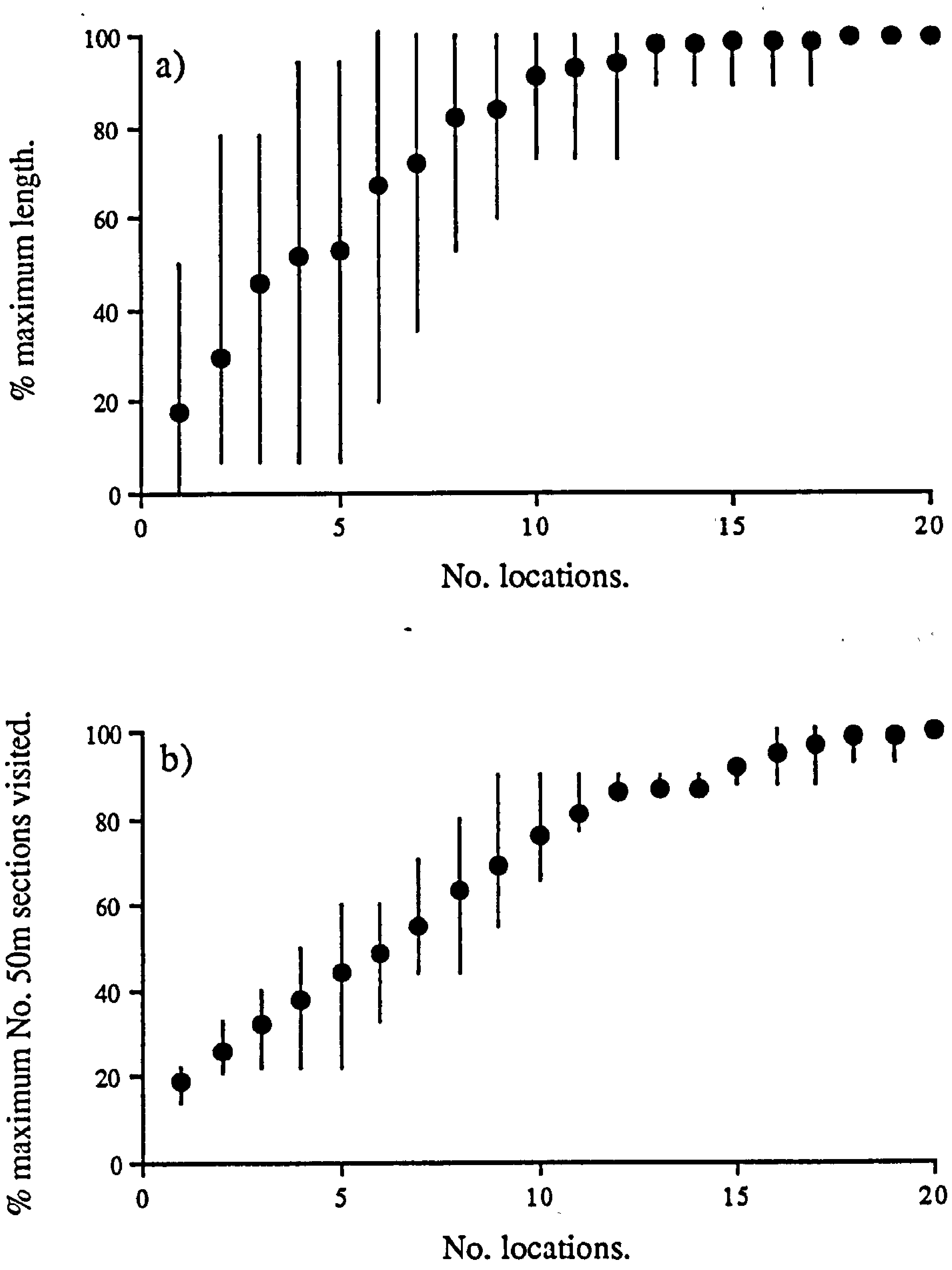


**Fig.4.2.** Functions of range size with sample size of location estimates. (a) range size measured as maximum length (n=10), and (b) number of 50m segments visited (n=6). Points and error bars indicate mean and range.

roosting at sites away from their daytime range were always located after a methodical search. Information on the locations of previously used sites (S. Newton *pers. comm.*) enabled searches to be concentrated on areas which the birds were likely to select.

Because of the background noise of running water, roosting birds could be approached very closely and illuminated without being disturbed. This enabled details of site selection to be recorded accurately.

### 4.2.4. Territory defense.

The dipper apparently defends its territory by evicting intruders and broadcasts its territorial status by means of year round song (Cramp 1988). Bryant & Tatner (1988) ranked singing the second most frequent activity for male and female dippers at rest during the months in which radio-tracking was carried out. Territorial behaviour was recorded only rarely during radio-tracking. Because of the need to stay out of sight of the individual being monitored however, some such behaviour may have been missed. Consequently it was not possible to record sufficient numbers of interactions to generate estimates of the length of water course that was being defended. The few instances that were recorded could be compared, in retrospect, with the estimates of the location and extent of the range estimated from radio-tracking data alone.

### 4.2.5. Habitat structure.

A survey of each of the study water courses was carried out, recording width to the nearest metre and scoring which 50 m segments contained broken water. This was water running over shallows (riffles) or among boulders (rapids). Such locations are preferred by foraging dippers (Cramp 1988). The detailed maps of the study areas used during tracking also provided information on the locations and angles of bends in the water courses. The increased erosion of banks at the sites of bends may provide suitable sheltered places for dippers to rest during the daytime.

## 4.3. Results.

### 4.3.1. Independence between ranges.

Twenty ranges of standardised sample interval and sample size were collected from 16 individuals of both sexes and various ages between August 1984 and December 1987

(Nutall 1988, D.M.Bryant unpublished data), and September to December 1990 (I.G.Johnstone). From these a random sample of standardised ranges were selected such that each individual only contributed one range, ensuring statistical independence. No individuals were tracked in more than one year. The times of the year that individuals were monitored are shown in Appendix 5. Nonparametric statistics were used unless otherwise stated due to frequent small and non-normally distributed samples.

### 4.3.2. Deriving measures of range use.

Since the dipper occupies a linear habitat, any estimates of range use must intuitively be based on length rather than, for example polygon area. This is true even for ranges that are classified as non-linear, since owners can only move within the linear constraint of their riparian habitat. Consequently, the simplest measure of range use in the dipper is the sum of the distance between the most outlying locations measured along the intervening water course. This was termed the maximum length. The median maximum-length is shown in Table 4.1. This definition is also suitable for individuals which occupied L-shaped or non-linear T-shaped configurations.

On examining the frequency of use of the different 50 m segments of water course visited by each individual it was clear that ranges were predominately non-uniform and multinuclear. An example of a range in presented in Fig.4.3. with a map of the water course occupied. As discussed in chapter 3, sequential cluster analysis is the most appropriate method of quantifying this type of range use. Following the methodology of chapter 3. therefore, sequential cluster analysis was carried out on each range, and core total lengths determined using the same techniques that were applied to location estimates from the robin. An example of a utilization distribution plot produced by sequential cluster analysis of a standardised sample of location estimates from a dipper is shown in Fig.4.4. The stepped effect, typical of dipper ranges, was due to the large size of the cells to which locations were assigned relative to the maximum-lengths of the ranges occupied. The median core length shown by the dippers in this study is shown in Table 4.1. Core lengths contained a median of 73 % of the location estimates (minimum 55 % maximum 90 %). This represented 29 % of the median maximum-length.

Of the core-lengths defined by sequential cluster analysis, 80 % produced more than one centre of activity (n=16). Modifying the partial area index of range patchiness ($A_p$)

**Table 4.1.** Median values of the different measures of range use for non-breeding dippers. Statistics refer to Mann Whitney U-tests between territorial and non-territorial individuals. Figures in parentheses show range.

| Class of individual and sample size # | Maximum-length (m) | Core-length (m) | No. nuclei | Usual-length (m) |
|---|---|---|---|---|
| All<br>(n=16) | 1025<br>(600-2650) | 300<br>(150-600) | 3<br>(1-4) | 850<br>(250-2450) |
| Territorial<br>(n=12) | 750<br>(600-2300) | 300<br>(150-600) | 2<br>(1-4) | 550<br>(250-1400) |
| Non-territorial<br>(n=4) | 2425<br>(1500-2650) | 425<br>(300-500) | 3<br>(3-4) | 2125<br>(1500-2450) |
| U | 2.0 * | 11.0 | 11.5 | 0.0 ** |

* $p<0.05$ ** $p<0.005$

\# The overlap of ranges is the basis for the definition of territorial and non-territorial space use.

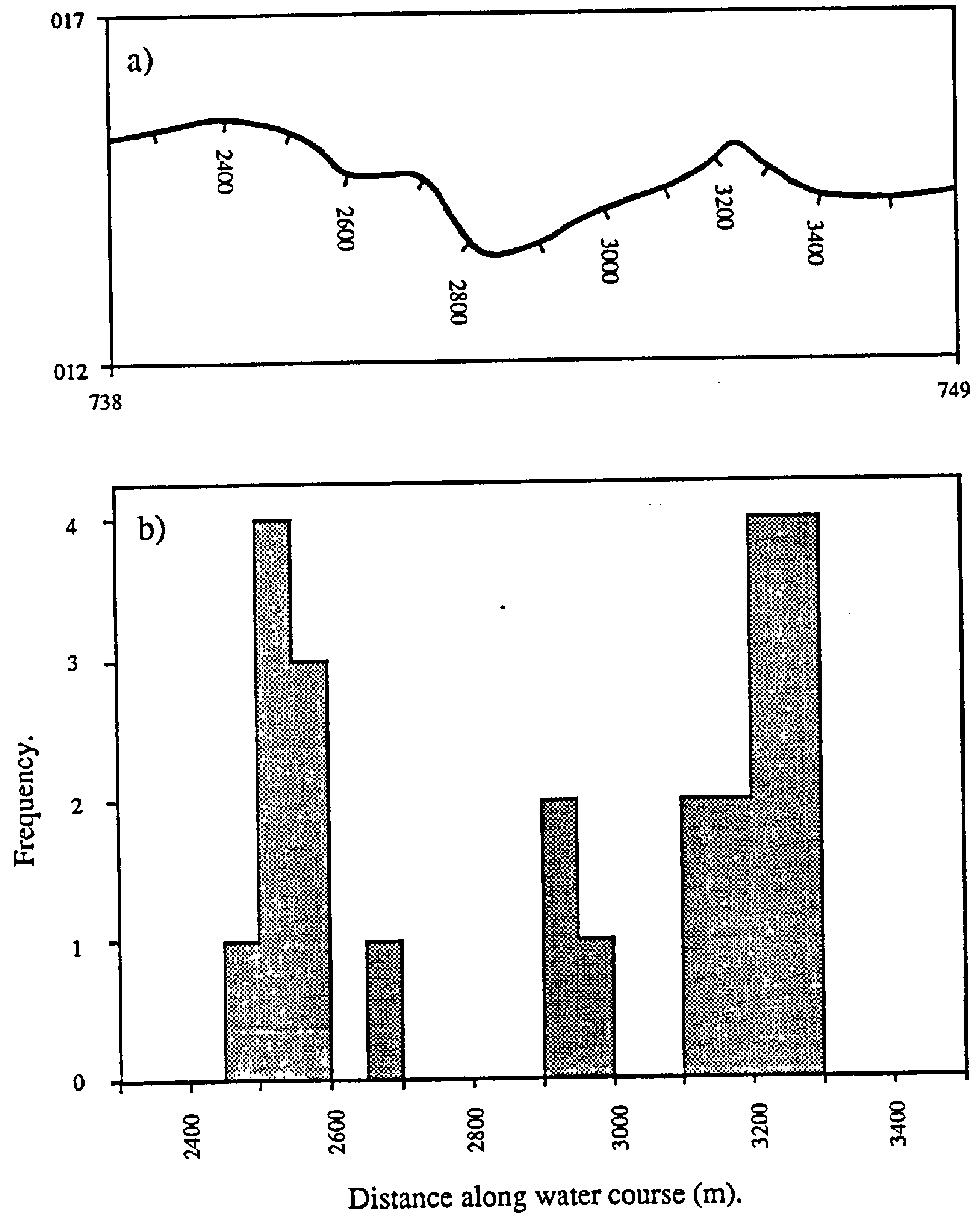


Fig.4.3. An example of the distribution of location estimates from radio-tracking (n=20) for juvenile male dipper RS03258 during November. In (a) is shown a map of the water course occupied. Axes correspond to the 100x100 km square NN of the British National Grid. The frequency of locations in each 50 m segment along the water course indicated is shown in (b).

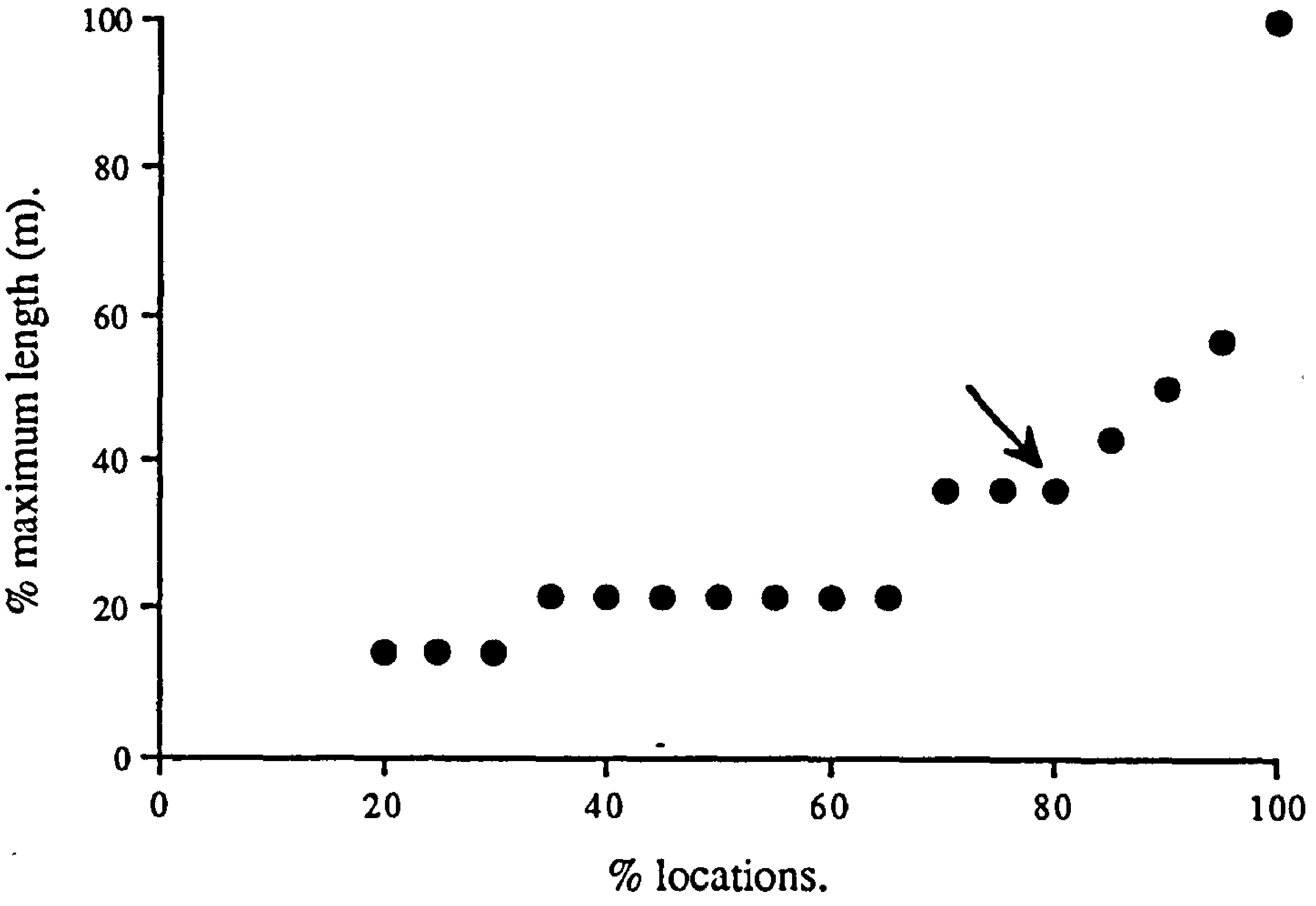


Fig.4.4. The utilization distribution plot (Ford & Krumme 1979) of the results from sequential cluster analysis. Data is represents a standardised sample of location estimates recorded from an non-breeding adult female dipper. The arrow indicates the percentage of locations beyond which additional locations do not contribute to the core regions.

(Kenward 1990), the degree of patchiness in the range use of dippers was quantified by calculating the partial length ($L_p$). $L_p$ equals the ratio of the total core-length to the distance along the water course which contained all core-lengths. $L_p$ can vary from one (locations uniformly distributed within range) to zero (locations concentrated in a number of infinitely small core-lengths). The values of $L_p$ are shown in the form of a frequency histogram in Fig.4.5. The median $L_p$ was 0.27 (range 0.15-1.0 n=16). Location estimates were therefore concluded to follow a highly patchy distribution. Each cluster of locations was termed a core nucleus. The number of core-nuclei occupied by each of the radio-tracked dippers is shown in Table 4.1.

Since dippers only moved between core-nuclei by following the twists and turns of the water course, the length which contained all core nuclei represented the length of water course within which individuals spent the majority of their time, either in core-nuclei or commuting between nuclei. This was termed the usual-length. The median usual-length is given in Table 4.1. The four measures of range structure developed to describe the use of space by the dipper are summarised in Fig.4.6.

### 4.3.3. Characteristics of the usual-length.

Of the locations at which dippers were observed to show behaviour associated with territorial defense and advertisement, all occurred within their usual-lengths (n=7 occurrences from 5 individuals). Although based on a small sample size, this may suggest that birds which were territorial were only attempting to defend their core-nuclei and the length of water course between them.

There was a significant negative correlation between the usual-length and the core-length as a percentage of the usual-length ($r_s$=-0.89 $p<0.005$ n=16 Fig.4.7.). The expected distribution if all ranges contained the same core-length (the median core-length of all birds tracked) is shown by the curve in Fig.4.7. The data closely approached this.

There was a slight but not significant tendency for the core lengths of each individual to be located in segments of the water course containing broken water compared to the usual-length (median % usual-length broken water=45, median % core-length broken water=67, Sign test binomial ns n=16 Fig.4.8.). There was no tendency for dippers to concentrate their activity in sections of the water course that contained bends of greater than an arbitrarily selected angle of 45° (% 50 m sections making up core length containing bends=25, % 50 m

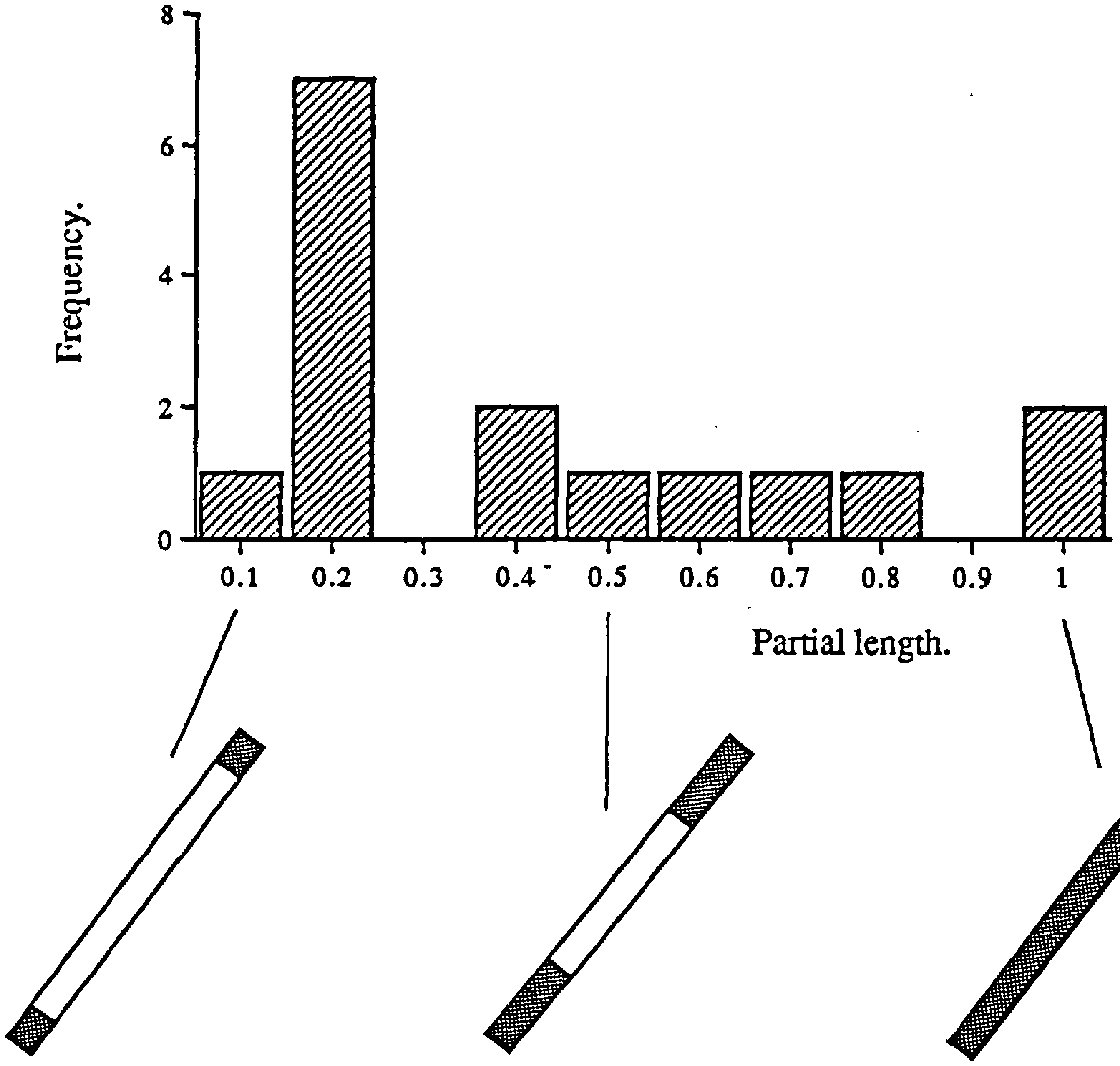


**Fig.4.5.** Partial length $L_p$ for the ranges of non-breeding dippers (n=16), shown in the form of a histogram. Also shown are hypothetical ranges of three different values of $L_p$, illustrating how decreasing $L_p$ reflects the increasing fragmentation of core regions.

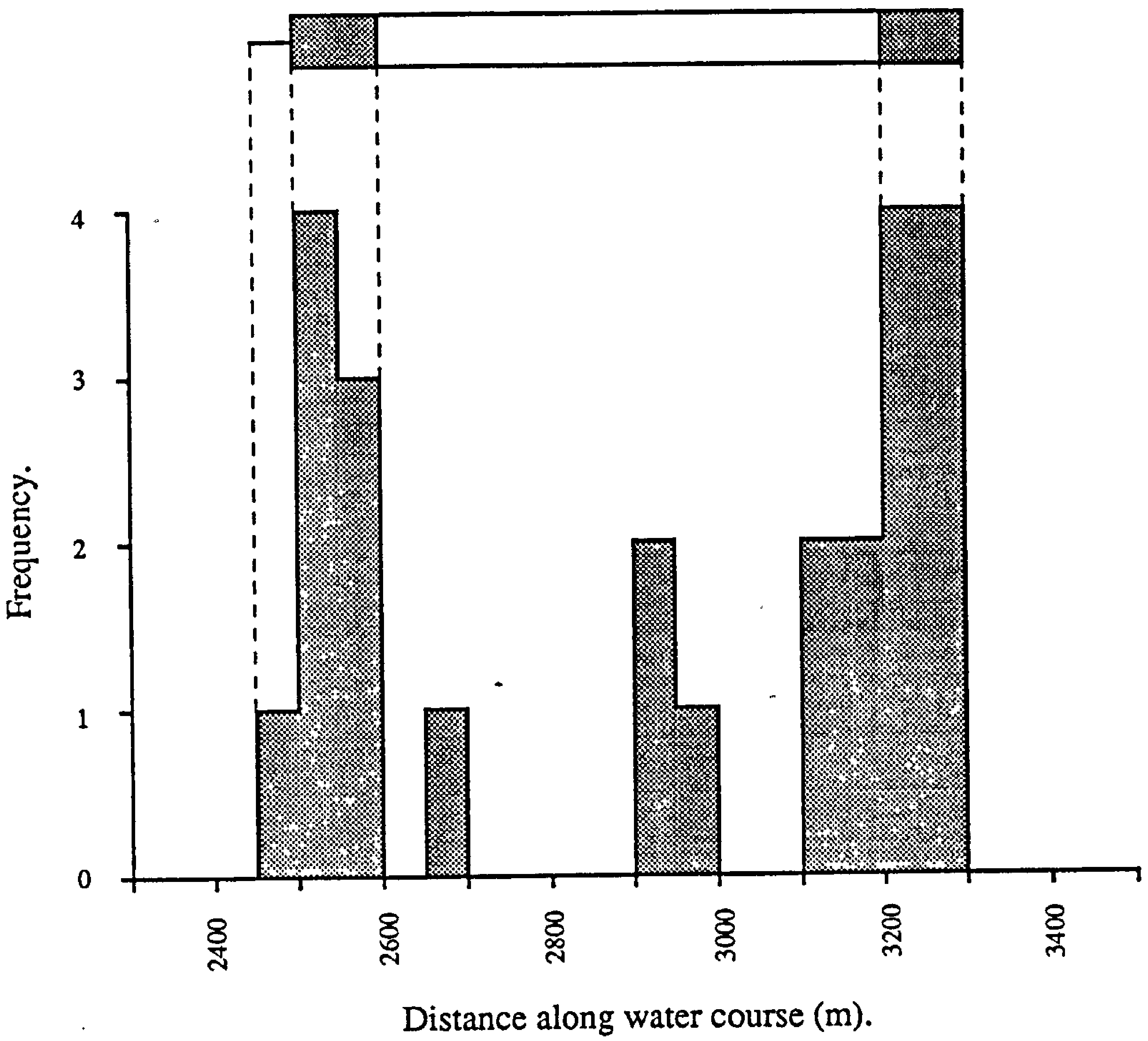


**Fig.4.6.** An example of the measures of range use developed for the dipper, and the location estimates from which they were calculated in the form of a histogram. The bar represents the usual-length, within which the shaded regions indicate two core-nuclei. The sum of the bar (usual-length) and the line (excursive length) equals the maximum-length.

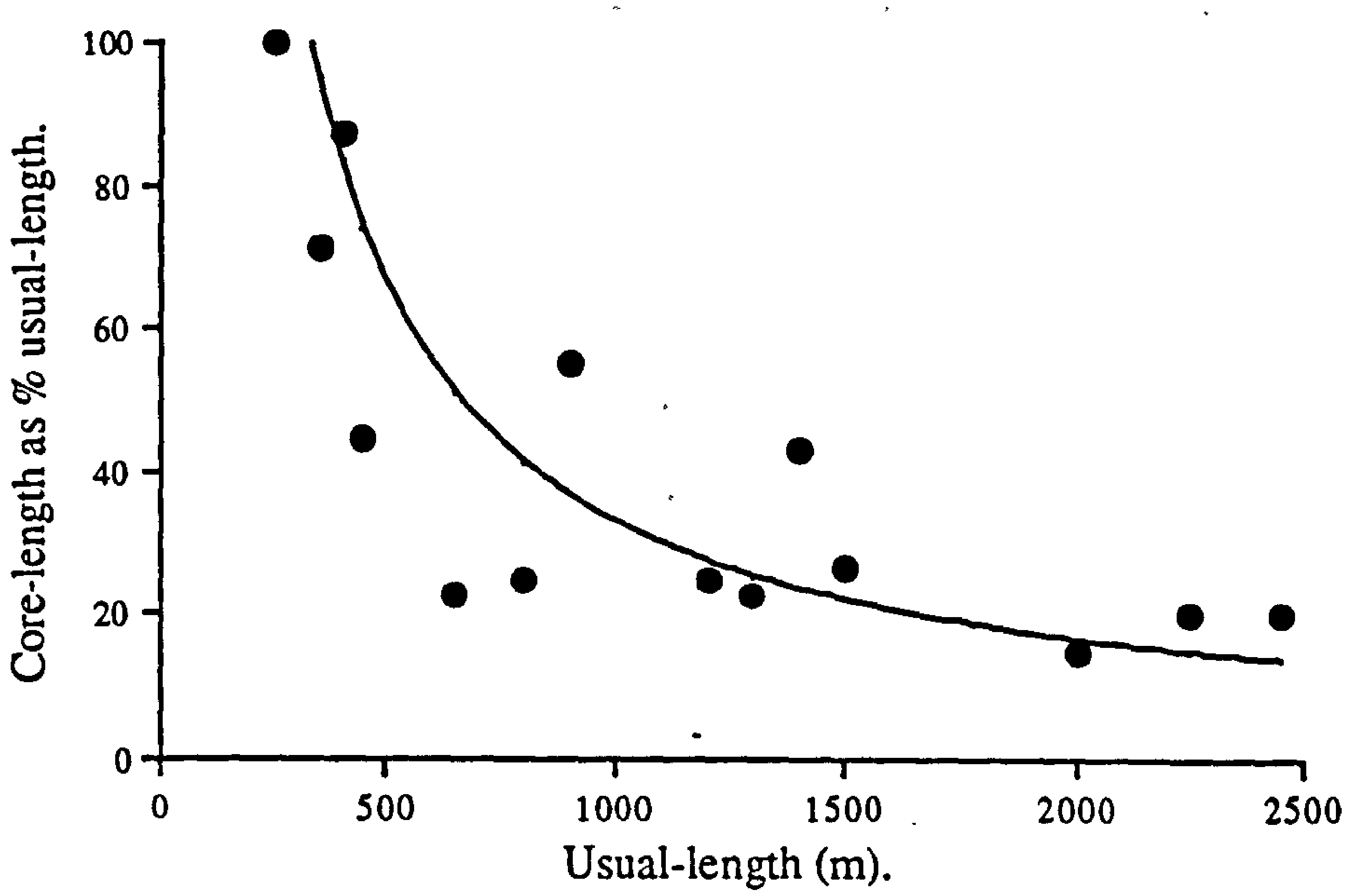


Fig.4.7. Total core length as a percentage of the usual-length for non-breeding dippers, plotted against the usual-length ($r_s$=-0.89 p<0.005 n=16). The line represents the expected distribution if all ranges contained the same core length (the median core length of all birds tracked).

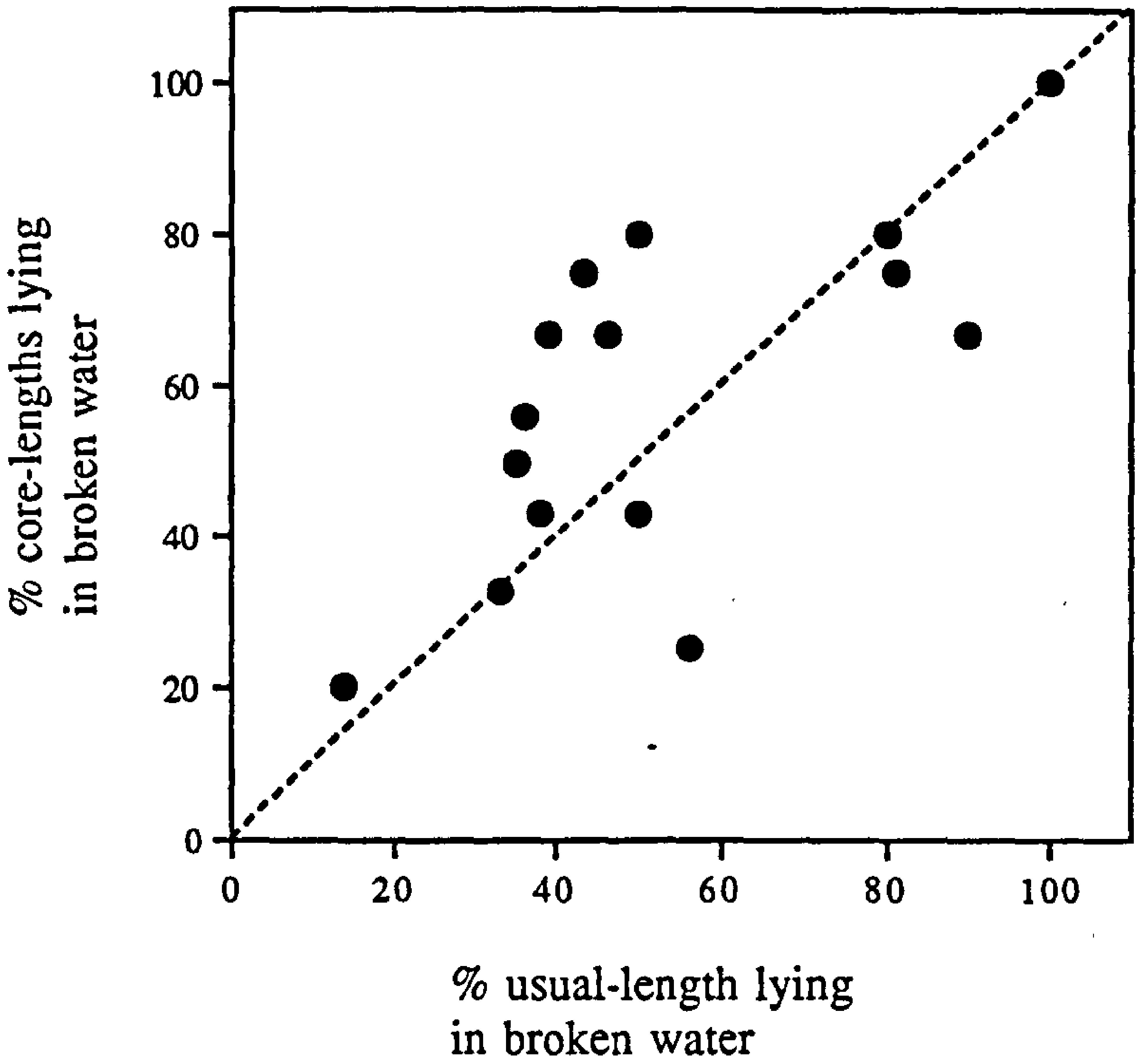


**Fig.4.8.** Percentage of usual-length lying in segments of water course that contained broken water plotted against the percentage of core-length lying in segments that contained broken water (Sign test binomial ns n=16).

sections making up usual-length containing bends=25, Sign test binomial ns n=16).

It was clear that the usual-lengths of some individuals were considerably longer than others occupying the same water course (Fig.4.9.). The usual-lengths of these individuals always overlapped the usual-lengths of one or more neighbours. Since this is unlikely to occur between neighbours that were defending territories, it suggests that individuals which were using large ranges which overlapped others were non-territorial. It was not possible to produce a definition for categorising individuals as territorial or non-territorial that was universally applicable, however the ranges of all individuals suspected to be non-territorial were distinctive in terms of length and overlap, when compared to their neighbours. Pooling the data between water courses, the maximum-lengths and usual-lengths of non-territorial individuals were significantly longer than those of territorial birds, while there was no difference in the core-lengths and number of nuclei between the two classes (Table.4.1.).

Although there was no difference between the number of territorial and non-territorial individuals which were of different sexes ($\chi^2$=0.262 ns df=1 n=16), individuals that were non-territorial were significantly more likely to be juveniles than birds which were defending territories ($\chi^2$=5.591 $p<0.05$ df=1 n=16). Here a juvenile is defined as an individual in its first year of life.

On comparing the proportions of the three study sites that were made up of broken water, it was clear that as the width increased, the proportion of 50 m segments that contained broken water decreased ($r_s$=-0.81 $p<0.005$ n=3). There was no increase in width along the length of each of the three study water courses (all $r_s$ $p>0.1$ $n>50$). As width increased between water courses however, usual-length decreased, core-length remained constant and core area increased (Table 4.2.). Core area was calculated by multiplying the total core length by the mean width of the water course occupied (Section 2.3.1.1. Table 2.27).

The sample size of territorial individuals within each study water course was too small for statistical comparisons of space use statistics to be made between different sex and age classes (for Lower Devon; male n=4, female n=2, adult n=6, juvenile n=0). The age, sex and statistics for the 16 dippers are presented in Appendix 5.

Only one territorial dipper out of the eleven that were radio-tracked, appeared to occupy a territory which could be classified as a non linear T-shaped configuration. In this individual, a small tributary was occupied briefly during a period of raised water levels. One out of eleven territorial and two out of five non-territorial dippers used core-nuclei on

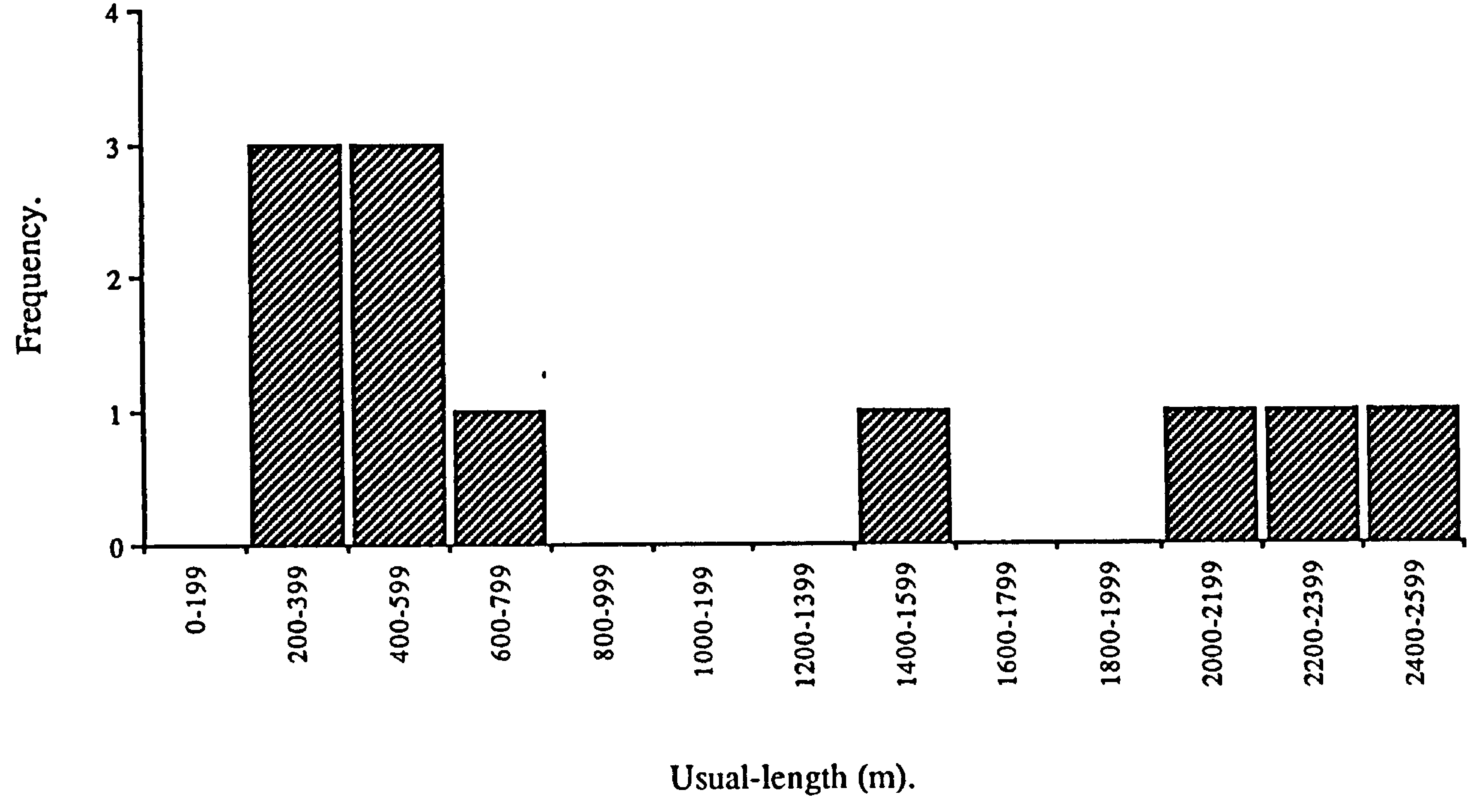


**Fig.4.9.** Histogram of usual-lengths occupied by dippers that were radio-tracked on the Lower River Devon (n=11).

**Table 4.2.** Spearman correlation coefficients between different measures of range size and the width of the water course occupied by non-breeding territorial dippers (n=11).

| Measure of range size | $r_s$ |
|---|---|
| Usual-length (m) | -0.59* |
| Core-length (m) | -0.13 |
| Core-area ($m^2$)# | 0.69* |

* $p<0.05$

\# Core-length multiplied by median width of water course occupied.

tributaries which joined the main water course some distance up-stream or down-stream of their other core-nuclei. This resulted in their using L-shaped usual-length configurations. This use of tributaries also occurred under spate conditions. The type of range configuration used by each individual is shown in Appendix 5.

Because of the small number of individuals radio-tracked concurrently in this study, the degree of short term range fidelity shown by territorial dippers could not be measured for comparison with that of non-territorial individuals. However, the percentage change in the utilization of 50m segments between two cohorts (Doncaster 1990) of location estimates is shown and compared to that for robins in Fig.4.10. In order to compare dippers and robins, for which range is measured in length and area respectively, the proportional change in grid segments/cells occupied was used. The sample size for the dipper was too small to allow statistical comparison between the two, although the ranges of both territorial dippers and robins appeared to change at a similar rate relative to their size. An example of the short term range fidelity for a territorial dipper is shown in Fig.11.a. There was only one individual for which ranges were available with an inter-cohort interval of sufficient length to assess longer term range fidelity. The two usual-lengths of the individual are illustrated in Fig.4.11.b. and show a change from territorial to non-territorial space use.

### 4.3.4. Individuals within the neighbourhood.

On modifying the definition of a near neighbour developed for use in a two dimensional system of territories, the near neighbour of a dipper may simply be defined as an individual for whom part or all of its usual-length lays within one median usual-range length of the edge of the usual-length of a focal individual. This was equal to 550m (Table 4.1.). This definition is also suitable for both linear and non-linear territories, the maximum number of near neighbours possible for these being two and three respectively.

The percentage length overlap for different measures of range overlap between the five dyads of concurrently tracked near neighbours that were recorded in this study is shown in Table 4.3. Clearly by definition, the maximum-lengths and usual-lengths of non-territorial individuals overlapped those of both territorial and non-territorial individuals, often to a large extent. The usual-lengths and therefore core lengths of territorial dyads never overlapped, although in one case the maximum-length overlapped the usual-length of a near neighbour to a small extent. An example of a group of near neighbours is shown in Fig.4.12. A median

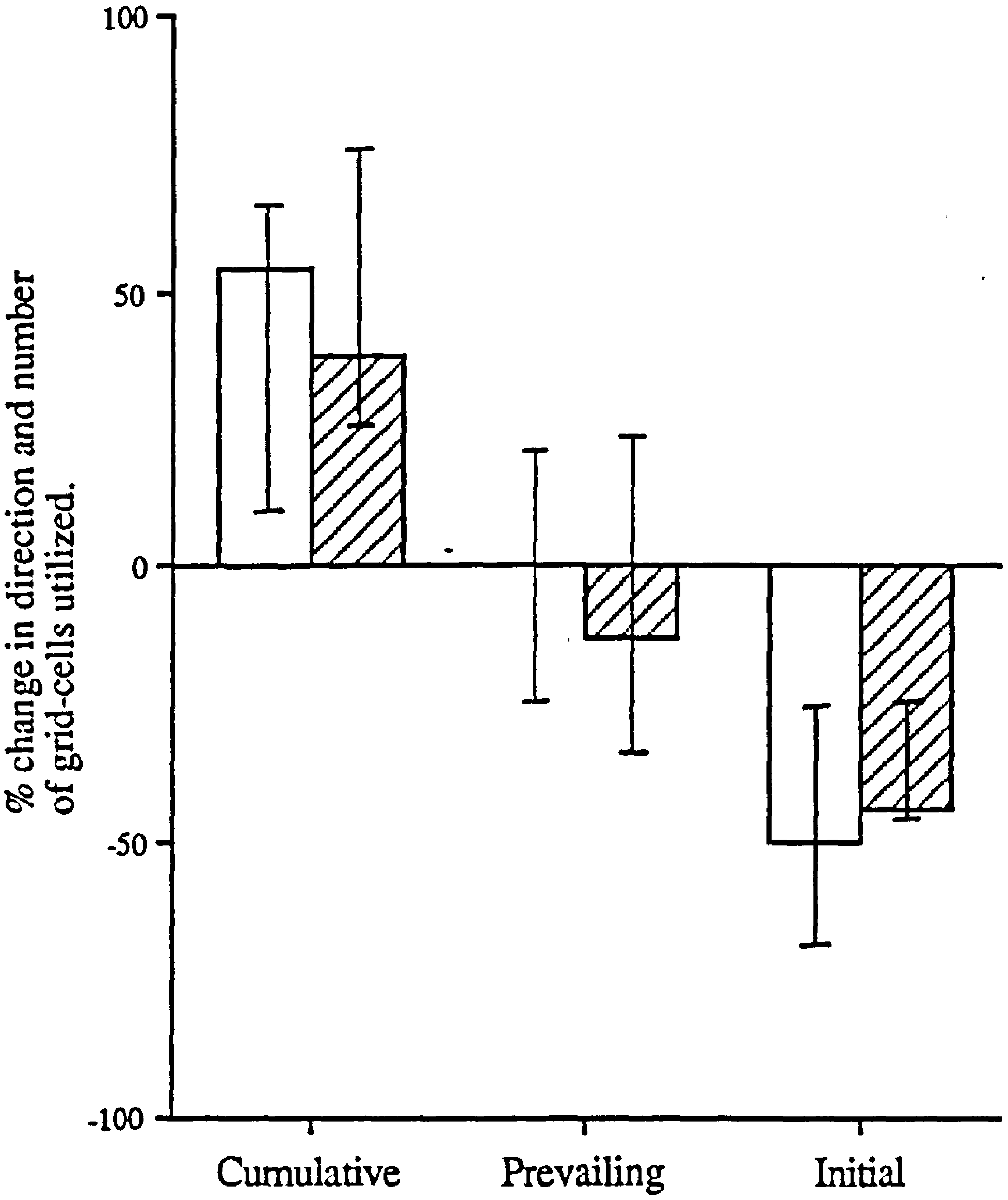
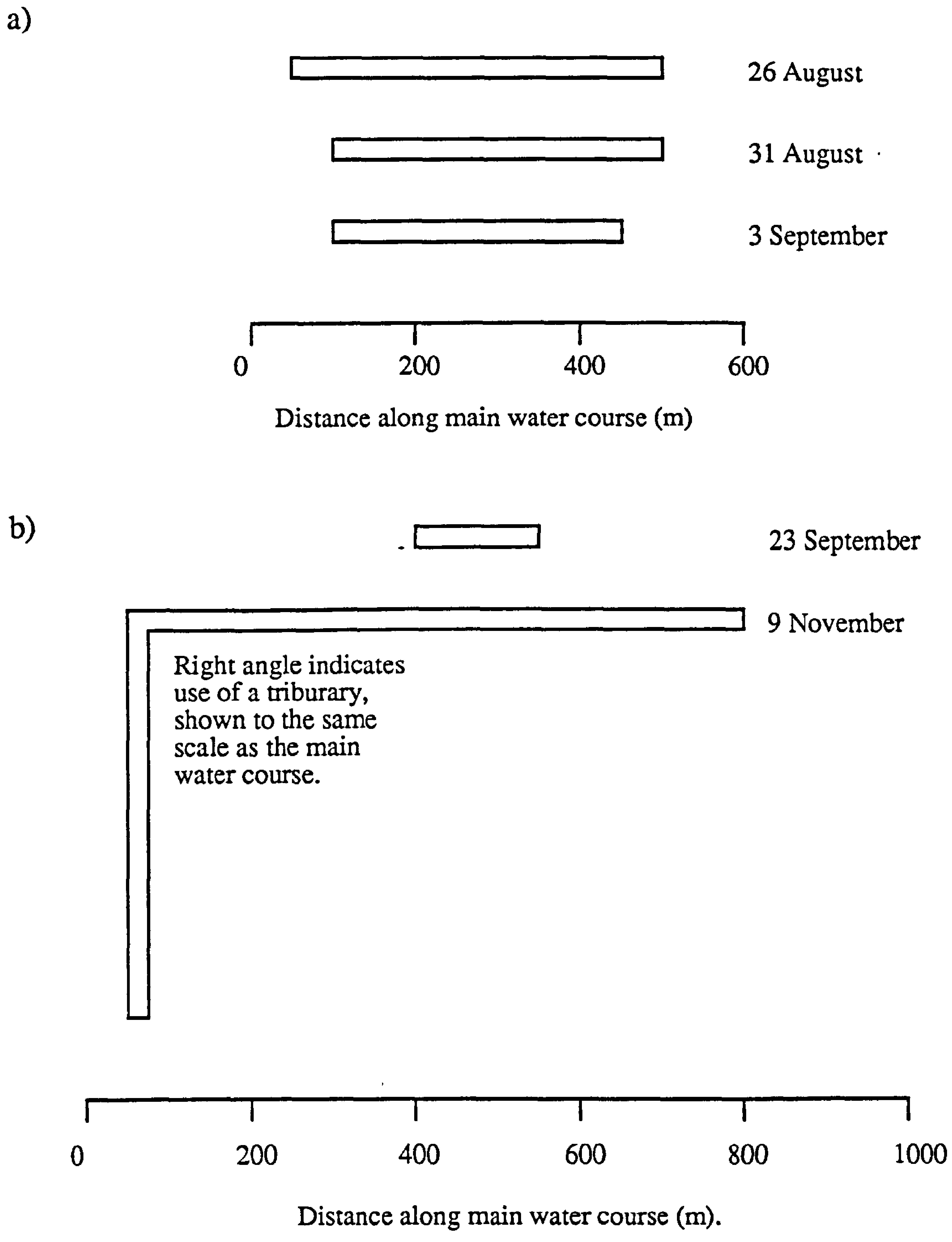


**Fig.4.10.** Comparison between the median percentage change in the number of grid cells/segments occupied by robins (hatched)(n=10) and dippers (open)(n=3). The inter-cohort interval was 6.4 days (robin) and 6.0 days (dipper). Error bars indicate ranges. The inter-cohort interval was the interval between the completion of sampling for the first cohort and the beginning of sampling for the second.



Right angle indicates use of a triburary, shown to the same scale as the main water course.

**Fig.4.11.** Examples of range fidelity in non-breeding dippers. Adult female RA84852 showed high fidelity to the segments of water course occupied over the short term on the Lower River Devon (a), while juvenile female XR68870 showed a change from territorial to non-territorial space use over the longer term on the River Ardoch (b). The open bars indicate usual-length and dates refer to the first day of sampling for each standardised sample.

**Table 4.3.** Measures of length overlap for five independent dyads of near neighbours.

| Types of individual in dyad and direction of overlap | % length overlap* | | |
|---|---|---|---|
| | Maximum-length on maximium-length | Maximum-length on usual-length | Usual-length on usual-length |
| Non-territorial XP05152 on non-territorial XP05010 | 100 | 100 | 100 |
| Non-territorial XR68870 on territorial RS03258 | 31 | 31 | 33 |
| Territorial XS44829 on non-territorial XS44849 | 69 | 69 | 62 |
| Territorial RS93655 on territorial XR68870 | 11 | 0 | 0 |
| Territorial 0XP5229 on territorial RS03258 | 0 | 0 | 0 |

* The % length of the second named measure which is overlapped by the first named measure.

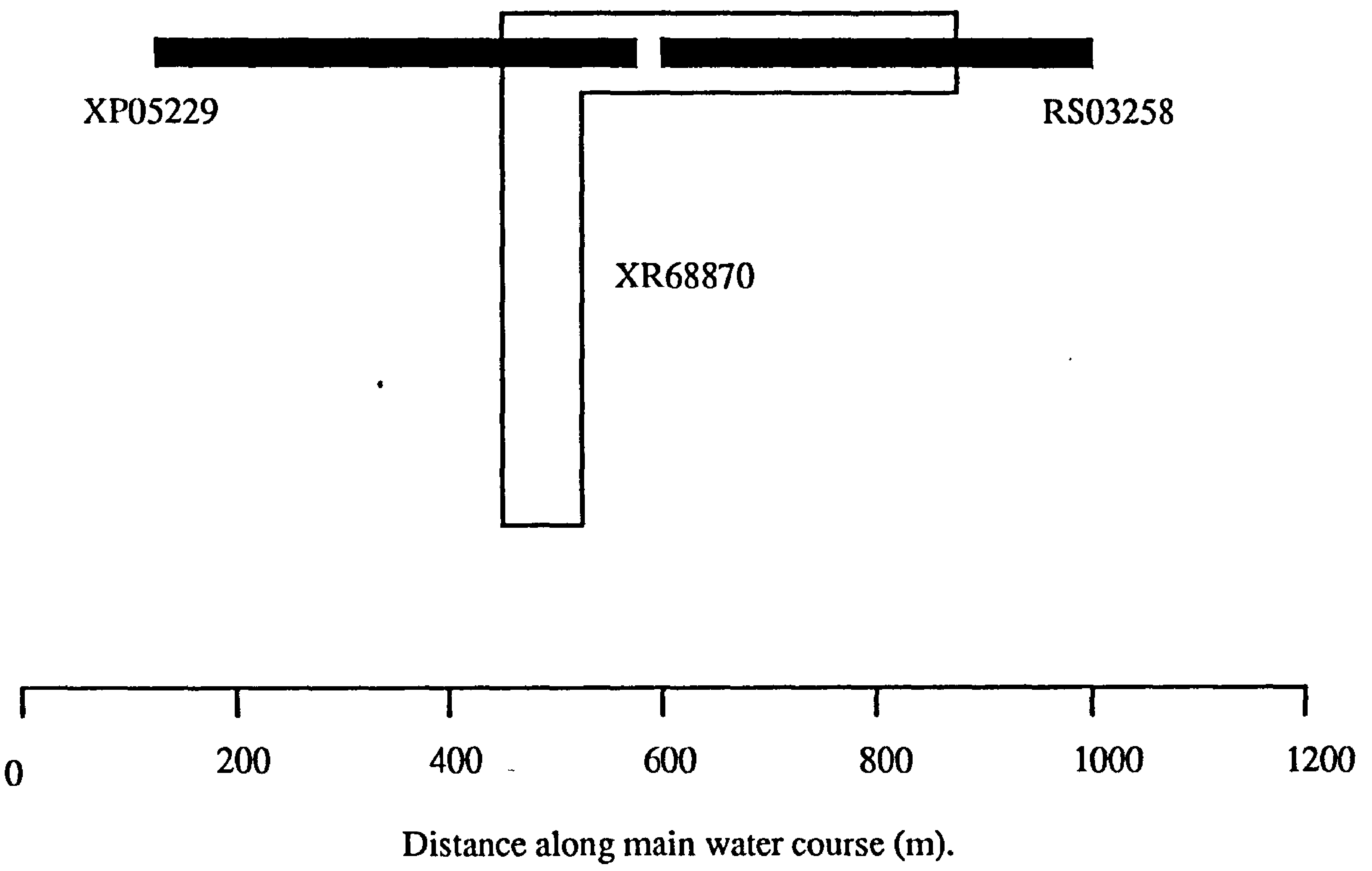


**Fig.4.12.** An example of a neighbourhood of non-breeding dippers on the river Ardoch. The solid bars indicate territorial individuals and the open bar non-territorial. Widths differ to highlight the region of overlap. Birds are identified by their ring numbers.

of 17 % of radio-locations occurred outside the usual-length of ranges of individuals that were classed as territorial. These were defined as excursive locations. Excursive locations of territorial dippers that were also intrusive in concurrently tracked neighbours were rare. Only one out of five dyads showed a small degree of intrusive activity in the core nucleus of a near neighbour.

### 4.3.5. Roost selection.

The roost sites selected by radio-tagged dippers could be assigned to two main categories. These were a) associated with artificial structures and b) in entirely natural situations. The range of situations observed within each category are illustrated in Fig.4.13., although they were not quantified to this level.

Some individuals were captured at night on their roost sites for the purposes of attaching radio-tags. Of these, a few selected a different site on the following night, suggesting that disturbance at roost sites may have effect on roost selection. One such individual selected a roost site two kilometres from where it was initially captured, returning to the first site after a few days. Other individuals merely selected a different position within the same site or occupied the same position on subsequent nights. Because of this the last night on which roost sites were recorded was used when looking for differences in selection between individuals, in order to reduce any disturbance-related biases.

There was a slight but not significant tendency for birds which selected artificial sites to travel further than birds which selected natural sites (Mann-Whitney U=9.0 ns, median distances artificial=300m range 0-2250 n=6, natural=50m range 0-950 n=4). There was also a slight but not significant tendency for dippers which roosted excursively to move upstream ($\chi^2$=1.28 ns 1df n=7, 5 moved upstream and 2 down stream). Birds which roosted excursively were however, significantly more likely to be located in a communal site than birds which remained on their usual-length to roost ($\chi^2$=4.0 $p<0.05$ df=1 n=10).

Because the effect on roost selection of capture at roost, the fidelity to particular sites over time was difficult to assess. Of two individuals which were initially captured on their territory during daytime however, both used the same sites over the five nights that they were monitored.

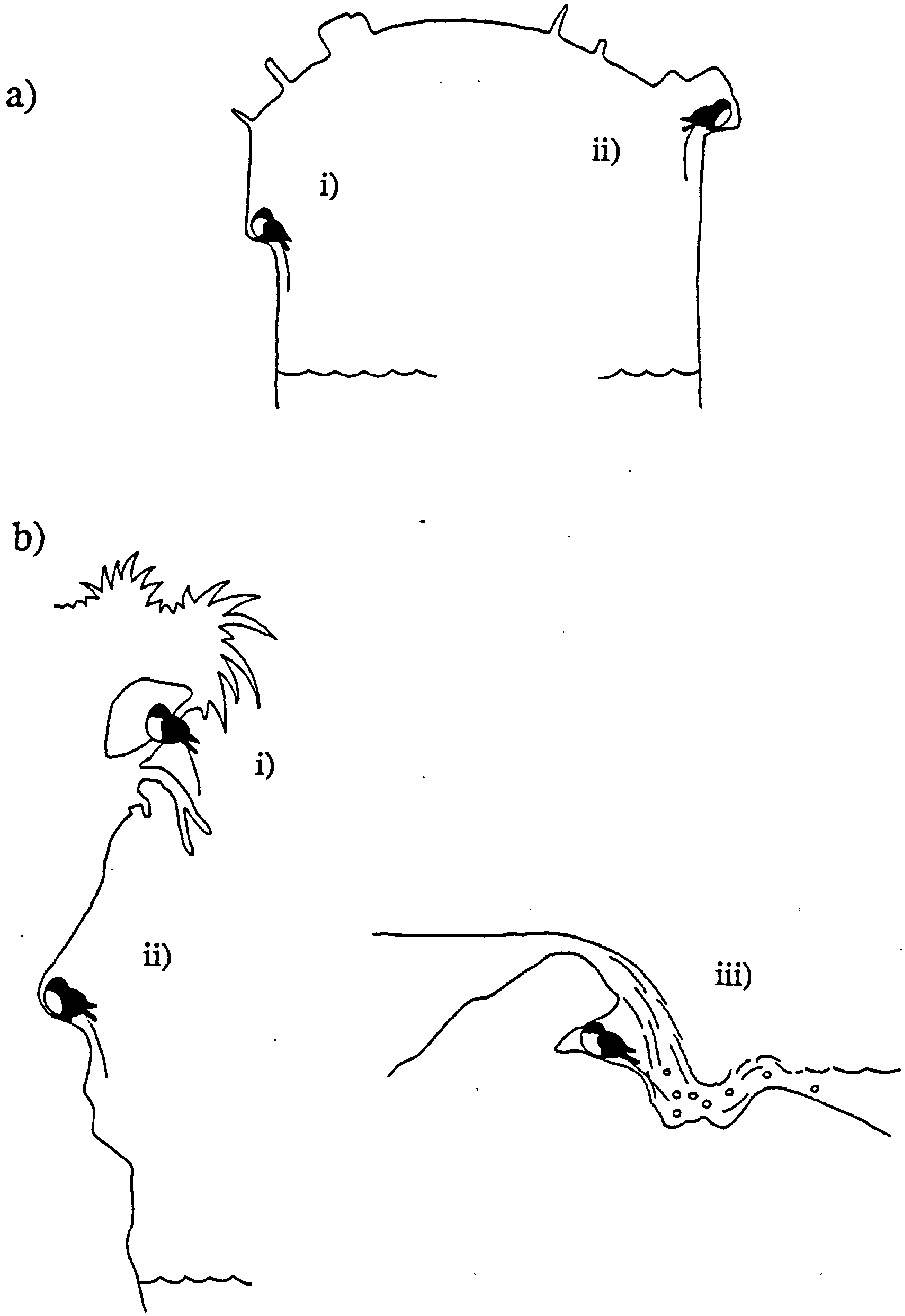


**Fig.4.13.** Categories of roost site selected by radio-tagged dippers. Artificial sites (a) contained individuals roosting on ledges (i) and in pipes and holes (ii) in bridges and culverts. Natural sites were more varied (b), with birds choosing sites under overhanging vegetation (i), on rock faces over water (ii) and even in dry cavities behind rapids (iii).

## 4.4. Discussion.

### 4.4.1. Structure of the territory and neighbourhood in the dipper.

In common with the robin, the utilization distribution of the dipper was highly non-uniform and multinuclear. Ranges contained a varying number of core nuclei separated by stretches of water which were overflown but rarely used. Together these core nuclei comprised the usual-length and represented the length of water along which each individual must travel in order to utilize its fragmented core regions. Behaviour associated with territorial defense was only recorded from dippers which were within their usual-length. This may indicate that, as in the robin, the latter measure of range use approximates the extent of the defended territory. In chapter 3. it was shown that the usual-area of the robin, the measure of range use analogous to the usual-length, also represented the space that was defended. The sizes of usual-length recorded in the present study are in general larger than the estimates of non-breeding territory length recorded by previous studies (Table 4.4.). This is possibly due to variation in the width of the water courses in the different studies, since usual-length was negatively correlated with width in the present study. This difference is however, more likely to be a result of the different definitions used to determine the lengths of territories in previous studies. Furthermore, radio-tracking allows the relocation of individuals which may have been missed by visual observations alone. This could lead to under estimation of range length, particularly if individuals were particularly widely ranging.

Some dippers were apparently non-territorial. As with the non-territorial element of the robin population however, individuals that were non-territorial could not be unequivocally identified. Nevertheless, the usual-ranges of those dippers that were classified as non-territorial were significantly longer than those of their territorial neighbours, with which they showed considerable range overlap. Although the robin study population also contained non-territorial individuals, the constraints of the riparian habitat occupied by the dipper and the resulting obligatory linear space-use, results in the non-territorial members of the population being forced to link remote core nuclei with flight paths which lay directly through the territories of one or more neighbours. Thus non-territorial dippers potentially experience a higher probability of unintentional aggressive encounters with territorial neighbours than robins, whose two dimensional pattern of space-use allows them the option of manouvering round neighbouring territories clustered in high quality habitat, when moving between remote core-nuclei. Dippers moving relatively long distances on the water course, for example when

**Table 4.4.** Comparison between the non-breeding usual-range length obtained by radio-tracking and territory length obtained by visual observations for two species of dipper.

| Species | Study | Range (m) |
|---|---|---|
| *Cinclus cinclus* | Vogt (1944) | 200-500 |
| | Balat (1962) | 100-200 |
| | Holmbring & Kjedemar (1968) | 220-830 |
| | Sudhaus (1972) | 150-200 |
| | Davenport (1983)* | 400-3200 |
| | Cousins (1985)# | |
| | Territorial | 100-775 |
| | Non-territorial | 250-1000 |
| | Present study using radio-tracking | |
| | Territorial | 250-1400 |
| | Non-territorial | 1500-2450 |
| *C. mexicanus* | Bakus (1959) | 55-963 |
| | Price & Bock (1983) | Aggression but no territoriality |

* Davenport (1983) concluded all individuals were non-territorial.

\# The definition of Cousins (1985) was "an aggressively defended area".

commuting to and from excursive roost sites, were often observed to fly very fast through the territories of neighbours or to fly much higher than territory owners that were moving between their core-nuclei. This may allow birds to move between remote locations along the riparian habitat while avoiding interactions with intervening aggressive territory owners.

The ends of territories can be considered as impermeable, through which there is no possibility of intrusions by neighbours, if they border on riparian habitat which is not occupied by other dippers. This may occur when birds occupy core nuclei on small tributaries, upstream of which there are insufficient resources to support a neighbour. When the ends of territories border on habitat that does contain neighbours, however, they must be viewed as being permeable, through which intruders can enter to trespass on the owners territory. All territory boundaries will be of this form on main water courses, where territories are of simple linear configuration. Regardless of simple linear, L-shaped or T-shaped territory configuration, therefore, it is possible that dippers may occupy usual-lengths with one, two or three permeable boundaries through which intrusions into their territories may occur.

Although the potential for occupying non-linear territories exists for the dipper, these results suggest that such configurations are rare. Some territorial and non-territorial individuals maintained core-nuclei on the main water course and on tributaries simultaneously in L-shaped configurations. It is possible, however, that these ranges represented two defended lengths occupied simultaneously or sequentially during the period of radio-tracking. Like the robin, non-territorial dippers may be nomadic and exhibit range drift. Only one dipper used core nuclei which conformed to a T-shaped configuration. This could similarly have been a transient feature or artifact of sampling protocol. Of the small tributaries present in the study sites, they were seldom used by more than one bird. Tributaries may therefore be considered "cul de sacs", containing additional foraging habitat but only hard boundaries. The edges of usual-lengths on the main water course, however, represent soft or permeable boundaries through which intruders may trespass from upstream or downstream. It is possible therefore, that intentional intruders or birds in transit between sites, may enter or pass through a neighbours linear territory without being detected while the owner is located in such a "cul de sac".

### 4.4.2. Range-use and habitat selection.

All the study water courses drained areas of similar geology, land use and climate. Any differences observed were therefore not a consequence of acidity-mediated variation in aquatic biomass on which the dippers depend for food (Vickery 1992, Ormerod *et al* 1985, Logie in press). Although the usual-length occupied by dippers varied, each contained a similar total core length. This suggests a minimum requirement of some habitat feature for survival. This phenomenon was also a characteristic of the usual-area of the robin and has been noted in a number of other studies of range use (Kenward 1982, Davies & Lundberg 1984).

It has often been suggested that dippers defend habitat which contains sufficient regions of preferred foraging habitat (broken water) to meet their energy requirements (Cramp 1988). There were, however, no significant preferences for core lengths to be located in such habitat features in the present study. Furthermore, there were no preferences for core lengths to be located on sheltered bends in the water course. Usual-lengths decreased as the width of the water course occupied increased. This has been recorded previously in the dipper (Robson 1956). The total core length however remained constant between different widths. The core area was therefore directly proportional to the width of the water course. It has been suggested that each dipper attempts to defend a particular area of broken water containing good foraging sites (Shooter 1970). The lack of clear selection for such shallow water and the varying core area indicated by this study, suggests that this is not the case. These results instead appear to show that the habitat which is defended is instead a critical length of water from which, for example, owners may have high visibility of neighbours or predators, shelter from the elements and access to broken water for foraging. Alternatively, from the proportion of time which is spent sitting quietly by the dipper during the non-breeding season (30%; Bryant & Tatner 1988) it is clear that that the radio-tracking data represent the locations of birds engaged in a wide range of activities. The resulting range statistics may therefore not correlate with the extent of any one habitat feature, if different features are utilized during different activities. The existing radio-tracking data are insufficiently detailed to measure this differential habitat utilization with behaviour.

The data were too few for a statistical comparison to be carried out between the territory lengths of dippers of different age and sex. The data do however, suggest that male dippers generally occupied longer usual-ranges than females. This has previously been shown in the dipper (Davenport 1983), although the reverse was found by Cousins (1985). The energy expenditure of dippers is positively correlated with body mass (Bryant *et al* 1985). Since male dippers are larger than females (Galbraith & Broadley 1980), the conclusion is that male dippers must defend a longer total core length in order to satisfy their daily energy requirements. Because total core lengths are fragmented into a number of core nuclei distributed along the water course, males must therefore defend a longer usual-length.

### 4.4.2. Short and long term changes in range-use.

The limited data available on the dipper in the present study suggest that like the robin, territorial dippers showed strong fidelity to the location and size of their territory over the short term. The degree of fidelity was similar to that of the robin, although lack of data from other species makes it difficult to draw a general conclusion. The fidelity shown by dippers in previous studies appears to vary. Price & Bock (1983) describe some individuals as highly sedentary, while others appeared to wander "seemingly at random". The latter presumably refer to nomadic non-territorial individuals. The non-territorial dippers recorded by radio-tracking were significantly more likely to be juveniles than birds which were defending territories. Price & Bock (1983) suggest that juvenile dispersal continues into the winter and the non-territorial dippers in the present study may have represented juveniles which had not yet managed to obtained a usual-length of sufficient quality for economic defense.

Qualitative observations in the present study suggest that dippers responded to raised water levels by establishing new core-nuclei in small tributaries, presumably where shallow water for foraging remained accessible. Such short term movements have been recorded previously in dipper populations (Balat 1962).

The data available for assessing long term range fidelity in the dipper were too few for quantitative conclusions to be drawn. It seems likely however, that territorial individuals showed high fidelity to their usual-lengths, compared to the more nomadic non-territorial birds. Switches between patterns of space-use are however to be expected as some birds gain territories and others are evicted or abandon territories that are no longer economically defendable and pursue a non-territorial existence in response for example to periods of spate. Such changes in space-use have been recorded by Bakus (1959) from observations of colour ringed dippers.

### 4.4.3. The selection of roost sites.

The types of roost site occupied by the radio-tagged dippers were similar to those recorded by other studies (Cramp 1988), with the exception of birds which roosted in natural cavities behind flowing water. These would have been impossible to locate without the aid of radio-tracking. Dippers not initially caught at roost, and for which the selection of roosts over successive nights was recorded, showed high fidelity to roost sites. This appears to be common in the dipper (Ormerod & Tyler 1990, Shaw 1979).

The dippers radio-tracked in this study showed a tendency to select roost sites that were further from their daytime range when in artificial structures such as bridges. If such artificial locations provide higher quality roost sites than are available on most territories, longer flights to and from territories would be energetically justified. Birds which chose roost sites in excursive locations were more likely to be in the company of other dippers, forming a communal roost. This phenomenon was similarly recorded in the robin. The conservation of energy during the long winter night has been suggested as a reason for the use of bridges for roosting (Shaw 1979, Ormerod & Tyler 1990). Since such high quality sites are relatively rare along the water course (only 6 bridges were used for roosting on approximately 10 km of water course), it would be expected that dippers from the surrounding area will commute to and roost communally within such structures. One individual commuted over two kilometres every dusk and dawn to reach its chosen roost site, further than the nearest natural site known to have been used at the same time. The large distances that some individuals were prepared to fly to reach an artificial roost site suggests the advantages of such behaviour is considerable. For example security from nocturnal predators and shelter from severe weather (Shaw 1979, Ormerod & Tyler 1990).

When roosting excursively, movements towards roost sites tended to be in an upstream direction. Hewson (1969) also observed this preference and suggested that is was due to the greater abundance of roost sites in the upper reaches of streams and rivers. This was probably true for the radio-tagged dippers occupying territories on the lower reaches of the widest water course, but for the other study sites suitable sites appeared abundant along their whole length.

# Chapter 5.

# 5. Short term territory use in the robin; predictions and tests.

## 5.1. Introduction.

Animals meet their energy requirements by foraging. For predators, the density of the prey they exploit may vary two ways. Firstly, the density of prey items exploited by some predators can vary due to events independent of the predators activity (Charnov 1976). An example of such prey is that exploited by the spotted flycatcher. This small bird catches flies in swarms during short flights from perches, where it scans for scans for prey items. The density of flies does not change during the time a perch is used, successive inter-catch intervals being similar (Davies 1978). Changes in availability of prey therefore depend on whether a swarm of flies happens to be within striking distance from a perch, rather than any effects of the predator on the swarm (Davies 1978).

Secondly, a predator may deplete the available prey in a local area either directly by consuming all the accessible items, or indirectly by disturbance of the remaining prey. Daily or seasonal changes in, for example prey mobility, will however, mean that both short and long term changes in the profitability of different areas may occur that are outside the predators control (Charnov 1976). Any small insectivorous birds such as the robin and the dipper are likely to experience this form of variation in prey density.

In situations where prey densities are reduced by the presence of a predator, the animal must at some point to move to an undepleted patch if it is to maximise its feeding rate (Charnov 1976). Once the predator has depleted and abandoned a patch, mobile prey items may redistribute themselves such that the patch is once more profitable to exploit. The phenomenon of patch recovery means that under certain circumstances the resource, represented by renewing prey densities within patches, can be exploited most efficiently by defending them as territories; owners can temporally schedule their visits to patches to coincide with maximum prey densities (Davies 1980).

Previous studies have discussed territorial defense in terms of concepts such as patrol time (Schoener 1987) or boundary patrolling (Dill 1978), often without quantitative field evidence. Consequently, there is little information on how territorial exploitation and defense is achieved and what behaviours, and therefore energy costs, are involved. Because of this, previous estimates of the form of the cost constraint on territory size cannot yet be considered accurate.

Radio-tracking can provide information not only about what habitat features are used by small territorial birds, but also how they are used over time. This presents an opportunity to determine; a) the pattern of resource exploitation within territories and b) what activities comprise territorial defense and the degree to which they are mutually incompatible with territory exploitation.

The robin was found to occupy territories of different shape, estimated by their eccentricity, which ranged from polygonal to highly linear. The dipper on the other hand occupied territories that were essentially only linear. Consequently it was considered more informative to focus on the energetic consequences of the large variation in the shapes of territories defended by the robin, rather than on a comparative study of the different territorial systems of both robin and the dipper.

## 5.2. The territory as a network.

### 5.2.1. Differential space-use within the usual-area.

In previous studies, robin territories have been assumed to consist of enclosed and usually fixed areas with abrupt but permeable boundaries (eg Lack 1965, Brindley 1991). This may be an unrealistic model since it is already apparent that territories are highly dynamic in location over time (chapter 3). Furthermore, the probabilistic model of territory use shows that the robins are normally located in a varying number of core-nuclei (78% of occasions), separated by areas that were rarely visited (1% of occasions)(Fig.3.31.). If the birds used all of their core nuclei on a regular basis (for the purposes of territorial exploitation and defense), they must therefore have been moving between nuclei very rapidly for them to have been recorded in transit so infrequently.

Continuous tracking data from robins of sample interval two minutes indicated that they moved significantly faster when commuting between nuclei than when travelling within nuclei (Wilcoxon signed rank matched pairs test $Z=-2.80$ $p<0.01$ $n=10$, median speed; within nuclei=2.5 m $\text{min}^{-1}$ range 0-5.4, between nuclei=19.5 m $\text{min}^{-1}$ range 12.4-70.0). Qualitative observations indicated that this was because movements between nuclei were predominately by means of flight, while within nuclei birds spent their time engaged in perch and drop foraging (East 1980, 1982), foraging by hopping on the ground and resting. The estimates of speed while engaged in the two different types of movement from continuous tracking were equal or lower than direct measurements of flight or hopping speed (flight 3.85 m sec$^{-1}$ and hopping 1.5-2.5 m min$^{-1}$, Tatner & Bryant 1986). This was because the two minute sample interval between continuous radio-tracking locations allowed time for birds to engage in activities such as pausing for vigilance during commuting and repeatedly quartering prey-rich areas within nuclei.

From the examination of samples of continuous tracking data, it was apparent that not only were inter-nucleus commuting movements rapid, but individuals tended to follow the most direct routes. An example of such movement is shown in Fig.5.2.1. Based on these observations the territory may be better considered simply as a number of core nuclei within which birds foraged, linked by a network of preferred flight paths.

### 5.2.2. The classification and shape of hypothetical networks.

Using this concept of a territory as a variable number of feeding patches linked by preferred flight paths, it is possible to construct a set of hypothetical territory networks in which core-nuclei are represented by points and are separated by commuting distances representing the preferred flight paths. These networks may vary in two ways; a) the number of core-nuclei being used and b) the commuting distances between nuclei. These two forms of variation are not mutually exclusive.

The simplest form for such models is the uniform mononuclear territory described by Grant (1969). As the initially mononuclear territory fragments into an increasing number of core-nuclei (increasing patchiness), owners must begin to commute between foraging patches in order to utilize their whole territory. When the number of nuclei increases, so does the number of potential configurations for the commuting paths. This is illustrated in Fig.5.2.2. for hypothetical networks for which all inter-nucleus commuting distances are the same distance d. The cost of moving between any pair of nuclei is therefore constant. At one extreme robins may select core-nuclei which constitute an ideal-linear configuration. In such territories, robins must pass through all nuclei when moving between the most distant points of their territory. This is essentially identical to the pattern of use shown by most dippers defending lengths of river. Alternatively, robins may select core-nuclei for which the network of flight paths enables it to reach the majority of its foraging patches without having to pass through intermediate nuclei. This was termed an ideal-polygonal territory configuration

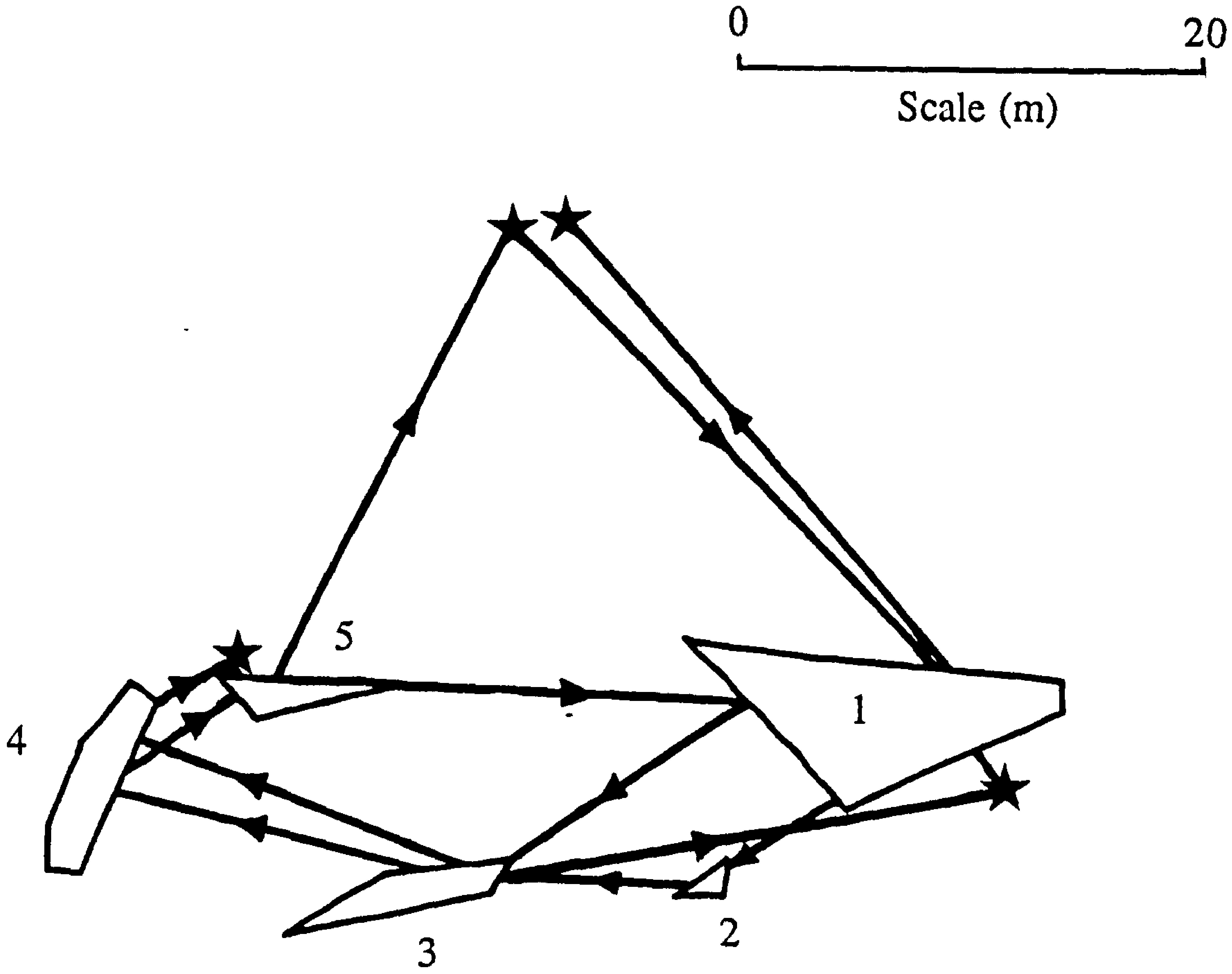
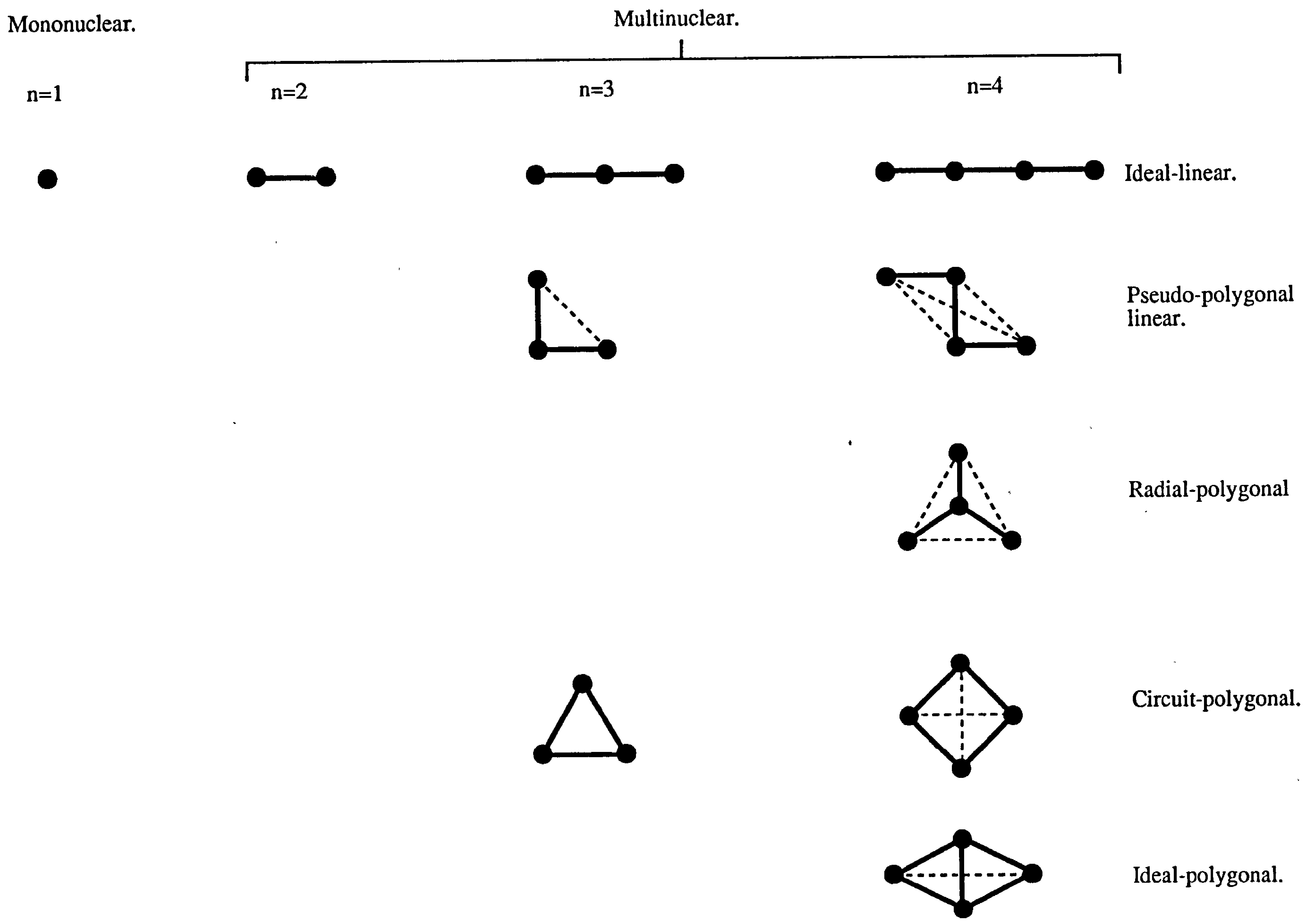


**Fig.5.2.1.** Continuous tracking data from non-breeding territorial robin F646594. In this example only 4 (10 %) of locations occured outside the core-nuclei polygons, here indicated by stars. Nevertheless some were very close to and therefore most likely still associated with the nearest nucleus. The sample interval was 2 min and the sampling period 1 hr.

**Fig.5.2.2.** The range of hypothetical territory configurations for different numbers of core-nuclei. Nuclei are depicted as points, connected by preferred flight paths. Solid lines indicate flight paths of distance d, dashed lines indicate potential flight paths of distance greater then d. Use of these longer flight paths can decrease the distance to the other nuclei within networks, but at the cost of increased individual commuting distances.


Mononuclear.
Multinuclear.
n=1
n=2
n=3
n=4
Ideal-linear.
Pseudo-polygonal linear.
Radial-polygonal
Circuit-polygonal.
Ideal-polygonal.

(Fig.5.2.2.). Between these two extremes lie a range of intermediate configurations, within which territory owners can reach varying numbers of their constituent foraging patches within a commuting distance d (Fig.5.2.2.).

In addition to the above variation, each of these networks may also vary simply by increasing or decreasing the individual commuting distances between nuclei (Fig.5.2.3.). As the individual flight distances between feeding patches increase so will the cost of each movement.

In chapter 3. the shape of robin territories was quantified using an index of eccentricity applied to irregular polygons. From the range of potential configurations however, it can be seen that some apparently polygonal territories (low $\epsilon$) may be utilised by a network of highly linear configuration (pseudo-polygonal linear). In order to compare the relative merits of polygons and networks in measuring the accessibility of patches within the territory, it was necessary to derive a measure of territory shape based on the configuration of flight paths. An index of linearity L was calculated by following the procedure in Fig.5.2.4., where examples for different configurations are also shown. L varies in a consistent manner for networks of different configuration and number of core-nuclei (Table 5.2.1. Fig.5.2.5.). Values of L greater than 0.25 indicate ideal-linear use, values equal to 0.25 indicate circuit-polygonal use and values less than 0.25 indicate varying degrees of polygonal use. The lowest values of L indicate ideal-polygonal use.

On applying the index of linearity, it is apparent that a polygonal territory is a network within which it is not necessary to pass through all the constituent core-nuclei in order to travel along its greatest length. For a robin occupying a particular core-nucleus therefore, L may be viewed as a measure of the accessibility of other nuclei in the individuals network. The proportion of nuclei accessible within the same flight distance within networks containing four core-nuclei and of different values of L are shown in Fig.5.2.6. The use of L therefore allows territory networks of different patchiness to be assigned to the different categories of configuration. Note that mononuclear territories are non-configurational, owners not needing to commute between patches during territorial exploitation and defense. The index L is therefore not relevant to such ranges. In Fig.5.2.2. therefore, both $\epsilon$ and L increase from left to right and from bottom to top.

In the network configurations illustrated in Fig.5.2.2. the commuting distances shown by solid lines represent the flight distance d. Dashed lines indicated distances greater than d.

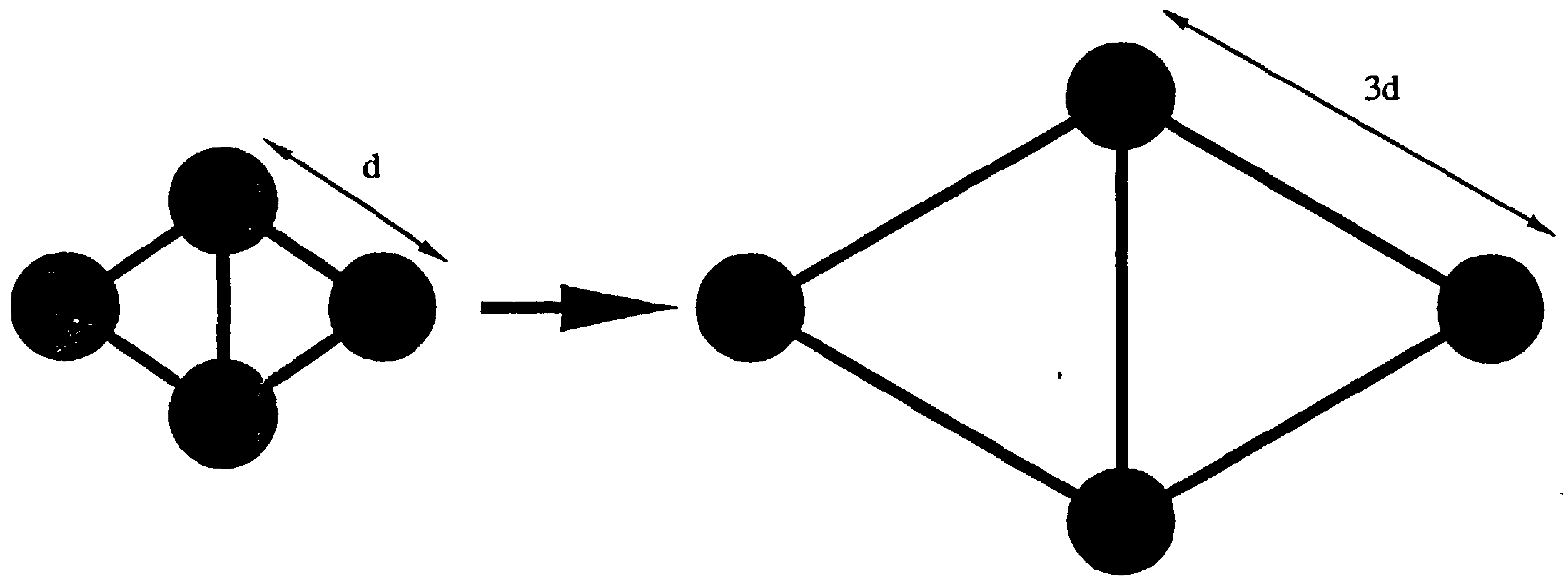


**Fig.5.2.3.** The configurations of core-nuclei can also vary by increasing or decreasing all the flight distances between nuclei. Increased flight distances will increase the cost of using the different nuclei during territory exploitation and defense.

**Fig.5.2.4.** Calculation of the index of linearity for quantifying the configurations of territory networks. The value of L is derived from the number of core-nuclei, and the matrix which decribes the movement possibilities within the network. Examples of networks, matrices of different values of L are shown in b) and c).

a)

$$\text{Index of linearity } L = \frac{(n/M_{tot})}{M_{max}}$$

*Where;*

*$n$ = No. core-nuclei in the territory network.*
*$M_{tot}$ = The total number of movement possibilities (the sum of the cells in the matrix describing the network).*
*$M_{max}$ = The maximum number of movement possibilities from one nucleus (the highest total of any column or row in the matrix).*

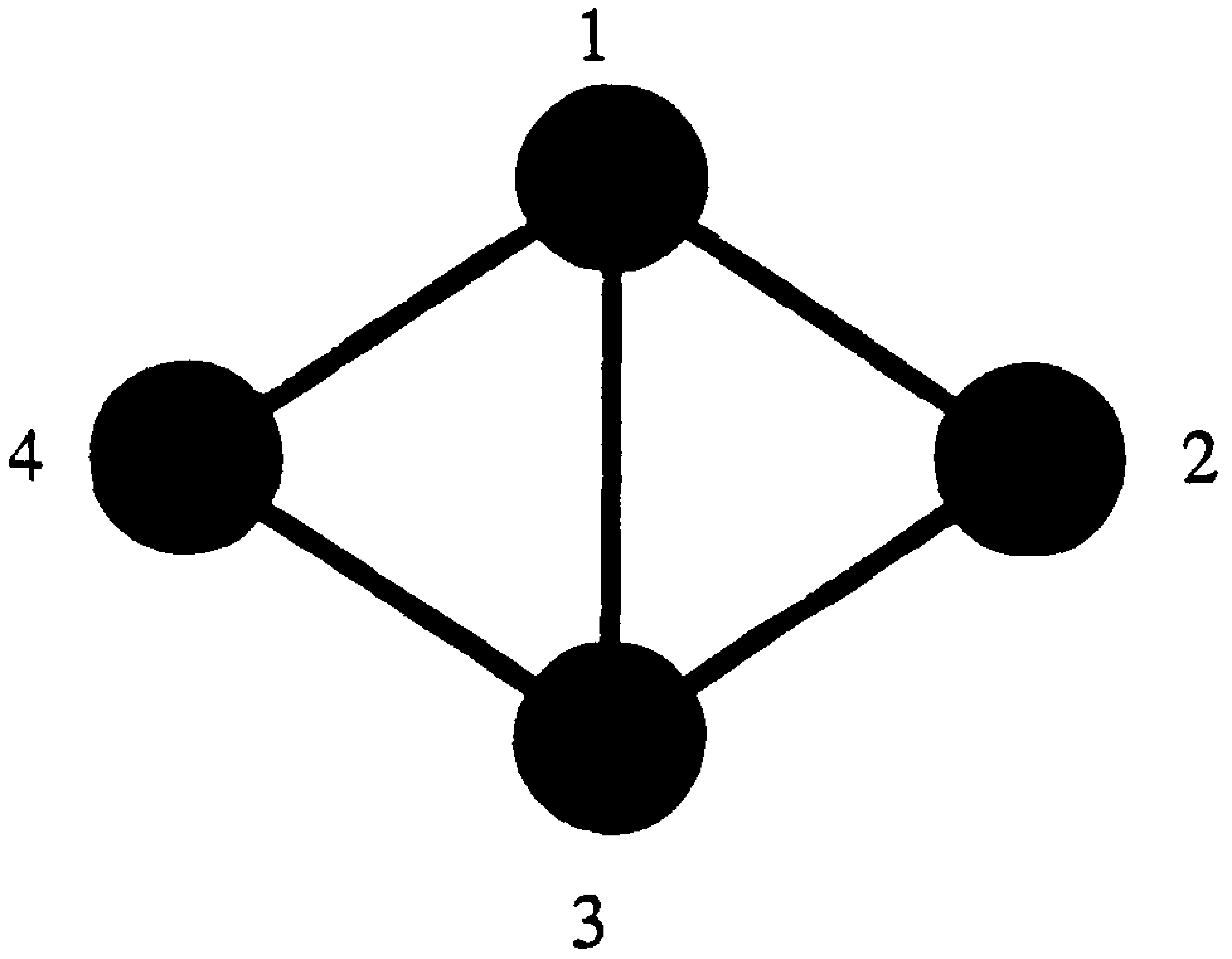
b)

Matrix of movement possibilities within network

$$\begin{array}{c|cccc} & 1 & 2 & 3 & 4 \\ \hline 1 & 0 & 1 & 0 & 0 \\ 2 & 1 & 0 & 1 & 0 \\ 3 & 0 & 1 & 0 & 1 \\ 4 & 0 & 0 & 1 & 0 \end{array}$$

$n = 4$
$M_{tot} = 6$
$M_{max} = 2$
$L = 0.33$

c)



Matrix of movement possibilities within network

$$\begin{array}{c|cccc} & 1 & 2 & 3 & 4 \\ \hline 1 & 0 & 1 & 1 & 1 \\ 2 & 1 & 0 & 1 & 1 \\ 3 & 1 & 1 & 0 & 1 \\ 4 & 1 & 1 & 1 & 0 \end{array}$$

$n = 4$
$M_{tot} = 12$
$M_{max} = 3$
$L = 0.11$

**Table 5.2.1.** Values of the index of linearity L for different configuration types containing different numbers of core-nuclei.

| Configuration type | No. core-nuclei | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Ideal-linear | - | 1.0 | 0.38 | 0.33 | 0.31 | 0.30 | 0.29 |
| Circuit-polygonal | - | - | 0.25* | 0.25 | 0.25 | 0.25 | 0.25 |
| Radial-polygonal | - | - | - | 0.22 | 0.16 | 0.12 | 0.06# |
| Ideal-polygonal | - | - | 0.25* | 0.13 | 0.09 | 0.07 | 0.06# |

* # Similar values of L indicate network configurations were identical.

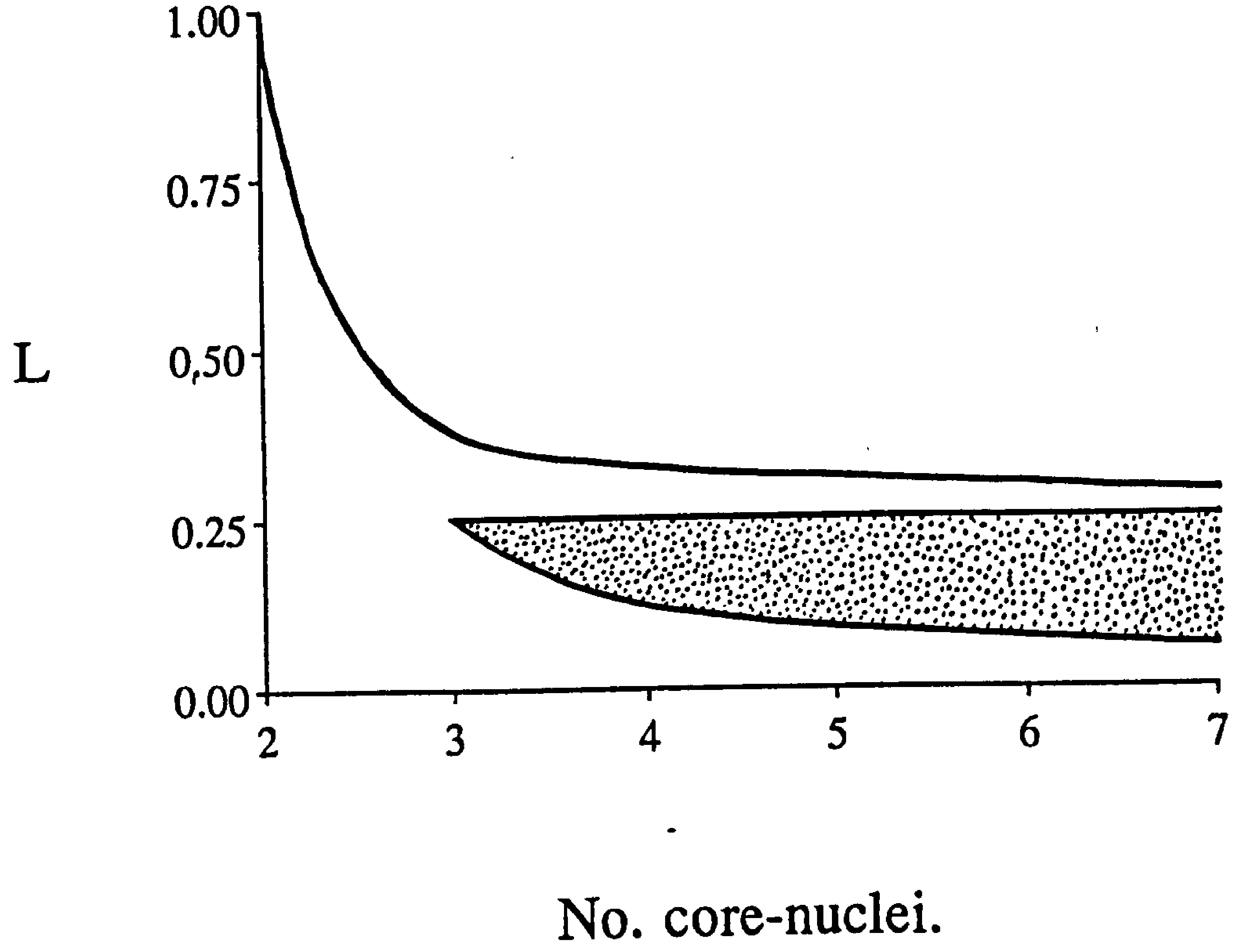


**Fig.5.2.5.** The behaviour of the index of linearity L for different classes of network configuration containing different numbers of core-nuclei. Values of L greater than 0.25 indicate ideal-linear configurations, values equal to 0.25 indicate circuit-polygonal configurations and the lowest values of L indicate ideal-polygonal configurations. Between circuit-polygonal and ideal-polygonal lie a range of possible hybrid configurations and range of associated values for L. Mononuclear territories were non-configurational and therefore L was not relevant to them.

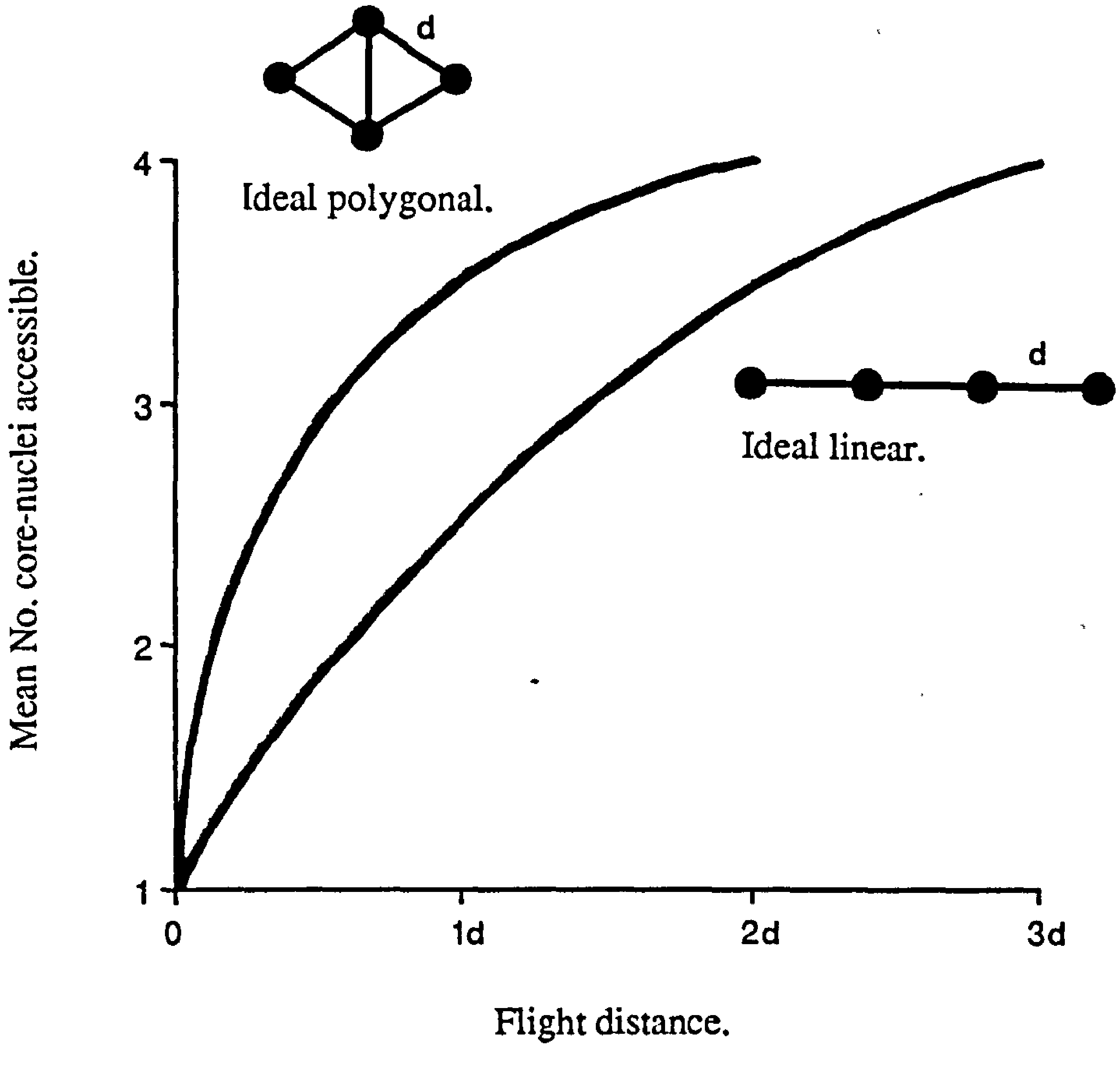


**Fig.5.2.6.** The mean number of core-nuclei accessible within different inter-nucleus commuting distances for ideal-linear and ideal-polygonal territory configurations, each containing four core-nuclei. More nuclei were accessible within a given commuting distance in the polygonal configuration than the linear.

Robins which choose to commute between nuclei along these longer routes will experience a decreased L. The total distance to their other foraging patches will therefore decrease, increasing the accessibility of the range as a whole. Individuals using longer flight paths will however incur an increase in the energy cost of individual commuting movements. Furthermore, longer flights may expose birds to a higher predation risk by giving aerial predators such as sparrowhawks longer to pinpoint and launch an attack on a flying bird (Newton 1986).

In ideal linear configurations of core-nuclei, the angle between pairs of flight paths is 180°. This represents the maximum angle possible between commuting routes and prevents occupants from using additional flight paths longer than d. The minimum angle possible between commuting paths of equal length is 60°. Angles equal this when flight paths take the form of equilateral triangles. In such situations L can be minimised. Values of angles between these extremes will provide opportunities for the use of longer flight paths as short-cuts to otherwise distant nuclei. This will produce intermediate effects on the accessibility of foraging patches within territories.

To recap, territories of high $\in$ must contain networks of high L. Territories of low $\in$ however, may contain networks of low or high L depending on the owners motivation to use inter-nuclei commuting paths of different cost. An apparently polygonal territory may be used in a highly linear manner.

### 5.2.3. The quantification of network use from field data.

The pattern of use of territory networks was measured using continuous tracking data. A sample interval of two minutes, the minimum interval feasible for manual radio-tracking, ensured that radio-location estimates showed high serial autocorrelation. This form of data can reveal how the configuration of core-nuclei suggested by sequential cluster analysis were used during each bout of continuous tracking. Because of the inevitable natural variations in robin movements however, it was necessary to construct a series of "movement rules" in order to define intra-nuclei activity, inter-nucleus commuting and excursive movements.

The core-nuclei defined by discontinuous tracking data often contained less than the proportion of continuous tracking locations that would be expected from the probabilistic model of territory structure (Fig.3.31.). This was considered to be due to territory drift and the effects of seasonal and weather induced micro-habitat selection (eg Walsberg 1993). For example during October each year, many acorns were squashed on the road running through the study site. This was exploited as a food source by the robins whose territories lay close to the road, resulting in a shift in activity to the edges of nuclei which provided the best access. Histograms of distance from the edge of core-nuclei both within and outside the usual-area for continuous tracking data are shown in Fig.5.2.7. These suggested that robins concentrated their activity in the area defined by a two metre wide boundary strip around each of the core-nuclei predicted by discontinuous tracking data. Of the 300 continuous tracking locations from 10 individuals which fell outside the core-nucleus polygons (Fig.5.2.7.), 59 % were within 2 m of the core polygon edges. When two nuclei were separated by less than two metres they were considered to have been used as one, forming a "complex nucleus". This occurred in 19% of territorial individuals (n=43) but had no effect on the median number of nuclei within networks (without boundary strip median=4 range 1-7 n=43, with boundary strip median=4 range 1-6 n=43). The mean area of the core-nuclei and boundary strip within each territory network were significantly correlated with the mean area of the bushes they occupied ($r_s$=0.77 p<0.005 n=10 Fig.5.2.8. Table 5.2.2.). The data lay close to the line expected if both were the same size. This suggested that the edge of the boundary strip corresponded with the edge of the bushes occupied.

Although this two metre boundary strip ensures that on average 76% of continuous tracking locations could be directly assigned to particular core-nuclei, there were still small numbers of locations which lay outside these areas. Some of these occurred within the usual-area while others were excursive. Robins may forage in the open for short periods while still being associated with and subsequently returning to a particular nucleus (for example during perch and drop foraging; East 1980, 1982), or may more rarely be recorded during a commuting movement to a different nucleus. Only one of these indeterminate locations would, if classed as being outside a nucleus, be sufficient to disrupt measurements of the duration of nucleus occupancy or sequences of inter-nuclei commuting. Since it is this information that is required to determine patterns of patch use, these locations must be further classified.

By constructing lines of equi-distance between nuclei, it was possible to assign the intermediate locations to the nearest nuclei on the assumption that such movements originated within or were directed towards them. This definition is based on the position in space of the intermediate locations. The locations that occurred outside the usual-area however, included brief movements just outside the boundary strip and true excursive activity, including

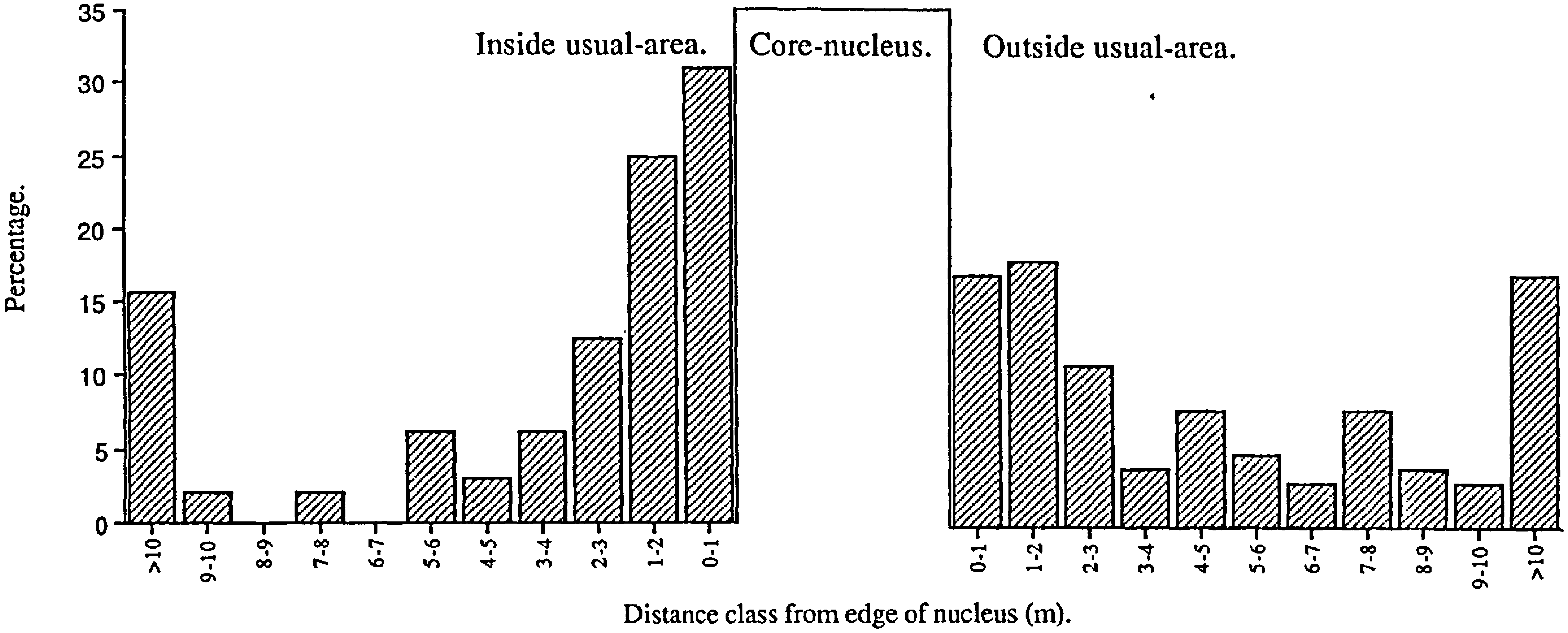


**Fig.5.2.7.** Histograms of distance from the edge of core-nucleus polygons for both inside (n=32 based on 1 hr continuous tracking from 10 individuals) and outside (n=93 based 1 hr continuous tracking of 10 individuals) usual-area polygons.

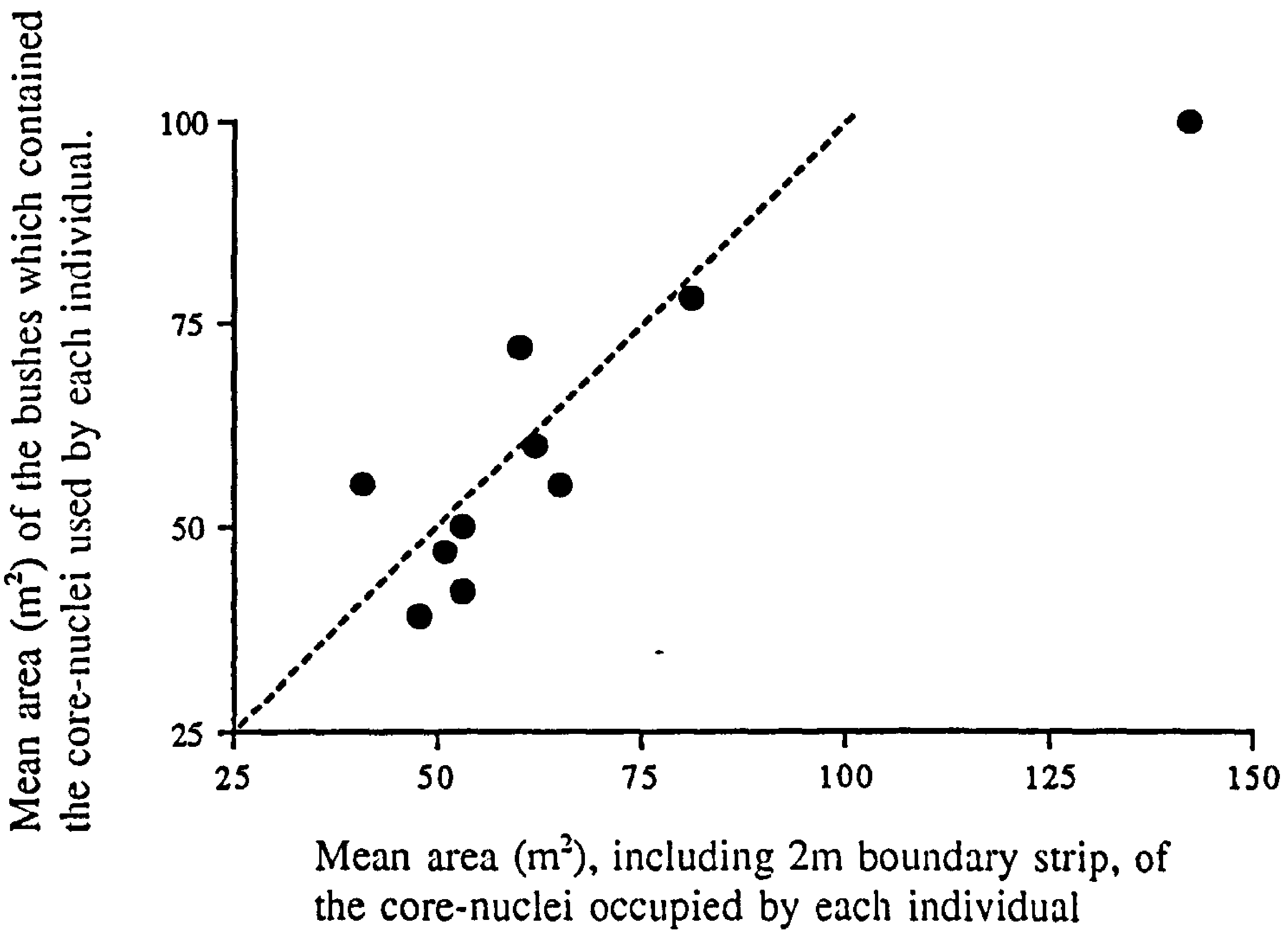


**Fig.5.2.8.** The relationship between the mean area of the core-nuclei within each territorial range and the mean area of each bush they occupied ($r_s=0.77$ $p<0.005$ $n=10$). The individual areas of the nuclei and bushes in each range are shown in Table 5.2.2. The line indicates the expected distribution if core-nuclei were the same area as the bushes in which they were located.

**Table 5.2.2.** The individual and mean areas of core-nuclei and the bushes in which they were sited. Since the sample sizes of means (No. core-nuclei) varied from 1 to 5, the mean was considered a more consistant measure of central tendancy than the median.

| Revised No. core-nuclei # | Areas of core-nuclei including 2 m boundary strip ($m^2$) | | Areas of bushes occupied ($m^2$) | |
|---|---|---|---|---|
| | Individual nuclei | Mean | Individual bushes* | Mean |
| 3 | 37,57,66, | 53 | 33,45,49, | 42 |
| 4 | 62,85,39,52 | 60 | 77,92,63,56, | 72 |
| 1 | 142, | 142 | 100, | 100 |
| 3 | 12,14,116, | 48 | 61,41,16, | 39 |
| 2 | 18,112, | 65 | 40,65, | 55 |
| 5 | 33,31,79,19,45, | 41 | 40,30,29,90,86, | 55 |
| 4 | 59,46,55,51, | 53 | 62,61,40,37, | 50 |
| 3 | 60,79,105, | 81 | 60,75,100, | 78 |
| 4 | 45,67,50,84, | 62 | 71,65,29,73 | 60 |
| 3 | 63,28,62, | 51 | 67,20,54, | 47 |

\# Includes complex nuclei.
* Order corresponds to that of core-nuclei.

intrusions into neighbouring territories. Here the duration of each excursion must be used in determining the category into which locations fall, leading to a definition based on time. The frequency with which excursive movements of different durations occurred, based on 35 excursions by 10 individuals, are shown in Fig.5.2.9. Although these data were not statistically independent, the majority of excursions (66 %) were equal to or of less than four minutes duration. Using a sub-sample of independent data, bouts of excursive activity were equal to or of less than four minutes duration significantly more often than excursions longer than four minutes (Goodness of fit test $\chi^2=3.6$ $p<0.05$ one tailed $n=10$). The test was one tailed because excursions of longer than four minutes were not expected to be more frequent. There was no relationship between the median duration of excursions and the median value of maximum distance individuals attained from their nearest nucleus ($r_s=-0.12$ ns $n=10$). More distant excursive movements therefore were not of longer duration. A duration of four minutes however, was adopted as the cut off point beyond which movement outside the usual-area and boundary strip was considered to be of excursive intent. This arbitrary period was judged to allow insufficient time for an individual to gain significant information concerning neighbours, or to have its own foraging success reduced by a simultaneous intrusion by a neighbour onto its own territory. This space and time based classification of intermediate locations is summarised in Fig.5.2.10.

It was not possible to determine the routes of all flight paths in observed ranges with a high degree of certainty. This was because their use varied in intensity, some nuclei were not visited during a window of continuous tracking and some birds may have used different flight paths in different situations. A measure of network accessibility (L) therefore, although useful in demonstrating the differences between hypothetical networks, cannot be directly applied to the dynamic pattern of space use shown by real territorial robins. Hence it was only possible to measure the lengths of the flight paths that a bird would use if minimising each commuting distance between its core-nuclei. The extent of the departure from this base line value in territories with low $\in$ and therefore potentially low L, will indicate the degree to which their use departs from that of an ideal-linear pattern.

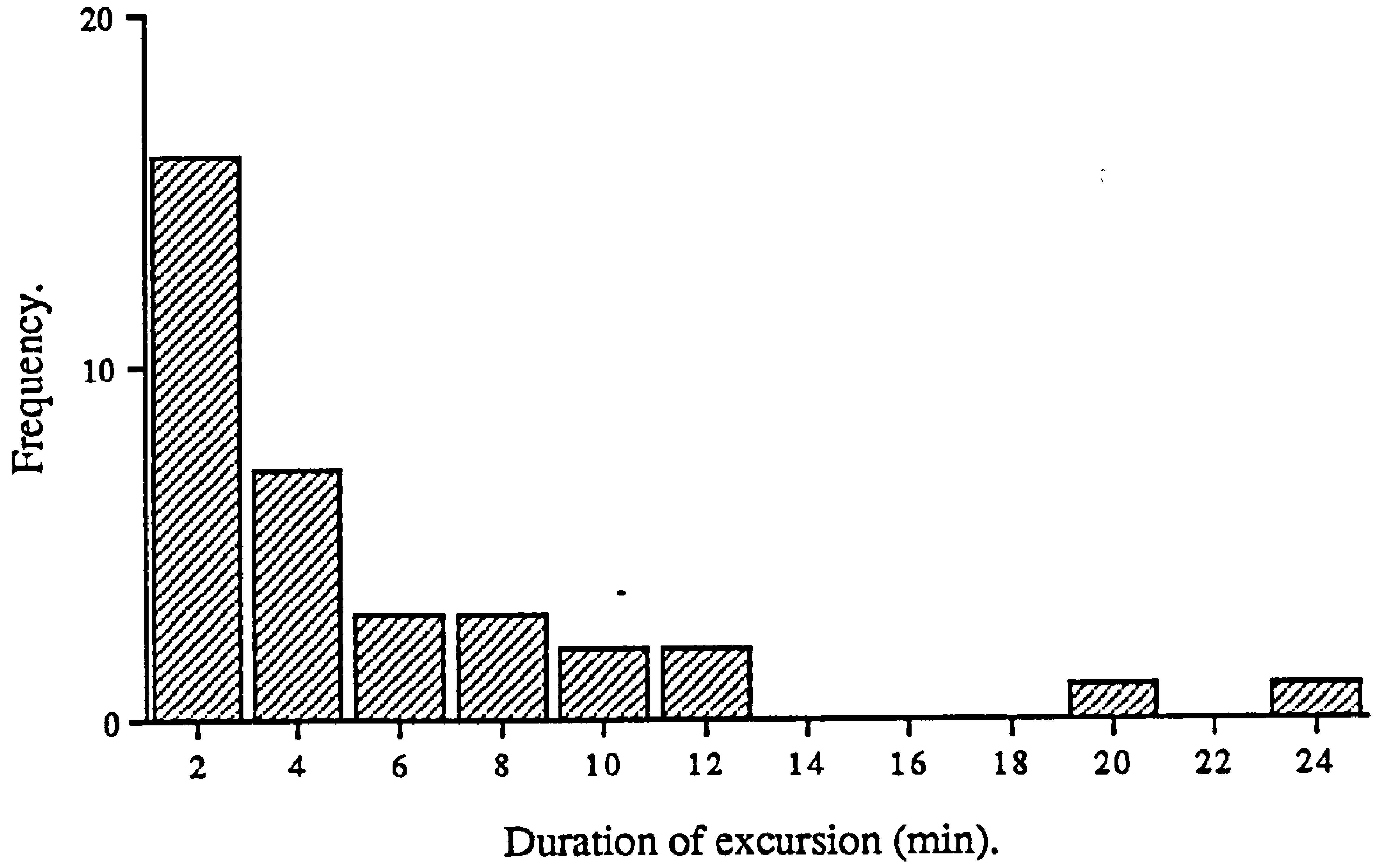


**Fig.5.2.9.** Frequency histogram showing the duration of bouts of excursive activity (n=35 from 10 individuals). The sample interval for continuous tracking data was equal to 2 min. One excursive location was assumed to represent activity of duration 2 min.

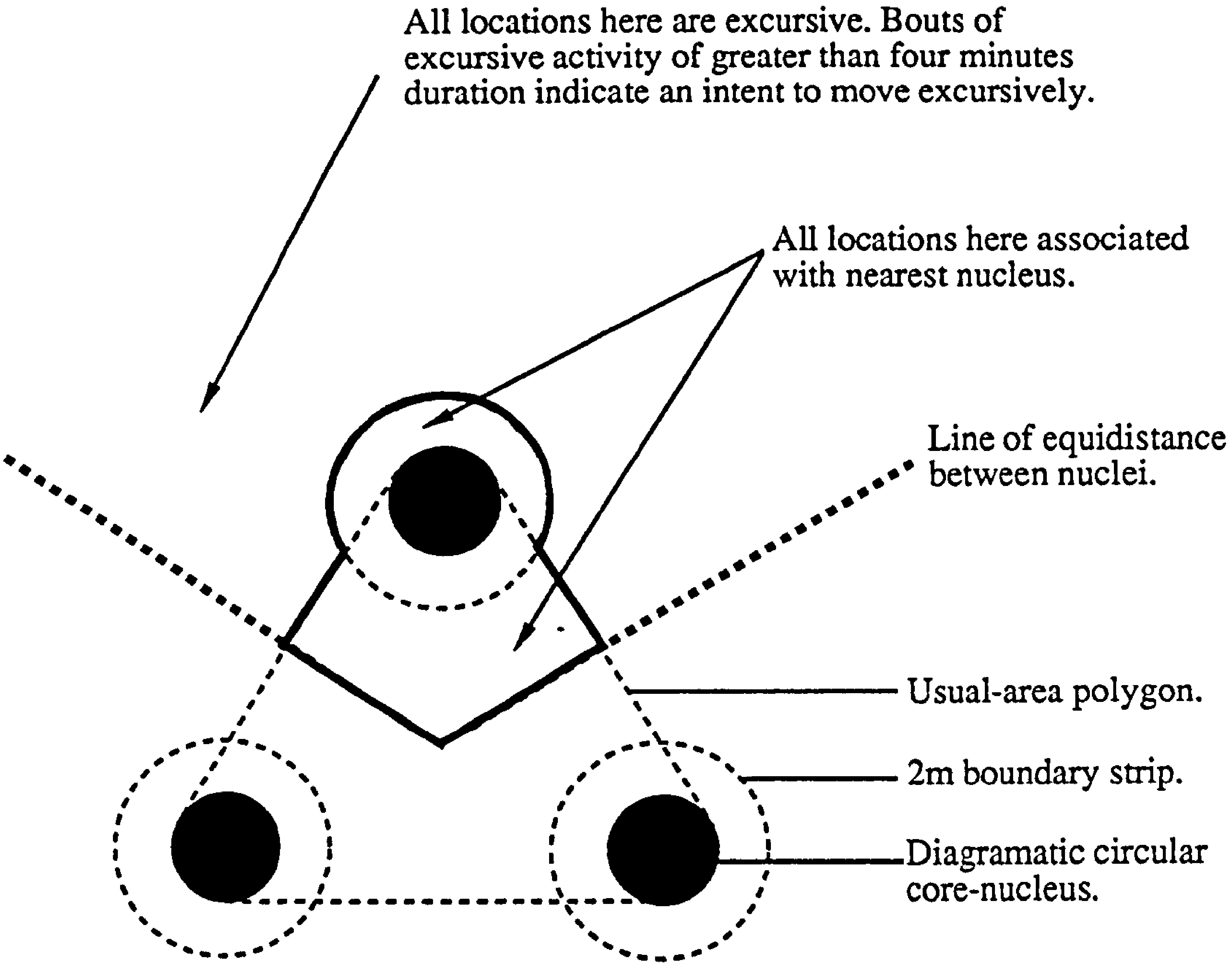


**Fig.5.2.10.** Summary of the movement rules applied to continuous tracking locations. Following these, intermediate locations could consequently be assinged to a particular core-nucleus, or to true activity of excursive intent.

## 5.3. The use of nuclei within networks.

### 5.3.1. Predation of a renewing food supply.

Previous studies have shown that the robin in winter preys mainly on small mobile invertebrates collected from the ground surface (Lack 1948, Cramp 1988, Grajetsky 1993), although fruit is also sometimes taken (Harper 1984). The size of prey items taken by robins has also been correlated to bill morphology (Herrera 1978). The remains of prey found in the stomachs of dead birds dissected for body composition analysis in this study supported these observations (Table 5.3.1. Appendix 6.).

From chapter 3 it was apparent that robins concentrated their foraging behaviour in a varying number of core-nuclei. These corresponded to the position of shrubs and bushes, which were considered habitat patches of high quality. On arriving in a patch, the capture rate experienced by a robin will follow a function of diminishing returns as the number of prey items available on the ground surface decreases. Such resource depression within a patch will occur primarily through the consumption of prey by the predator (Charnov *et al* 1976). The resource may also be depressed simply by the presence of the predator in the patch; the mobile invertebrate prey moving into cover and becoming inaccessible to the predator (microhabitat depression; Charnov *et al* 1976). This has been shown to occur in the robin (Grajetsky 1993), its effects being reduced by birds employing perch and drop foraging behaviour (East 1980, 1982) instead of hopping along the ground. So, within a particular patch the feeding rate of a robin will decline exponentially with time until it reaches zero, by which time all the prey initially available have been consumed; have moved out of sight; or have adopted a cryptic posture. If the non-breeding robin is assumed to be maximising its rate of energy intake over the day (energy maximiser with a time constraint; Schoener 1969), individuals must at some point make the decision to give up foraging in a depleted patch and incur the short-term cost of commuting to an undepleted patch where its foraging rate is likely to be higher. The time period between arriving in a new patch and leaving after giving up foraging has been termed the "giving-up time" (Davies & Houston 1981).

Once abandoned, the number of prey available in a depleted patch will start to recover as previously hidden invertebrates move into sight. The time that it takes for the prey availability in a depleted patch to return to its initial value is the recovery time (Davies & Houston 1981). Assuming that the giving-up time is considerably shorter than the recovery time for foraging robins, the most profitable behaviour is that which ensures the time elapsed

**Table 5.3.1.** Percentage of robin stomachs which contained each of the different items. See Appendix 6. for stomach contents of individuals.

| **Phylum**<br>Class<br>*Order* | % stomachs containing each category | |
|---|---|---|
| | Present study (n=28) | Lack(1948)(n=13) |
| **Mollusca** | | |
| Gastropoda | | |
| *Pulmonata* | 4 | 8 |
| **Annelida** | | |
| Oligochaeta | | |
| *Lumbricidae* | 0 | 8 |
| **Arthropoda** | | |
| Arachnida | | |
| *Acarina* | 7 | 8 |
| *Pseudoscorpiones* | 4 | 0 |
| *Araneae* | 11 | 23 |
| Crustacea | | |
| *Isopoda* | 4 | 0 |
| Myriapoda | | |
| *Diplopoda* | 11 | 0 |
| *Chilopoda* | 11 | 0 |
| Insecta | | |
| *Thysanoptera* | 4 | 8 |
| *Hemiptera* | 7 | 38 |
| *Coeloptera* | 74 | 77 |
| *Lepidoptera* | 0 | 15 |
| *Diptera* | 56 | 38 |
| *Hymenoptera* | 11 | 31 |
| *Dermaptera* | 19 | 31 |
| Vegatable matter | 22 | 23 |
| Seeds | 11 | 46 |
| Grit | 52 | - |

between giving-up and returning to the same patch (the return time; Davies & Houston 1981) is equal to the patch recovery time. Shorter than this and the robin will incur a cost in the from of a reduced feeding rate, by trying to exploit patches that have only partially recovered. Longer than this and the robin will spend more time travelling to other patches than is necessary in order to return to a fully replenished patch. This will also have associated cost. For example, failure to harvest fully recovered patches may make the territory relatively more attractive to intruders. Alternatively, robins may need to visits patches as soon as they have fully recovered simply to fuel their energy requirements. Perhaps because of a processing constraint (Schoener 1971), such as stomach size, robins may be constrained into consuming prey items in small quantities and thus more frequently. Consequently in the absence of any behaviour associated with resource defence, a territorial robin should commute between the core-nuclei within its territory network in a sequence such that each is depleted of prey after a regular time period. Assuming patches only begin to recover once the predator has left and the prey densities are uniform within and between patches of different size, this regular sequence of visits would be expected for robins using networks containing few high quality patches or many low quality patches. The reason for this is that both types of patch will recover at the same rate after depletion, leading to the adoption of the same return time by owners. The results from chapter 3 already suggest that usual-areas tended to contain similar total core areas. As the number of nuclei increases therefore, the area of individual nuclei would be expected to decrease along with the duration of visits required to harvest the available prey.

Based on the networks of patches described in section 5.2., the most economic configurations will be those that allow access to all patches in a sequence of visits that minimises the total commuting distance. Such configurations are those classified as circuit-polygonal, ideal-polygonal and to a lesser extent pseudopolygonal-linear if owners choose to use longer and more costly individual flight paths as short cuts (Fig.5.2.2.). In these configurations linearity L is equal to or less than 0.25. Assuming individuals only exploit patches that are, or based on their return time would be expected to be, fully recovered, robins using ideal-linear configurations (L greater than 0.25) must at some point pass through a number of the patches within its network without pausing to forage in order to reach the next recovered patch.

### 5.3.2. Methods.

The ranges comprising the independent sample of utilization distributions analyzed to determine the locations of core-nuclei and usual-areas, were inspected to determine the linear-length of each range. This was the total of the commuting distances that individuals would use if minimising the lengths of individual movements between nuclei. Individual commuting distances were measured to the nearest metre between the geometric centres of each relevant pair of nuclei.

Robins commonly leave their roost sites well before sunrise (Harper 1985), often when it is still dark. Birds could not be continuously tracked this early since to a large extent continuous tracking data represented radio-assisted visual observation. Nevertheless, it was considered important to monitor birds as early in the day as possible since most singing in the robin has been reported to occur at dawn (Harper 1984). Accordingly, periods of continuous tracking were carried out, each lasting one hour, at dawn (starting within a few minutes of sun rise), dusk (timed to finish when the birds went to roost) and during the middle of the day. The timing of the latter period varied but was always within a couple of hours of noon. Foraging and singing are mutually exclusive activities in the robin (East 1982). The cost of singing at dawn, therefore, may be low since the benefits of foraging are limited. This is because low temperatures or light levels make invertebrates less detectable (Kacelnik & Krebs 1982). Although prey items are less be less likely to initially escape if chilled, prey densities will take longer to recover once depleted. Ten minutes was always allowed to habituate the focal bird to the presence of the observer. In addition to the location of individuals, a note was made of the locations at which focal birds engaged in vocalisation (song and tic-calls) or evicted intruders. The total time spent singing was also recorded to the nearest second on a stopwatch.

The continuous tracking data and behavioral observations were superimposed onto the core-nuclei and usual-area polygons measured for each individual. The latter were based on discontinuous tracking data collected not less than one week before the continuous tracking was carried out. For these ranges, the angles between the individual commuting paths that minimised distances between nuclei were also measured. These were measured to the nearest degree at the geometric centres of the core-nuclei from which they originated. The pattern of use of the core-nuclei was then quantified by applying the movement rules described in section 5.2. The measures of range and network use are described in Table 5.3.2. These were

**Table 5.3.2.** Descriptions of the measures of range and network use by which continuous tracking data was quantified after applying the movement rules in section 5.2.

| | |
|---|---|
| **Proportion of time on usual-area;** | The proportion of continuous tracking locations that were inside the usual-area polygon of each individual. |
| **Commuting rate between core-nuclei (movements $hr^{-1}$);** | Number of occasions per hour that birds left one nucleus and commuted directly to another.* |
| **Visit duration of birds to core-nuclei (min);** | The mean duration of those visits to nuclei in which birds were observed to arrive and leave. |
| **Time singing (sec $hr^{-1}$);** | Total time singing per hour. |
| **Proportion of locations at which birds vocalised;** | The proportion of continuous tracking locations at which birds sang or tic-called. |
| **% departure from ideal-linear use of nuclei;** | The percentage decrease in total distance moved between nuclei from that expected if birds always minimised individual commuting distances.* |
| **Proportion of movements that were back-tracks;** | The proportion of inter-nucleus commuting movements in which the bird returned to the nucleus that it had left in the previous movement.* |

* Using a 2 min sample interval, every visit to core-nuclei could be recorded. Any situations in which an intermediate nucleus was not visited, therefore, indicated departure from ideal-linear territory network use.

selected to quantify parameters of space use both within and outside territory networks.

If robins foraging within their territory networks follow the predictions for exploitation of a renewing food supply within patches, it would be expected that they should visit their core-nuclei in a regular sequence or circuit, such that the return time of the individual equals the recovery time of the prey within patches. The degree of randomness of direction in the commuting movements between core-nuclei could not be assessed directly using a statistic such as the Runs test of serial randomness (Zar 1984). This was because such a test requires the two categories of movement (move to new nucleus or "back-track" to previously visited nucleus) to occur with approximately equal frequency. Since robins visiting nuclei of a polygonal network in a regular sequence will never back-track as long as the number of nuclei is greater than two, such a test is inappropriate. The proportion of a particular individuals movements that are backtracks however, does provide a crude measure of the departure from the predicted regular sequence of exploitative visits to core-nuclei.

### 5.3.3. Results.

#### 5.3.3.1. Network structure.

The number of core-nuclei occupied by each territorial individual was positively correlated with the size of the usual-area within which they were contained ($r_s$=0.47 $p<0.001$ n=43). This relationship was more significant when the number of nuclei was replaced by the number revised to include complex nuclei, formed by the addition of two metre boundary strips to the edges of core nuclei ($r_s$=0.62 $p<0.001$ n=43). From section 5.2. it was clear that robins spent most of their time within this area during continuous tracking and when considering the size of individual patches used by robins therefore, this area must be included. Furthermore, this relationship was less significant than the correlation between the "revised" number of nuclei and the linear length of each territory network ($r_s$=0.68 $p<0.001$ n=43 Fig.5.3.1.). Also shown for comparison are the data for non-territorial robins. All subsequent references to the core area and number of core-nuclei refer to the revised number and area including 2 m boundary strip.

The average individual commuting distance (the linear-length divided by the number of commuting paths) was not correlated with the number of nuclei in ranges ($r_s$=0.01 ns n=43), indicating that within territory networks of different numbers of nuclei, the individual minimum commuting distances were similar (median 20 m range 8-52). If territory networks

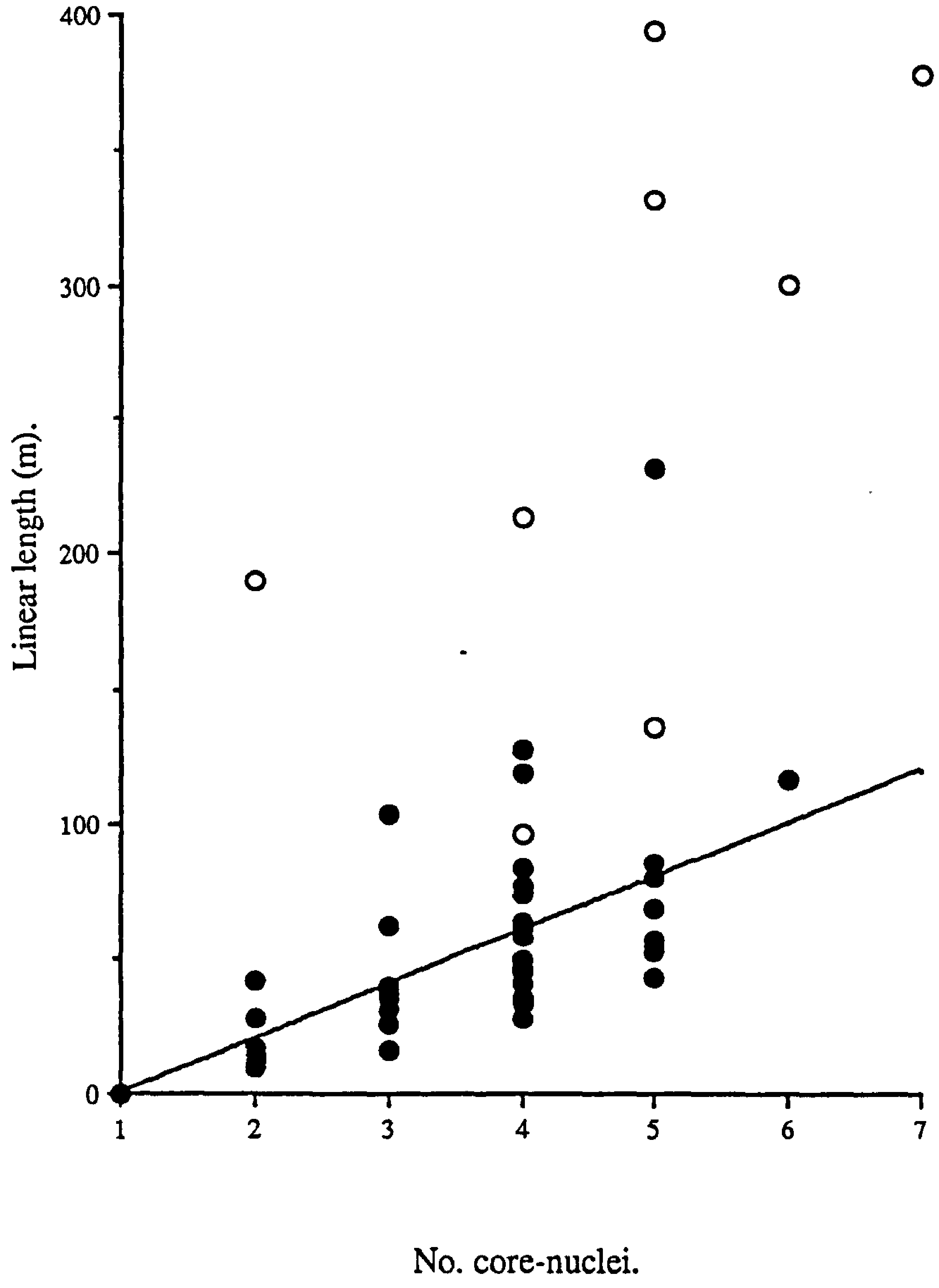


**Fig.5.3.1.** The relationship between the linear-length of ranges and the number of core-nuclei within ranges. The linear-length was the sum of the individual commuting movements if robins always minimised the distances moved between core-nuclei. Solid symbols indicate territorial individuals ($r_s$=0.68 p<0.001 n=43), open symbols indicate non-territorial (n-8). The line shows the expected distribution if all individual commuting distances were equal to the median value of 20 m (range 8-52).

Equation for line is;

Linear-length = 20 x No.core-nuclei -20

containing different numbers of nuclei were separated by the same total linear-length, the individual commuting distances would be negatively correlated with the number of core-nuclei. The solid line in Fig.5.3.1, about which the data from territorial individuals were clustered, shows the expected distribution if all the core-nuclei in territories were separated by the median value of 20m. The networks occupied by non-territorial robins did not conform to this pattern, core-nuclei being much more widely separated.

The number of core nuclei was negatively correlated with the mean area of individual nuclei within networks (the total core area divided by the number of nuclei into which it was fragmented) ($r=0.39$ $p<0.01$ $n=43$ Fig.5.3.2). If all ranges contained the same total patch area, the distribution will follow curve (a). This was calculated by extrapolation from the median nucleus area of the median number of nuclei within territorial ranges. Although as would be expected, curve (a) fitted the observed data well around the median value of four core-nuclei, the fit is less good at the extremes of the observed data.

The total core area showed a slight but significant increase as it fragmented into increasing numbers of core-nuclei ($r_s=0.42$ $p<0.005$ $n=43$ Fig.5.3.3.). The data were considered sufficiently normally distributed for a linear regression equation to be fitted. Of the variation in core area, 15 % was explained by variation in the number of nuclei (Fig.5.3.3.). This suggested that for each additional core-nucleus occupied and 20m commuting flight path used by a territorial robin, the total core area of the territory network increased by 26 $m^2$. In Fig.5.3.2. curve (b) represents the expected distribution if the median area of the median number of core-nuclei was adjusted by this value between networks of lower or higher numbers of nuclei. The median discrepancy between the observed and expected values of mean nucleus area were 29.3 (range 1.5-157.0 n=43) and 19.2 (range 0-73.3 n=43) for curves (a) and (b) respectively. Curve (b) therefore represents a closer fit to the observed data (Fig.5.3.2.).

### 5.3.3.2. Patch use within networks.

It is already apparent that the area of individual core-nuclei was similar to the area of the patches of vegetation they occupied (section 5.2.), suggesting that the edges of core-nuclei and the edges of occupied bushes and shrubs occupied the same locations. It is possible that the density of prey varies between large and small bushes and between the centre and edge regions within bushes. This difference would have implications for the foraging quality of

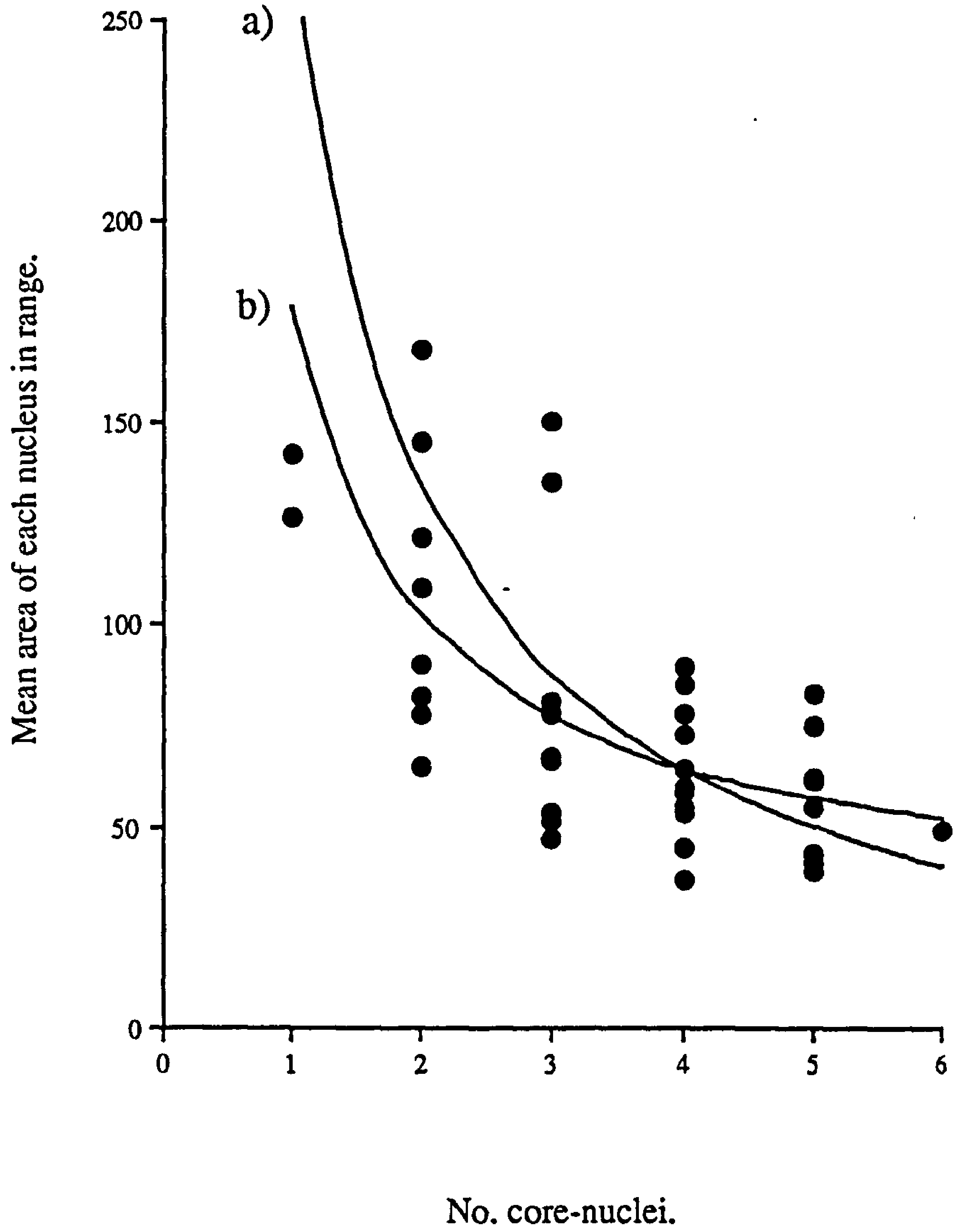


**Fig.5.3.2.** The relationship between the mean area of core-nuclei (m$^2$) and the number of core-nuclei within ranges for non-breeding territorial robins ($r_s$=-0.61 $p<0.001$ n=43). Line (a) shows the expected distribution if all ranges contained the same total core area, the median core area of all ranges. Line (b) shows the expected distribution if for each additional nucleus used, there is a 26 m$^2$ increase in total core area (see text). The median discrepancy between the observed and expected values of mean core area were 29.3 m$^2$ (range 1.5-157.0) and 19.2 m$^2$ (range 0-73.3) for curves (a) and (b) respectively.

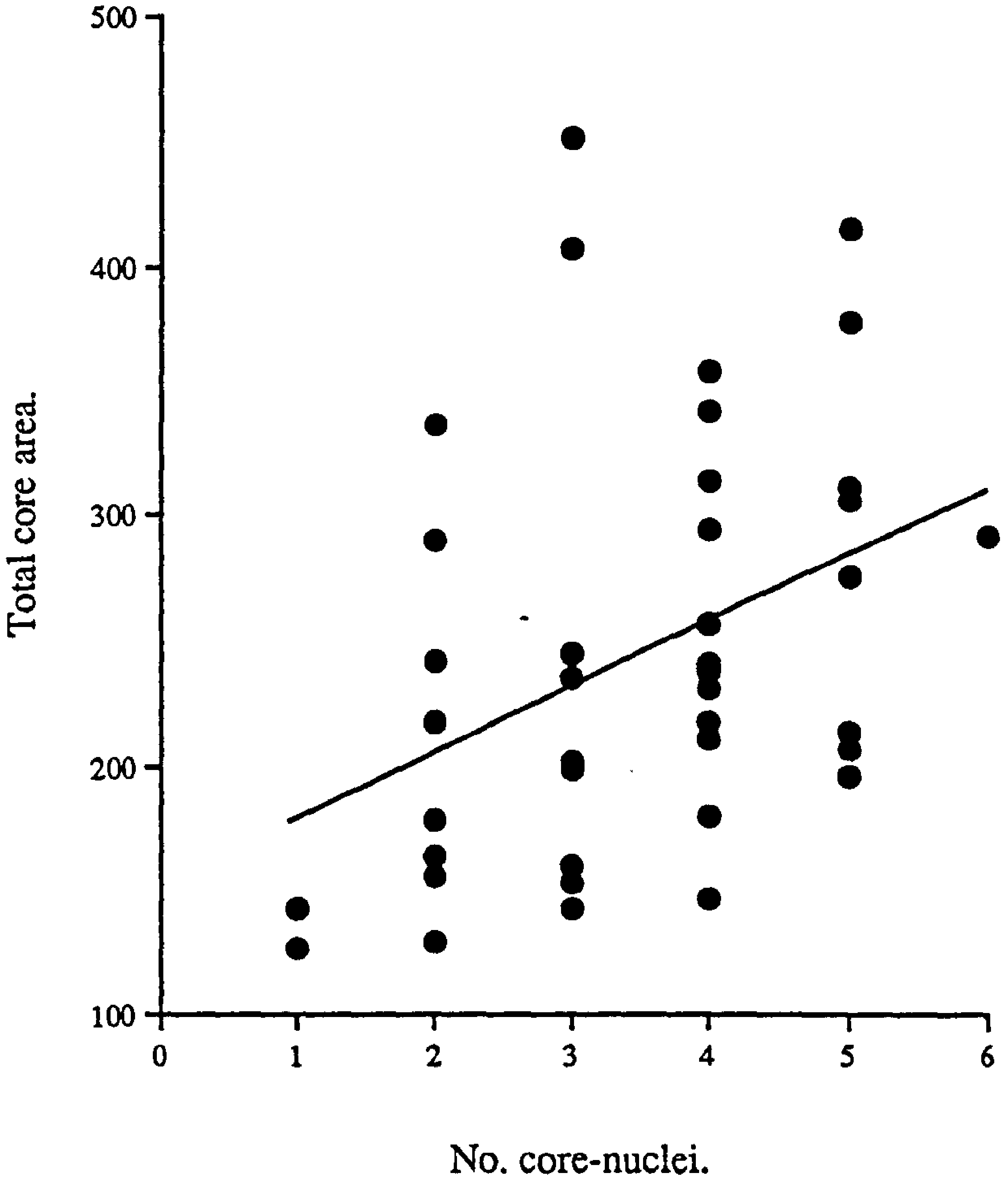


Fig.5.3.3. The relationship between the total core area and the number of core-nuclei into which it was fragmented in the ranges of non-breeding territorial robins($r=0.39$ $p<0.01$ $n=43$). The line is the fitted linear regression equation; Core area=26.19xNo.nuclei+152.31 ($p<0.01$ $r^2=0.15$ $n=43$).

bushes of different size. This is because, assuming nuclei are circular, the total edge length increases at 1.7 times the rate of the total core area as the number of nuclei are increased. The data on prey densities, estimated from the number of prey items captured in pitfall traps in a 24 hr period, were normally distributed. There were no differences between the prey densities within bushes of different size (Table 5.3.3.). Because of this, data from the different sites within bushes could be pooled between bushes of different size to test for any difference between the prey density in different sites (T-test T=-1.62 ns df=1 n=60). Since there were no differences in prey density between bushes of different size nor between different sites within bushes, patch size may be considered a measure of the number of prey available in the undepleted state. As the area of a bush doubles so does the number of available prey and hence the patch quality.

Data concerning the patterns of movement of robins were based on over 900 radio-locations collected during discontinuous tracking and three one hour samples of continuous tracking from each of seven territorial individuals during October and November 1991. Each sample was analyzed to determine values for the measures of range and network use described in Table 5.3.2. The data are presented in Appendix 7. There were no significant differences between the different times of day for the different measures of range and network use (Table 5.3.4.). The mean values of the three samples were therefore used in subsequent analysis. Because each individual was represented by only three sampling periods, the mean value was preferred over the median since the latter would only represent the middle observation and therefore only one third of the available information would be used compared to all for the mean. The utilization distribution statistics for the seven ranges derived from discontinuous tracking data are shown in Table 5.3.5. Correlations between these and the measures of range and network use are shown in Table 5.3.6. The number of core-nuclei was the measure of network size that was most consistently correlated with measures of network use, closely followed by linear-length (Table 5.3.6.). Usual-area was only correlated with one measure of network use and eccentricity with none (Table 5.3.6.). The measures of range and network use were poorly correlated with the environmental variables experienced by the robins during and previous to the period of continuous tracking (Table 5.3.7.). Although more correlations were significant at the five percent level than would be expected at random, all the correlations were weak or inconsistent and do not warrant detailed consideration (Table 5.3.7.).

**Table 5.3.3.** One-way ANOVA between numbers of prey items found in pitfall traps after 24 hrs, for traps located in different sites within bushes of different size. Values indicate mean with standard deviation in parentheses. Both results were non-significant at the 5 % level.

| Bush size | No. prey items trapped over 24 hr period | |
|---|---|---|
| | Centre of bush | Periphery of bush |
| Small (<50 $m^2$)<br>(n=20) | 6.55<br>(5.65) | 7.65<br>(4.65) |
| Intermediate (50-100 $m^2$)<br>(n=20) | 7.60<br>(6.48) | 10.65<br>(9.05) |
| Large (>100 $m^2$)<br>(n=20) | 6.30<br>(3.69) | 5.75<br>(5.08) |
| F | 0.33 | 2.83 |

**Table 5.3.4.** Nonparametric one-way ANOVA between the different measures of network use and time of day. Data show median and range for seven robins at the three different times of day. See appendix 7. for individual data.

| Measure of network use | Dawn | Midday | Dusk | Kruskal Wallis | |
|---|---|---|---|---|---|
| | | | | H | p |
| Proportion of time on usual-area | 1.0<br>(0.7-1.0 | 0.93<br>(0.47-1.0) | 0.6<br>(0.42-1.0) | 4.46 | 0.11 |
| Commuting rate (Movements hr$^{-1}$) | 9.0<br>(5.0-19.5) | 6.8<br>(0-18) | 6.7<br>(0-21) | 1.07 | 0.59 |
| Time singing (seconds hr$^{-1}$) | 11<br>(0-148) | 0<br>(0-12) | 0<br>(0-139) | 0.57 | 0.75 |
| Proportion of locations at which birds vocalised | 0.13<br>(0-0.36) | 0.1<br>(0-0.17) | 0.07<br>(0-0.37) | 0.50 | 0.82 |
| % departure from ideal linear use | 13.8<br>(0-59.7) | 15.9<br>(0-16.9) | 1.9<br>(0-20.7) | 0.61 | 0.74 |
| Proportion of movements that were backtracks | 0.42<br>(0.08-1.0) | 0.36<br>(0-1.0) | 0.25<br>(0.2-1.0) | 1.0 | 0.50 |

**Table 5.3.5.** Utilization distribution statistics for robins which were continuously tracked at different times of the day.

| Ring No. | No. core-nuclei[#] | Total core area ($m^2$)[$] | Usual-area ($m^2$) | Linear-length (m) | Eccentricity (Є) | Angles between commuting paths (degrees)[*] | |
|---|---|---|---|---|---|---|---|
| | | | | | | Mean | Range |
| F646581 | 4 | 239 | 543 | 49 | 0.30 | 133 | 115-150 |
| F646569 | 5 | 415 | 812 | 68 | 0.53 | 123 | 70-165 |
| F646546 | 6 | 268 | 608 | 61 | 0.37 | 130 | 80-155 |
| F646551 | 3 | 183 | 268 | 29 | 0.54 | 105 | - |
| H227546 | 5 | 377 | 632 | 52 | 0.28 | 142 | 130-150 |
| F646547 | 3 | 252 | 513 | 55 | 0.18 | 160 | - |
| F646590 | 2 | 164 | 165 | 15 | 0.26 | - | - |

[#] Revised number to include complex nuclei.
[$] Including 2 m boundary strip around each nucleus.
[*] A territory network of two core-nuclei only contains one commuting path.

**Table 5.3.6.** Correlations between measures of network use by robins averaged over the day and measures of territory size and shape (n=7).

| Measure of network use | $r_s$ | | | |
|---|---|---|---|---|
| | No. core-nuclei | Linear-length (m) | Usual-area ($m^2$) | Eccentricity (∈) |
| Proportion of time on usual-area | 0.05 | -0.21 | -0.11 | -0.43 |
| Commuting rate (movements $hr^{-1}$) | 0.87 *** | 0.64 * | 0.46 | 0.39 |
| Time singing (sec $hr^{-1}$) | 0.22 | -0.04 | 0.25 | -0.25 |
| Proportion of locations at which birds vocalised | 0.69 * | 0.52 | 0.45 | 0.13 |
| % departure from ideal linear-use | 0.74 * | 0.90 *** | 0.54 | 0.13 |
| Proportion of movements that were backtracks | -0.80 * | -0.70 * | -0.85 ** | -0.20 |

* $p<0.05$ ** $p<0.01$ *** $p<0.005$

**Table 5.3.7.** Spearman correlation coefficients between measures of network use and the environmental variables experienced by robins during and previous to the period of continuous tracking (n=7).

| Measure of network use | Weather on day | | | Weather on previous day | | | Weather averaged over previous five days | | |
|---|---|---|---|---|---|---|---|---|---|
| | $T_{mid}$ (°C) | Rainfall (mm) | Wind speed (knots) | $T_{mid}$ (°C) | Rainfall (mm) | Wind speed (knots) | $T_{mid}$ (°C) | Rainfall (mm) | Wind speed (knots) |
| Proportion of time on usual-area | 0.50 | 0.33 | -0.80 * | -0.11 | -0.45 | 0.42 | 0.36 | -0.13 | 0.46 |
| Commuting rate (Movements $hr^{-1}$) | -0.11 | 0.33 | -0.13 | 0.21 | -0.26 | -0.45 | 0.61 | -0.04 | 0.50 |
| Time singing (sec $hr^{-1}$) | 0.67 | 0.28 | -0.52 | 0.23 | -0.80 * | 0.20 | 0.63 | -0.14 | 0.68 * |
| Proportion of locations at which birds vocalised | 0.07 | -0.04 | -0.22 | 0.27 | -0.56 | -0.22 | 0.72 * | -0.09 | 0.77 * |
| % departure from ideal-linear use | -0.77 * | -0.64 | 0.34 | -0.14 | 0.10 | -0.49 | 0.09 | 0.26 | 0.14 |
| Proportion of movements that were back-tracks | -0.31 | 0.12 | 0.07 | -0.43 | 0.78 * | 0.34 | -0.77 | 0.09 | -0.66 |

* $p<0.05$

Commuting rate was positively correlated with the number of core-nuclei used by each robin (Table 5.3.6., Fig.5.3.4.). Each point represents the data averaged over the three periods of continuous tracking during the day. Ranges were omitted from all figures for clarity, the individual data being shown in Appendix 7. The line in Fig.5.3.4. represents the distribution if each bird exhibited the same return time. This would be expected for a bird exploiting a renewing food supply by visiting a series foraging patches in a regular sequence. The line was calculated by extrapolating from the median number of nuclei and median commuting rate, and represents a median return time of 31 min (range 19-40). Return times for each individual were estimated by multiplying the number of nuclei by; duration of tracking divided by commuting rate. The durations of commuting movements were assumed to be negligible. There was no relationship between the return time and the number of core-nuclei being used ($r_s$=0.43 ns n=7). The fitted line predicts that a robin occupying four core-nuclei will move between nuclei about twice as often as a robin occupying only two nuclei (Fig.5.3.5.).

The duration of nucleus visits was negatively correlated with the number of core-nuclei in each territory network (Table 5.3.6. Fig.5.3.6.). As in Fig.5.3.4. the fitted line shows the expected distribution if each bird showed the same return time. This equalled the visit duration multiplied by the number of nuclei (median 25 min range 17-35). The discrepancy between the return times calculated from the visit duration and commuting rate for each individual was because birds could be recorded as commuting from one nucleus to another without the duration of both nucleus visits being known (the tracking began or ended during a visit). Furthermore, sequences of nucleus visits and movements between nuclei may be interrupted at any time by excursive activity, amplifying this effect. Commuting rate was negatively correlated with the duration of visits to nuclei ($r_s$=-0.88 $p<0.005$ n=7). As expected therefore, robins which exhibited short giving up times commuted between their foraging patches more often.

If the area of patches is a measure of the number of available prey items, the duration of visits to individual nuclei by robins will be positively correlated with their area. The observed data support this prediction ($r_s$=-0.78 $p<0.05$ n=7 Fig.5.3.6. Table 5.3.8.). The fitted line extrapolated from the median values shows the expected distribution if the duration of visits by robins was twice as long in patches that were of twice the area (Fig.5.3.6.).

Robins which occupied networks containing larger numbers of nuclei were observed to vocalise at a greater proportion of continuous tracking locations ($r_s$=0.69 $p<0.05$ n=7

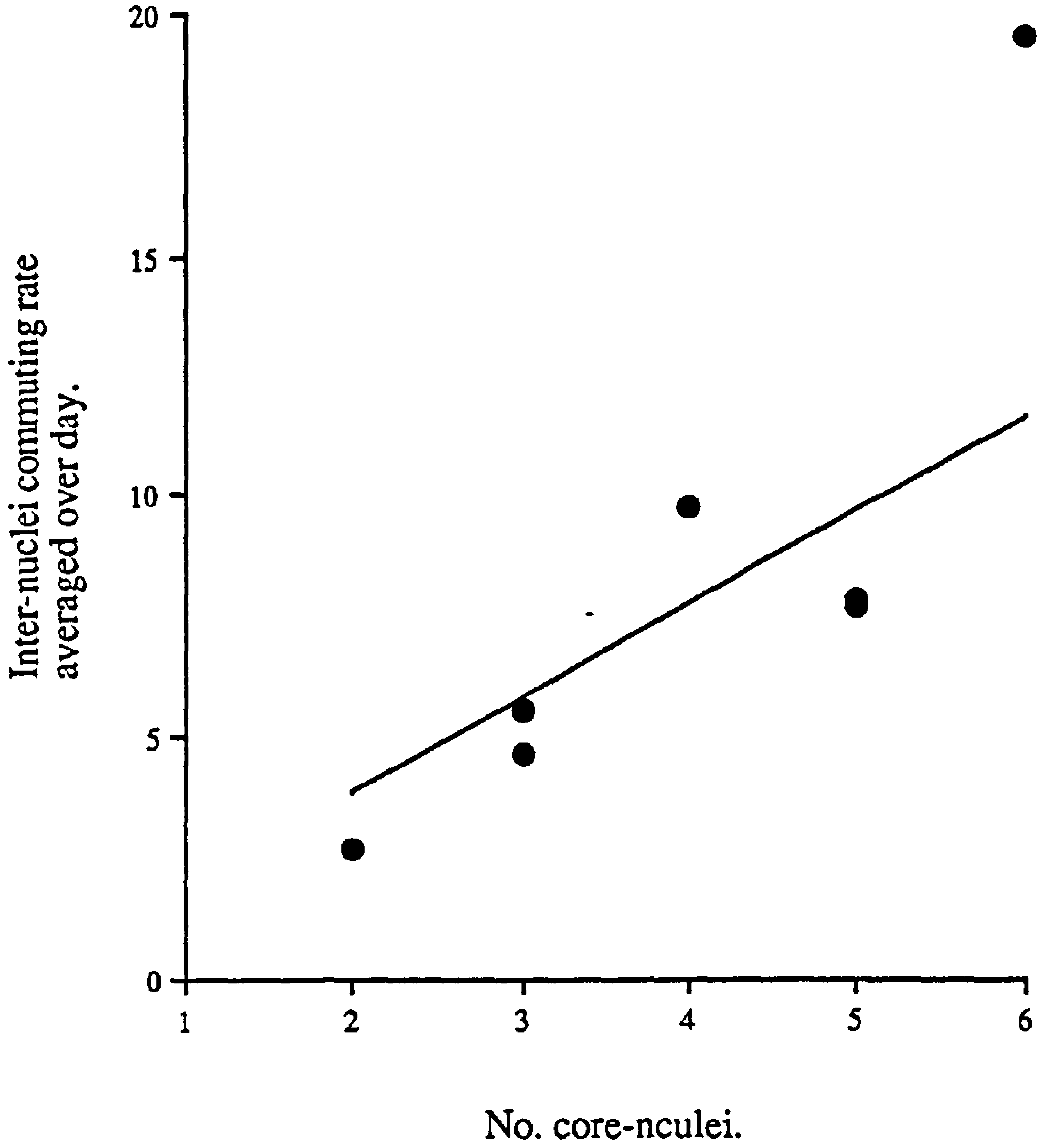


**Fig.5.3.4.** The inter-nucleus commuting rate averaged over the day (movements $hr^{-1}$) as a function of the number of core-nuclei within ranges ($r_s$=0.87 p<0.005 n=7). The line shows the expected distribution if all robins showed the median return time of 31 min (range 19-40). The individual data for the commuting rate are shown in Appendix 7.

Equation for line is;

Commuting rate = 1.93 x No.core-nuclei

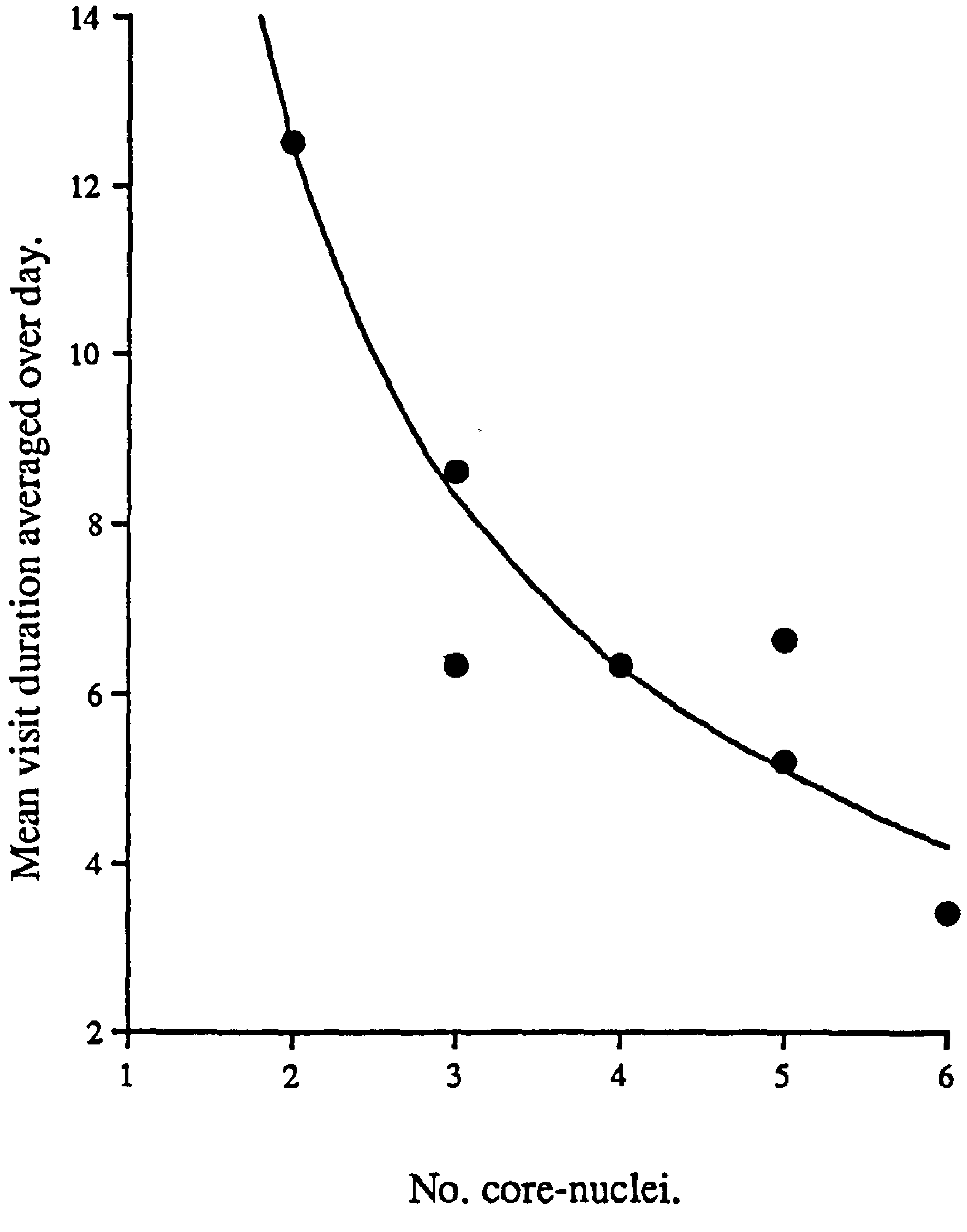


**Fig.5.3.5.** The mean duration of visits to core-nuclei averaged over the day (min) as a function of the number of nuclei within ranges ($r_s$=-0.80 p<0.01 n=7). The line shows the expected distribution if all robins showed the median return time of 25 min (range 17-35). The individual data for the mean visit durations are shown in Table 5.3.8.

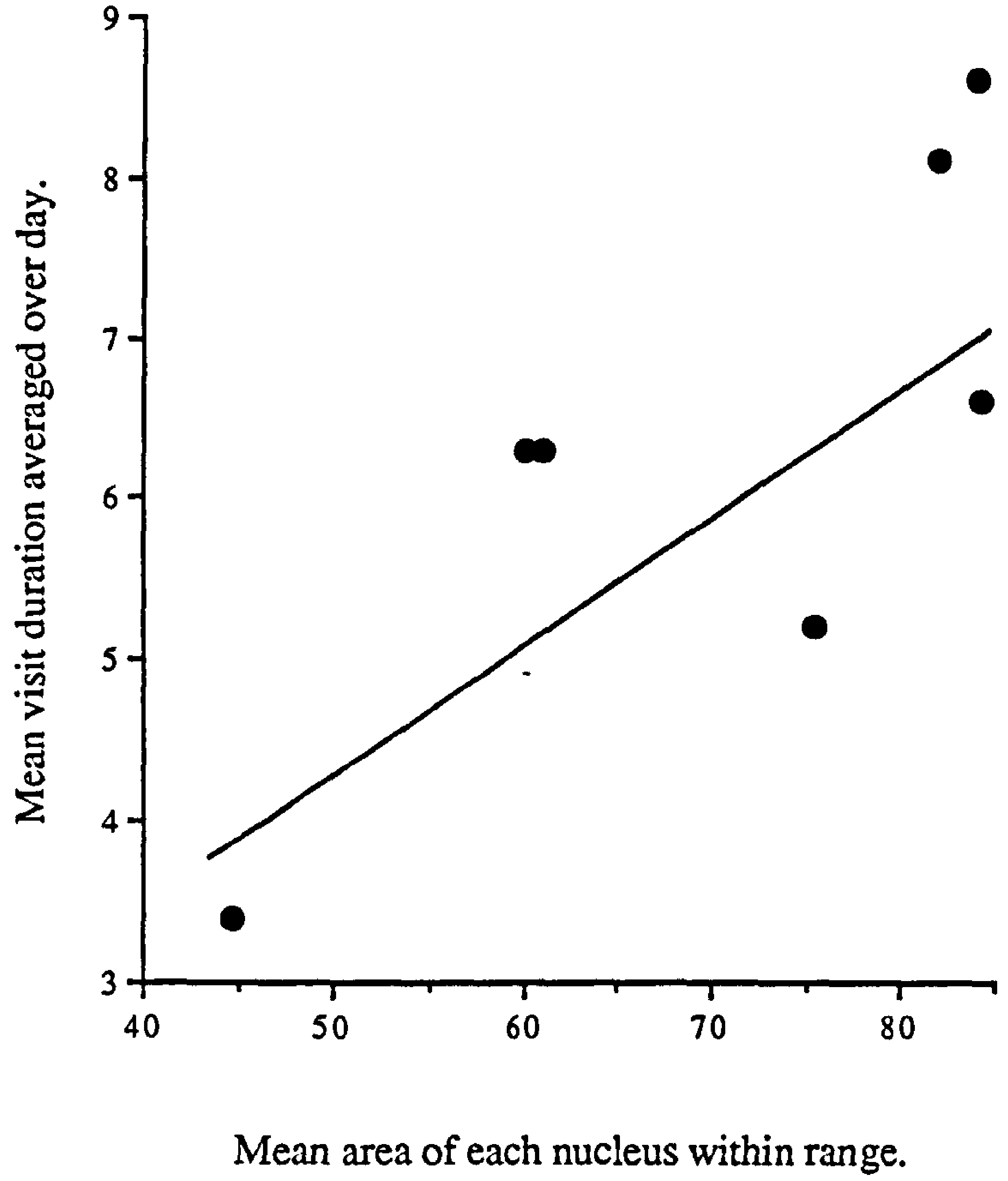


**Fig.5.3.6.** The relationship between the mean duration of visits to core-nuclei averaged over the day (min) and the mean area of nuclei within ranges ($m^2$) ($r_s$=0.78 $p<0.05$ n=7). The fitted line extrapolated from the median values shows the expected relationship if the duration of visits by robins was twice as long in foraging patches that were of twice the area. The individual data are presented in Table 5.3.8.

Equation for line is;

Visit duration = 0.08 x Nucleus area

**Table 5.3.8.** Mean visit duration and mean nucleus area for networks of different numbers of core-nuclei. Data was averaged for each nucleus over the three periods of continuous tracking during the day.

| Ring No. | No. core-nuclei | Mean visit duration (minutes) |  | Mean area of core-nuclei ($m^2$) |  |
|---|---|---|---|---|---|
|  |  | Individual nuclei[*] | Mean | Individual nuclei[#] | Mean |
| F646581 | 3 | 3.3,5.6,8.8,7.6 | 6.3 | 25,56,77,81, | 60 |
| F646569 | 5 | -,3.4,2.5,13.3,7.0, | 6.6 | 48,128,159,48,38, | 84 |
| F646546 | 6 | 6.0,3.3,2.8,2.6,2.7,2.8, | 3.4 | 25,34,36,40,63,70, | 45 |
| F646551 | 3 | 6.8,2.0,10.0, | 6.3 | 30,41,112, | 61 |
| H227546 | 5 | -,8.5,5.0,2.4,4.7, | 5.2 | 2,79,3,30,29, | 75 |
| F646547 | 3 | 13.0,9.3,3.5, | 8.6 | 22,10,2, | 84 |
| F646590 | 2 | 6.0,20.0, | 12.7 | 27,17, | 82 |

[*] A dash indicates a nucleus was not visited during continuous tracking.

[#] Order corresponds to that of visit durations.

Fig.5.3.7.). The fitted line shows the expected relationship if robins vocalised twice as often when occupying double the number of nuclei. When robins vocalised, they were significantly more likely to do so during the first third of a visit to one of their core-nuclei and least likely to do so in the middle third of a visit. The likelihood of vocalisations in the last third was intermediate (Goodness of fit test for visits longer then 4 minutes $\chi^2=15.23$ $p<0.01$ df=2 n=50 Fig.5.3.8.). There was no significant tendency for robins to vocalise during nucleus visits more often at different times of day ($\chi^2=4.55$ ns df=2 n=151).

### 5.3.3.3. Network use.

If the most efficient way for robins to visit renewing foraging patches is to ensure that return times are equal to the recovery time of prey density within patches, they should adopt a regular sequence of patch visits. The most economic configurations will be those that allow access to all patches used in a sequence of visits that minimises the total commuting distance. The degree to which robins achieve this will depend on the shape and configuration of the network of foraging patches they use.

The mean angle between the pairs of flight paths constituting the linear length, along which birds would commute when following ideal linear use, were consistently high (median 139° range 105-160°). There was no relationship between the median angle and number of nuclei in each network ($r_s=0.13$ ns n=6). High values for angles between commuting paths would indicate that the distance saved by taking the short cut and avoiding the intermediate nucleus is minimal, the maximum possible angle being 180°. The networks occupied by the robins that were continuously tracked therefore presented few opportunities for the exploitation of short cuts and pseudo-polygonal network use.

Excluding any individuals which occupied only two nuclei, a configuration which can only be used in an ideal-linear manner, the departure from ideal linear use increased with the number of nuclei within the territory network ($r_s=0.74$ $p<0.05$ n=6 Fig.5.3.9.), although the departure was small (median 13.1 range 0-30.4). Also shown in Fig.5.3.9. is the percentage departure from ideal-linear use achieved for networks of different numbers of nuclei separated by commuting distance (d) if they were instead used in a circuit polygonal manner (line b). For example, a robin using a network of three nuclei would reduce the distance required to travel to its most distant nucleus by 50 % if it could use three instead of two commuting paths. This indicated that although the robins to some extent took advantage of short cuts

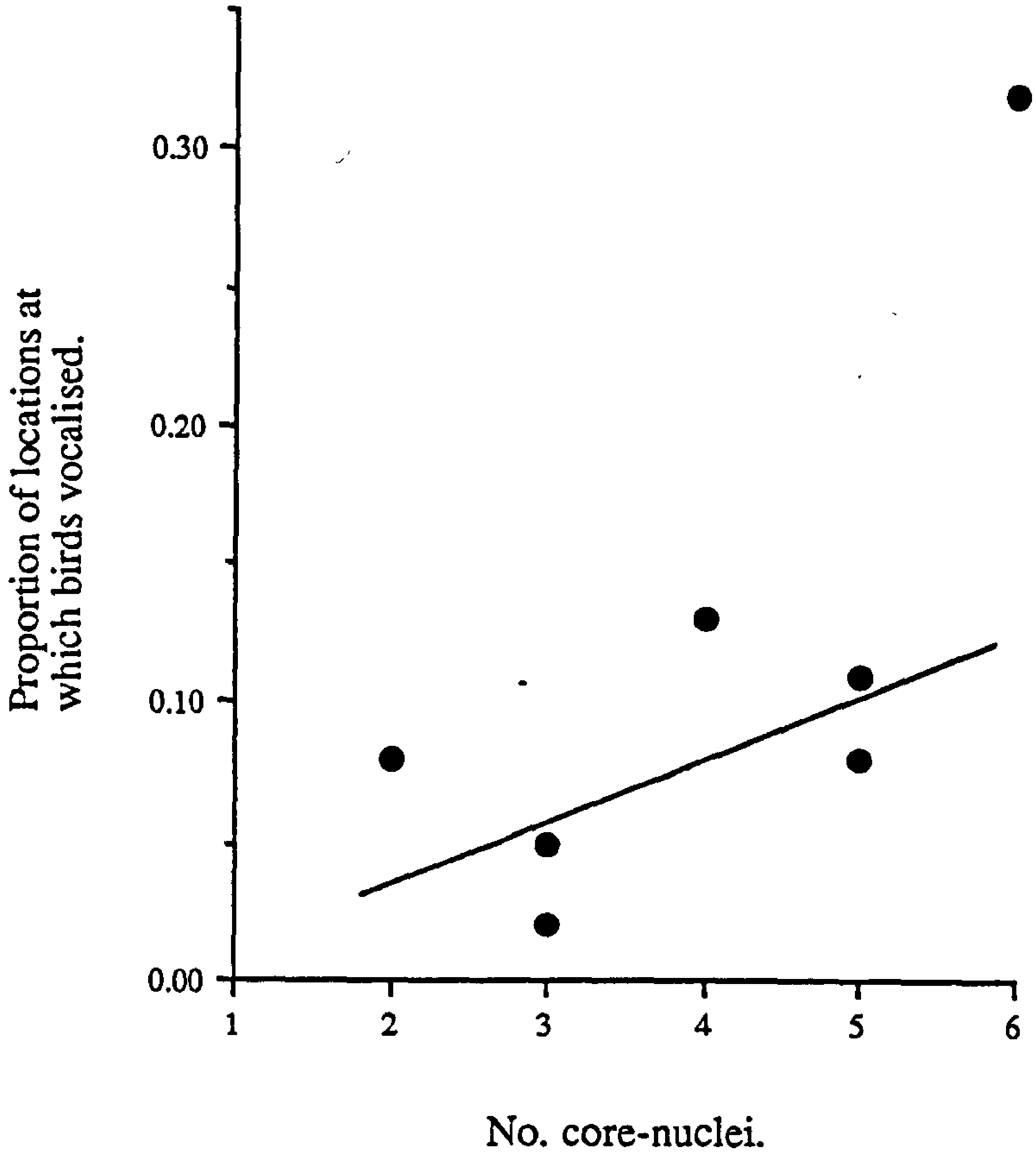


**Fig.5.3.7.** The proportion of locations at which robins vocalised (sang or tic-called) during continuous tracking averaged over the day plotted against the number of core-nuclei within each range ($r_s$=0.69 $p<0.05$ n=7). The fitted line represents the expected relationship extrapolated from the median values, if robins which used twice the number of nuclei were observed to vocalise at twice the number of locations. The individual data for the proportion of locations at which birds vocalised are shown in Appendix 7.

Equation for line is;

$$\text{Proportion} = 0.02 \times \text{No.core-nuclei}$$

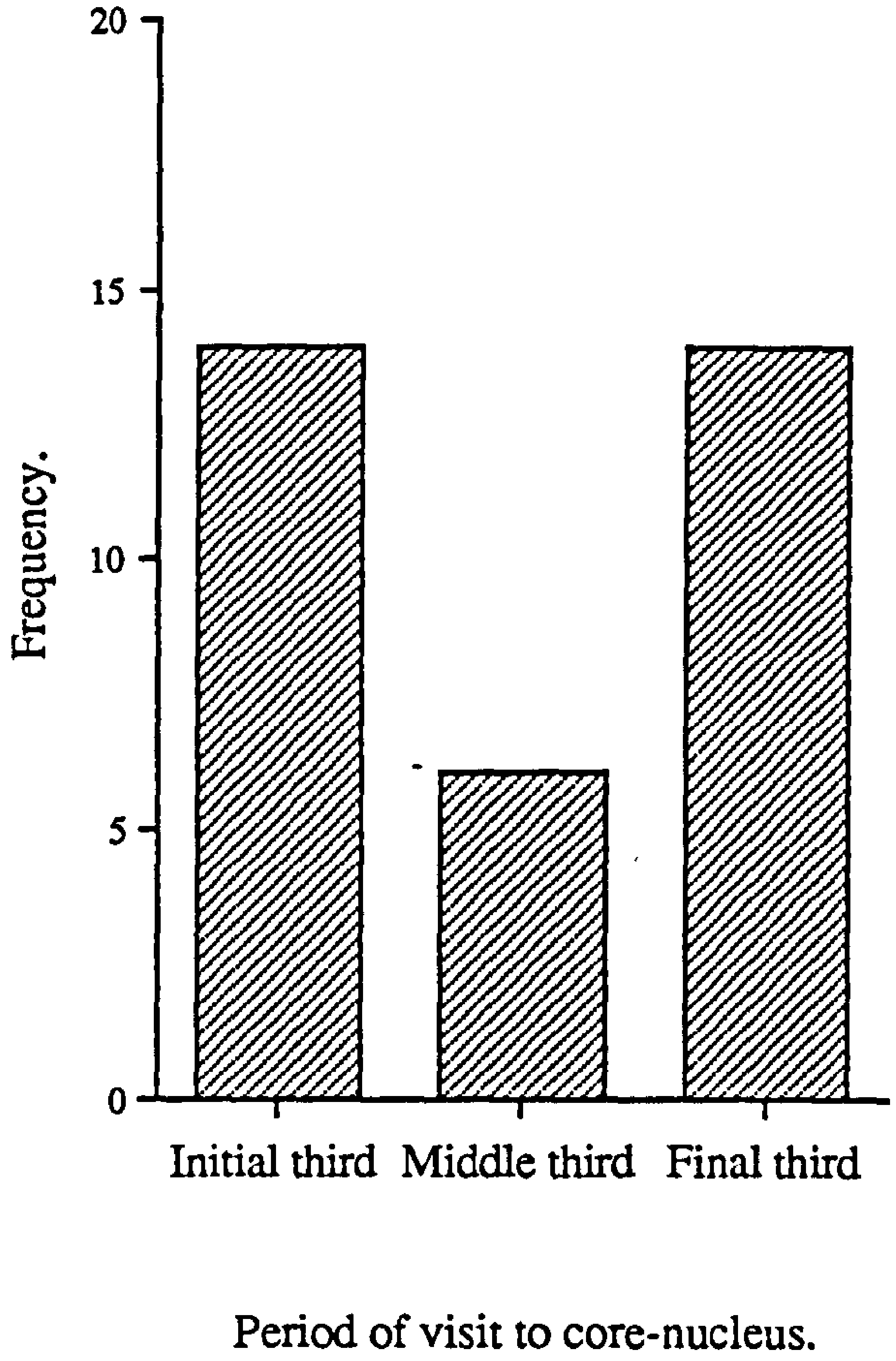


**Fig.5.3.8.** The frequency with which robins vocalised (sang or tic-called) during different portions of visits to their core-nuclei that were longer than four minutes (Goodness of fit test $\chi^2$ 15.23 $p<0.001$ df=2). Visits shorter than this could not be divided into thirds.

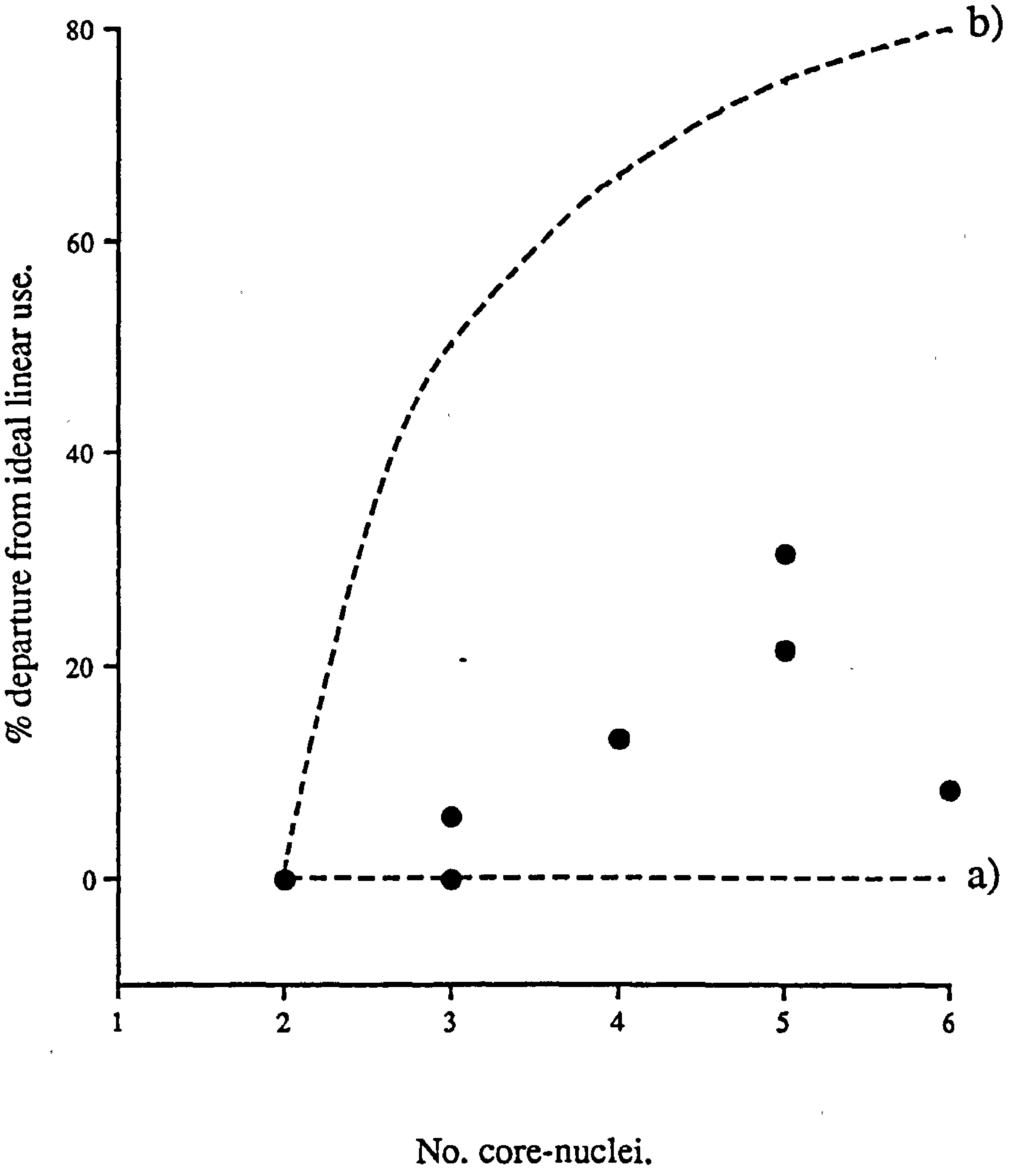


**Fig.5.3.9.** The departure from ideal-linear use averaged over the day plotted against the number of nuclei within ranges ($r_s$=0.74 $p<0.05$ n=6).If the robins had used their networks only in an ideal-linear manner the data would follow line (a). Line (b) shows the expected distribution if all nuclei were separated by distance d, and the robins changed their pattern of use from that of ideal-linear to circuit-polygonal (see text). The individual data for the % departure from ideal-linear use are shown in Appendix 7.

when moving between distant nuclei, their pattern of use was close to that expected if they always minimised the individual commuting distances.

The randomness of the direction of movements by robins using their networks can be assessed by measuring the proportion that were back-tracks (Table 5.3.2.). Excluding those individuals which used networks containing more than two nuclei and visited more than two nuclei during continuous tracking, the proportion of movements that were back-tracks was not correlated with the number of core-nuclei used ($r_s$=-0.56 ns n=5). If robins were following a predictable sequence of nucleus visits, the proportion of movements that were back-tracks would be zero for circuit-polygonal networks (always move forwards and never backwards; Fig.5.3.11. line a). If robins moved randomly between nuclei the expected proportion of movements that were back-tracks would be equal to 0.5 for circuit polygonal use (equal probability of moving forwards or backwards; line b). For networks used in an ideal-linear manner, a number of commuting movements must be back-tracks if birds are to return to fully recovered patches (visits to terminal nuclei must always be followed by a backtrack). From Fig.5.3.9. it is already apparent that the robins did use their territory networks in a way that closely approached ideal-linear use. The effects of this on the probability of making a backtrack during ideal-linear network use are shown in Fig.5.3.11. by lines (c) and (d) for regular and random patch visits respectively. The predicted lines were calculated by averaging the probability of the next movement being a backtrack for each nuclei in networks of different size and during different types of movement. The departure of the observed data from ideal-linear random use (median 0.42 range 0.15-0.48 n=5) was greater than the departure from ideal-linear regular use (median 0.07 range 0.02-0.35 n=5). Examples of temporal and spatial foraging circuits being used by territorial robins recorded during the study are shown in Fig.5.3.12. Although the robin occupying a network of two nuclei can only visit them in a regular sequence, the individual using five nuclei could visit them randomly. Clearly the latter follows a much more regular sequence of core visits. Both birds showed similar return times of 25-30 min (Fig.5.3.12.), similar to the values predicted from commuting rate between and visit duration to core-nuclei.

The results therefore suggest that the movement of robins around their network of foraging patches is intermediate between regular sequences of patch visits and a random sequence of visits.

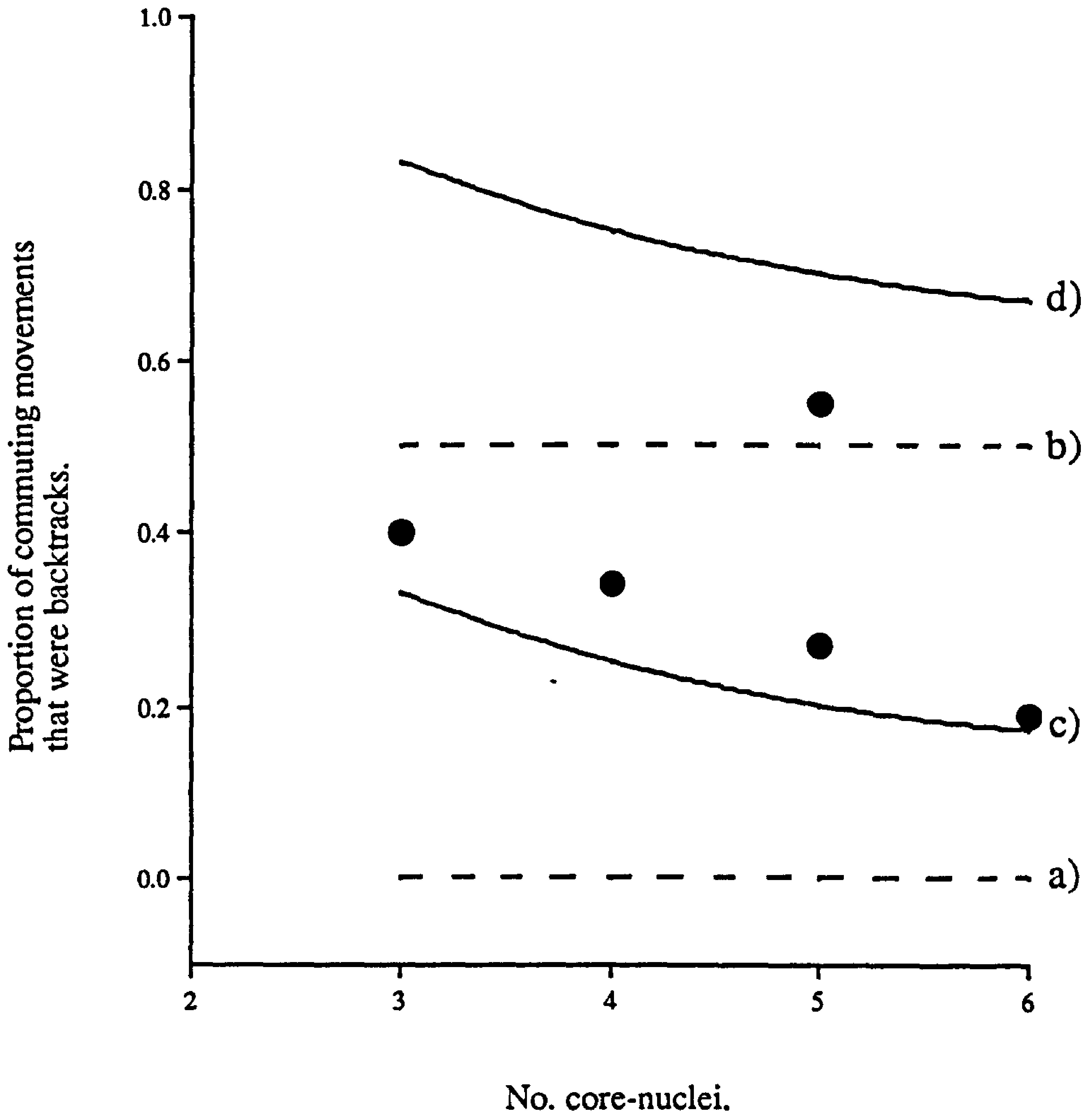
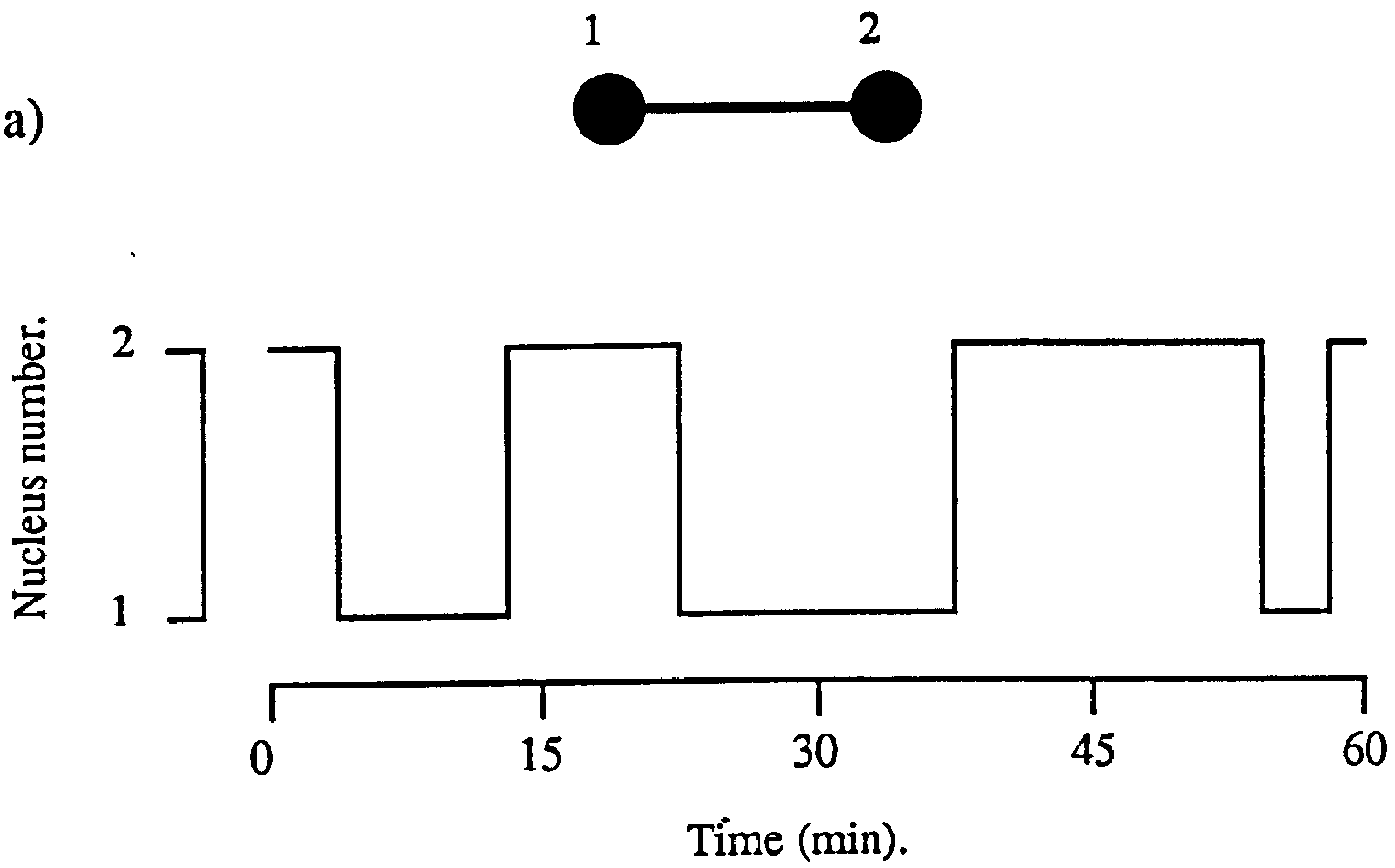


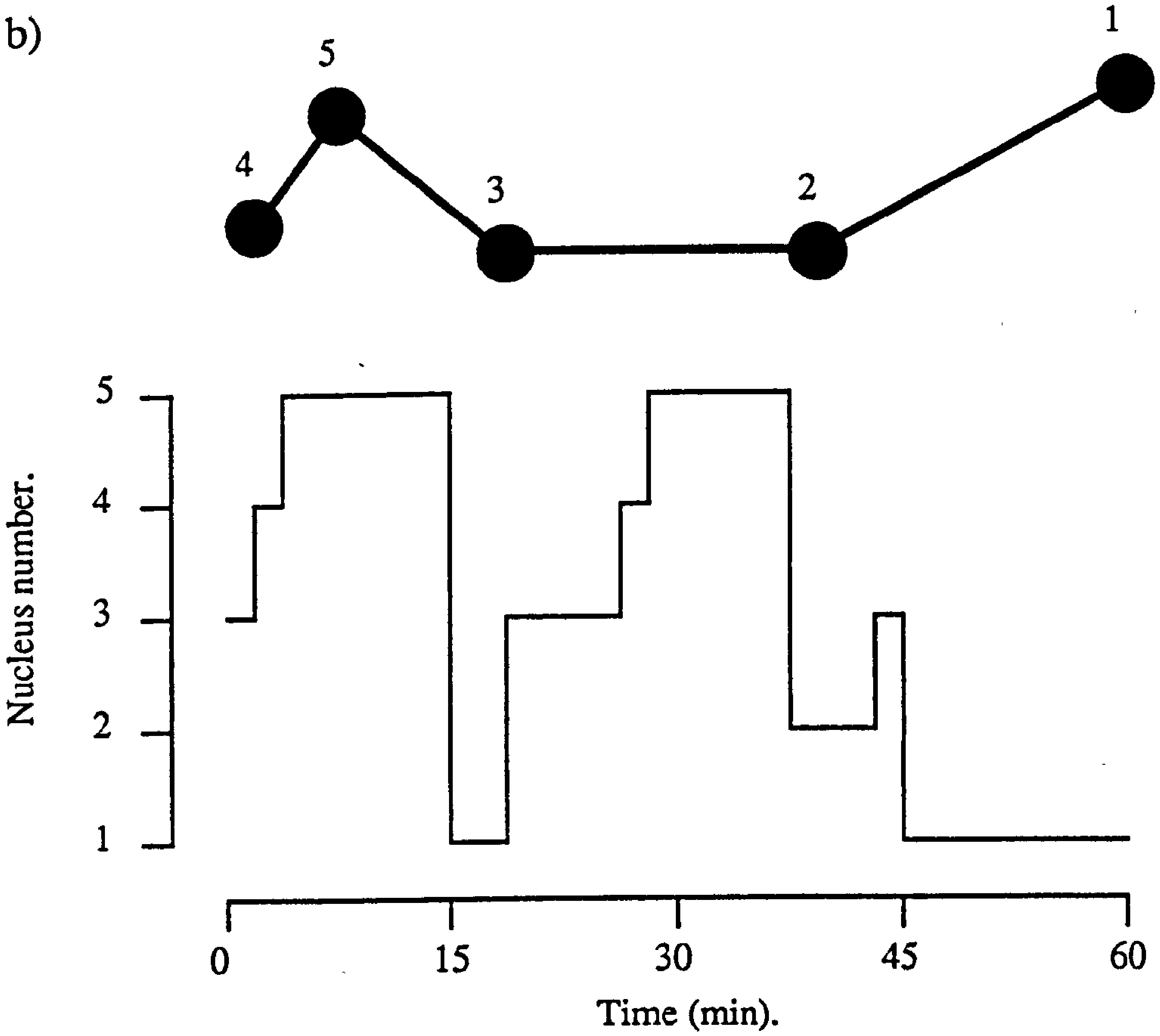
**Fig.5.3.11.** The proportion of movements that were back-tracks averaged over the day plotted against the number of core-nuclei within ranges ($r_s$=-0.56 ns n=5). Line (a) represents regular movement by robins occupying circuit-polygonal territory networks. Line (b) represents random movements between core-nuclei that were used in an circuit-polygonal pattern. Line (c) represents regular sequences of visits to nuclei in ideal-linear configurations, and line (d) represents random movements between nuclei in ideal-linear networks. Predicted lines were obtained by averaging the probability of making a backtrack on the next commuting movement for each nucleus in networks of different size and configuration. The individual data for the proportion of movements that were back-tracks are shown in Appendix 7.

Fig.5.3.12. Two examples of movement between nuclei by non-breeding territorial robins. In (a) two nuclei were being used and therefore could only be visited in a regular sequence. The five nuclei used in (b) however could be visited randomly. The observed sequence of visits is nevertheless remarkably regular. Both birds showed a return time of 25-30 min.

a)


1
2
Nucleus number.
2
1
0
15
30
45
60
Time (min).

b)


1
5
4
3
2
Nucleus number.
5
4
3
2
1
0
15
30
45
60
Time (min).

### 5.3.4. Discussion.

#### 5.3.4.1. Network structure.

Within territories, pairs of feeding patches represented by the core-nuclei were separated by minimum commuting flights of similar length. Bigger territories contained a larger number of core-nuclei separated by similar distances, rather than the same number of nuclei separated by longer flight distances. Large territories with long linear-lengths therefore contained feeding patches that were more fragmented. This perhaps reflects the selection of patches by robins that minimise individual commuting distances between patches rather then the minimisation of the average commuting distance between all patches. This might be expected if moving across the open ground between patches was an energetically costly or a risky activity.

As the number of core-nuclei within the network increased, the total core area also increased by a small and constant increment, while the area of individual core-nuclei decreased exponentially. Each increment possibly represents the additional feeding area required to provide enough energy to fuel the additional flight distance needed to reach the patch. Nevertheless, the total core area was very similar between networks containing different numbers of core-nuclei. This constant resource amount appears to be a common element in the territories of birds which exploit renewing resources; nectar feeders defend territories of very different area but similar number of flowers (Gill & Wolf 1975, Kodric-Brown & Brown 1978) and the insectivorous pied wagtail defends a similar length of river bank on which insects are washed up (Davies & Houston 1981).

#### 5.3.4.2. Patch use within networks.

Since there was no difference in the prey density between or within bushes of different size, large bushes contained more available prey in the undepleted state than small bushes. Large bushes therefore represented feeding patches of higher quality. This may however, depend on the degree of microhabitat depression caused by robins foraging by hopping along the ground (Grajetsky 1993). In large patches, mobile invertebrate prey items may move out of reach or adopt a cryptic posture by sensing an approaching robin some distance away.

If the foraging behaviour of robins was organised to ensure patches were only revisited after they had fully recovered, the duration of visits to nuclei (giving up time) would decrease and commuting rate increase as the core area became more fragmented in large networks. The observed trends in commuting rate and nucleus visit duration with number of core-nuclei clearly support these predictions. The data showed that birds occupied networks of similar total patch area which was fragmented into individual patches to different extents. In networks containing a greater number of patches, individual patches were smaller. Robins using such patches exhibited shorter giving up times and commuted to new patches more often indicating that they contained fewer prey items and were of lower quality. This suggests that the robin is exploiting a renewing food supply within the foraging patches which it defends. It would be useful to understand more fully the depletion of prey within patches by foraging robins and the response to a such predator by the invertebrate prey.

Robins occupying large territory networks with high numbers of nuclei vocalised more often than those occupying small networks. Since birds tended to vocalise when arriving on or leaving nuclei, it would be expected that vocalisations would increase with commuting rate, as observed. The function of vocalisations in this context is perhaps the announcement by the owner of its' arrival in and use of a feeding patch. Robins may also vocalise just prior to leaving since this their last chance to signal ownership before moving on. Such information may targeted towards both intruders who may already occupy nuclei used by the owner, and neighbours to discourage them from initiating intrusions into the patches exploited by the owner. The song of the robin is structurally highly complex (Hoelzel 1986, Brindley 1991) and serves to identify particular individuals within the neighbourhood (Brindley 1991), probably through individual voice characteristics (Weary & Krebs 1992). So, neighbourhoods of robins may continually monitor the position of each other as they move round their respective networks of feeding patches. Tic calls are structurally much simpler (Cramp 1988) and tend to replace song during the winter months (Rae 1979). Over the course of the Autumn and Winter robin populations decline through emigration and mortality (Adriaensen & Dhondt 1983, Harper 1984, this study). New individuals do not arrive and establish territories until the following spring. During the Winter therefore, territory owners may monitor neighbours simply by the location rather than auditory characteristics of their vocalisations. The communication of individual identity through song would therefore be less important. Furthermore song projected from preferred singing perches may be costly in terms of predator attraction (section 3.3.7.). In this situation, therefore, tic calls, which unlike song are often issued from the safety of dense cover, may be enough for robins to monitor the location and movements of a closed population of neighbours. The use of vocalisations in this way may also have costs associated with territory use. By singing or calling, owners will reveal their location to potential intruders which may then target their intrusive activity elsewhere in the owners territory to avoid an encounter. Clearly it is necessary to understand more about the frequency and behaviour of conspecific intruders into the territories of robins.

### 5.3.4.3. Network use.

It is possible that territories of low eccentricity may be utilised by a network of feeding patches of high linearity (pseudopolygonal-linear; Fig.5.2.2.). These results suggest that the robins departed very little from the network of flight paths that would be used if birds were minimising individual flight distances between nuclei. The robins therefore rarely used "short cuts" when commuting between distant foraging patches to reduce their total commuting distance per circuit. The large values of the median angles between pairs of flight paths indicated that the majority of networks approached ideal linear configurations irrespective of size as indicated by the number of nuclei. The study site contained few artificial linear elements such as hedges (Fig.2.1.). The robins therefore, were not constrained into selecting core-nuclei which were arranged in network configurations that approached ideal-linear. It appears, however, that all habitats preferred by robins contain natural linear elements such as streams, banks, and woodland edges and clearings, along which suitable bushes and shrubs develop. A preference for such potentially linear habitat has been previously recorded (Lack 1948; Fig.5.3.13.); non-breeding territories being clustered along roads and around the edges of woodland where such habitat is likely to occur. The linear robin territory may therefore be the norm rather than the exception, even though they may be less efficient in terms of length of foraging circuit.

Although the robins did not appear to move between foraging patches in a perfectly regular sequence, their pattern of movement was closer to that expected for regular movement than for random movement. It would be naive to expect real robins to visit the patches within their ranges in a perfectly regular sequence geared only to food availability, since they must also carry out other activities such as territory defense and predator avoidance. The extent to which their behaviour departs from the most economic way of exploiting renewing food patches will have implications for the costs of territory maintenance.

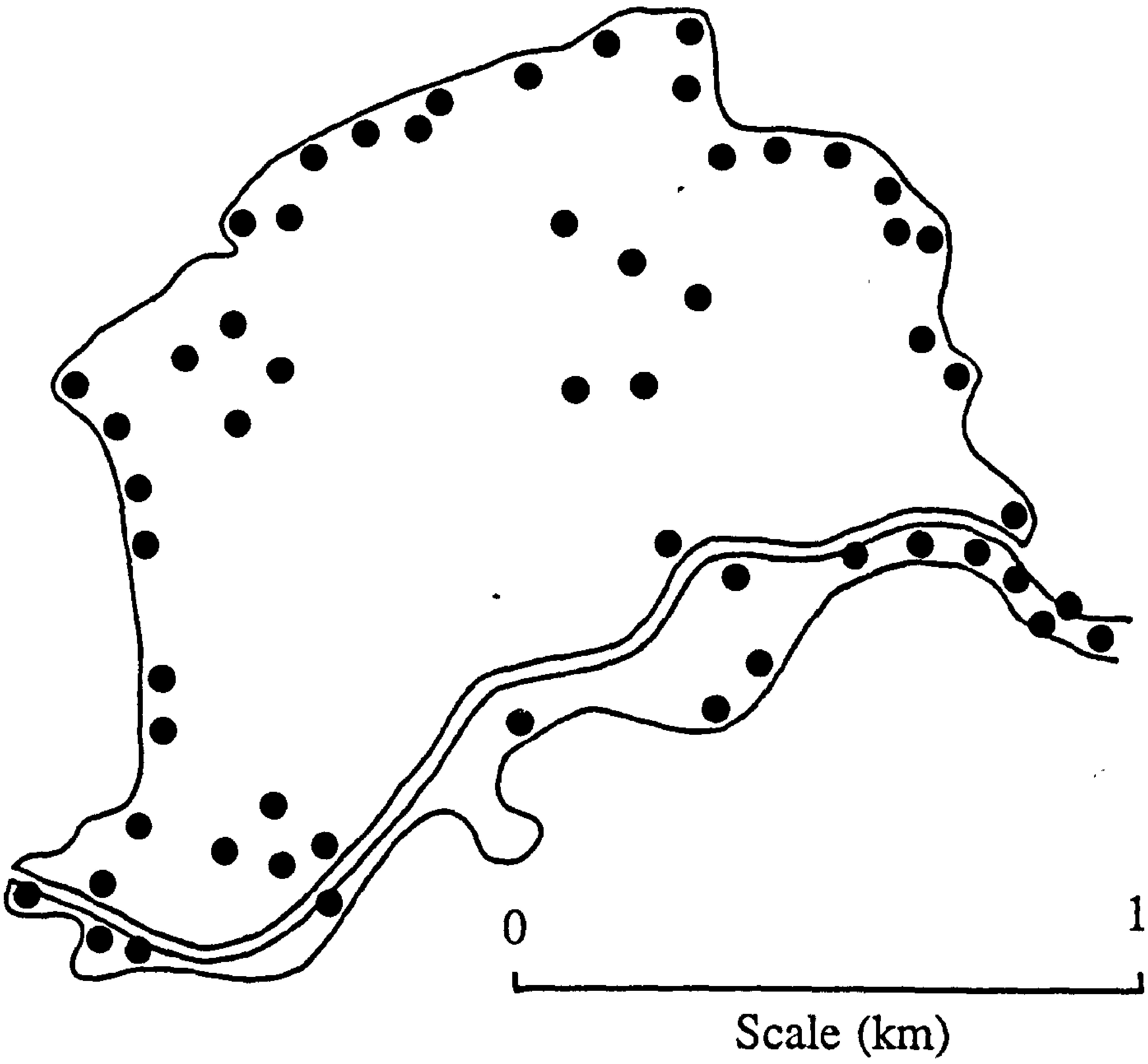


Fig.5.3.13. The distribution of resident robins in Wytham Great Wood during October 1945 (from Lack 1948). Note how the territories are clustered along the road and around the woodland edge.

## 5.4. Intrusions and evictions.

### 5.4.1. Methods.

Continuous radio-tracking provides the first technique by which small birds may be monitored continuously regardless of their activity or movements. Previous to this studies of the robin have relied on visual observations, which unavoidably are subject to biases towards focal individuals which are easy to observe, or which by their behaviour draw attention to themselves (East 1982). The levels of intrusion and eviction recorded by this study therefore represent the first rigorous assessment of the frequency and duration of this behaviour in the robin.

Hour long samples of continuous tracking data were examined for intrusive activity. This was defined as activity during which one bird spent a period of time inside the usual-area of another. Because all robins concentrated their activity in bushes and shrubs, intruders were almost always located within the core-nuclei of neighbours. In this analysis intrusions of less than four minutes duration, which following the movement rules for quantifying network use, would not be classed as intentionally excursive, were included. This is because these very short intrusions may represent instances of encounters with and eviction by owners, and therefore successful defense.

Although continuous tracking data were available for five non-territorial robins, it was not possible to determine when any intrusive activity was initiated since these individuals ranged widely into areas in which the ranges of territorial robins were not regularly monitored. However, the rate at which non-territorial robins were evicted could be assessed and compared with that for territorial birds.

### 5.4.2. Results.

The results summarised in Table 5.4.1. show intrusions by territorial robins into territorial neighbours, which were monitored from the moment the bird entered a neighbours' usual-area, to the moment it left of its own accord, or was forcibly evicted by the territory owner. The data contributing to the three sampling periods were not statistically independent; three individuals intruding into the same neighbour at different times of the day. It was not possible therefore, to compare statistically the intrusion pressure experienced by territorial robins at these different times. Intrusion pressure was, however, highest during midday and lowest at dusk (Table 5.4.1.).

**Table 5.4.1.** Intrusive actvity of territorial robins in the territories of neighbours during different times of the day.

| | Dawn | Middle | Dusk | Total |
|---|---|---|---|---|
| No. hour long observation periods | 15 | 35 | 15 | 65 |
| No. intrusions recorded | 4 | 11 | 1 | 16 |
| No. of intrusions that were terminated by an eviction | 1 | 2 | 0 | 3 |
| No. of intrusions that were targeted at near neighbours | 4 | 9 | 1 | 14 |

The proportion of hour long continuous tracking samples during which intrusions occurred (a measure of intrusion rate) was positively correlated with the number of nuclei in the territory network into which the intrusions were directed ($r_s=0.97$ $p<0.005$ $n=5$ Fig.5.4.1.). There was never more than one intrusion recorded per hour. The form of the function relating intrusion rate to number of core-nuclei must be exponentially accelerating, since even robins which only used one core-nucleus must have experienced some intrusions however brief. The curve shows a second order polynomial passing through the origin and fitted to the data (Fig.5.4.1.). The number of nuclei making up the networks from which intrusions were initiated, however, was not significantly correlated with the intrusion rate ($r_s=0.50$ ns $n=5$).

Dyads of non-breeding robins were only seen close together, without one attempting to evict the other, during bouts of mutual display. These always occurred in the neutral interstices between territories (n=18). The foraging behaviour of intruders was similar to that of owners, concentrating their time in bushes and shrubs. Intruding robins however, never vocalised. Intruders that were encountered were evicted by aggressive chasing until they left the territory. An impression formed during observations of chases was that intruders flew in any direction to escape. This resulted in the intruder entering another nucleus of the owner or a nucleus of a neighbour, rather than an obvious retreat across a discrete territory boundary to neutral ground. All intruders visited only one nucleus in the target territory before being evicted or leaving of their own accord (n=16), whereupon they returned to their own territory. Intrusions were more likely to be directed towards the territories of near neighbours (Table.5.4.1.). The durations of intrusions which were terminated by the intruder leaving the nucleus of its own accord were positively correlated with the area of the nucleus visited (data from middle of day $r_s=0.78$ $p<0.01$ $n=9$ Fig.5.4.2.). Also shown are the two intrusions by robins which occurred during this period, that were encountered by owners and the intruder evicted.

The median area of nuclei visited during intrusions was 38 $m^2$ (range 27-85 n=9). The median area of nuclei used by owners, however, was 75 $m^2$ (range 44-84 n=7). This reflects the higher intrusion pressure experienced by territory networks which contain large numbers of nuclei, each of which has a small area. From section 5.3., the median duration of nucleus visits by territory owners which occupied networks containing greater than one nucleus was 6.5 min (range 3.3-8.5 n=41). The median duration of intrusions during midday that were not terminated by eviction was two minutes (range 2-8 n=9), while the median time until being

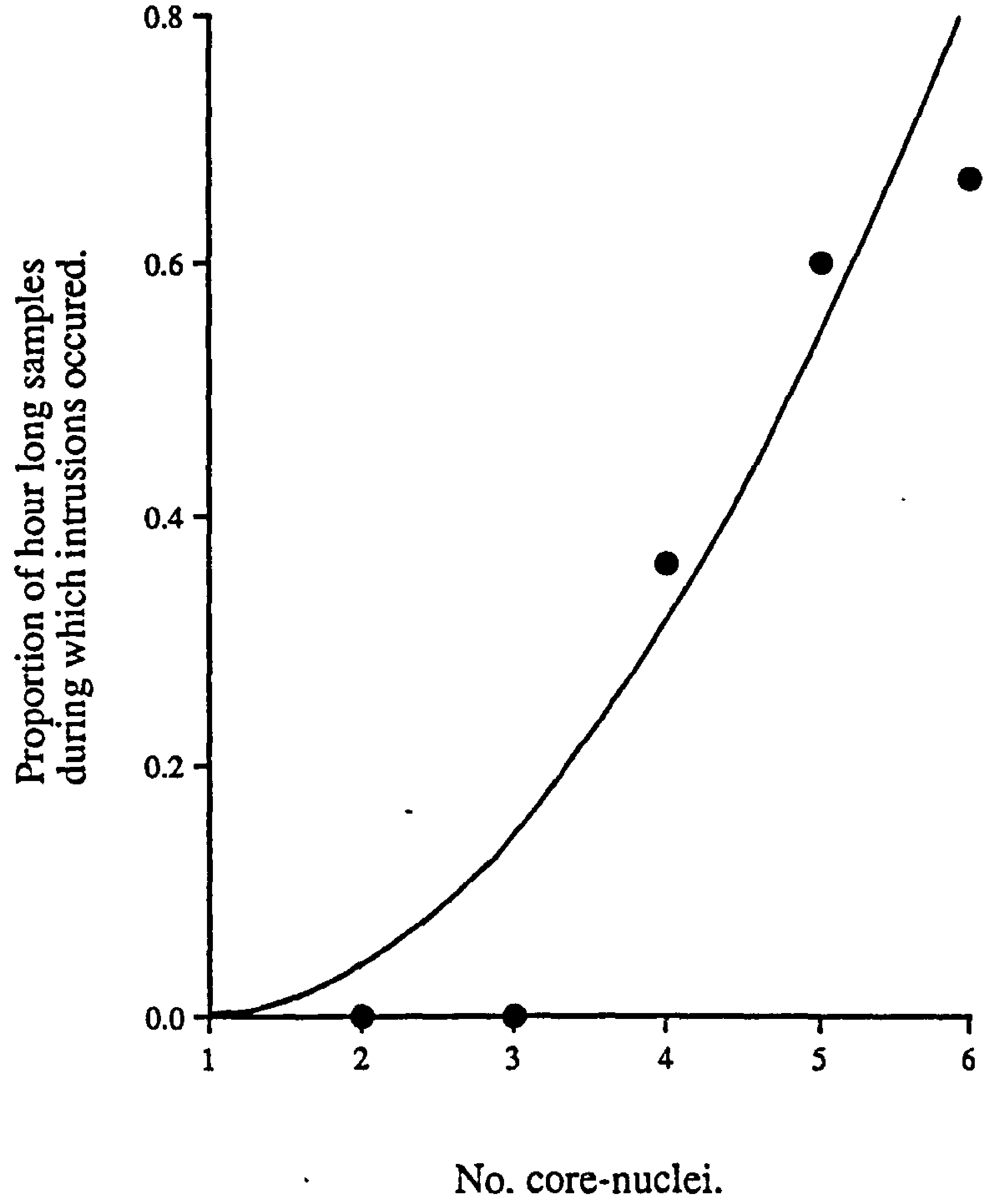


**Fig.5.4.1.** The relationship between the proportion of hour long samples of continuous tracking during which intrusions into neighbours occurred, and the number of core-nuclei within the usual-areas into which intrusions were targeted for non-breeding robins ($r_s$=0.97 $p<0.005$ n=9). The curve shows the polynomial equation;

$$\text{Proportion} = 1 - 0.04\ \text{No.nuclei} + 0.03\ (\text{No.nuclei})^2 - 1$$

**Table.5.4.2.** Comparison of the number of evictions experienced by territorial and non-territorial robins.

| | Territorial | | | | Non-territorial | | | |
|---|---|---|---|---|---|---|---|---|
| | Dawn | Middle | Dusk | Total | Dawn | Middle | Dusk | Total |
| No.hour long observation periods | 15 | 35 | 15 | 65 | 3 | 6 | 3 | 12 |
| No.evictions recorded | 1 | 2 | 0 | 3 | 2 | 7 | 0 | 9 |

**Table 5.4.3.** Comparison between the number of evictions of intruding robins by territory owners during an eight hour winter day.

| Study | No. evictions per territorial robin per day | No. evictions per non-territorial robin per day |
|---|---|---|
| Harper (1986) | 1 | 15 |
| This study | 0.5 | 9 |

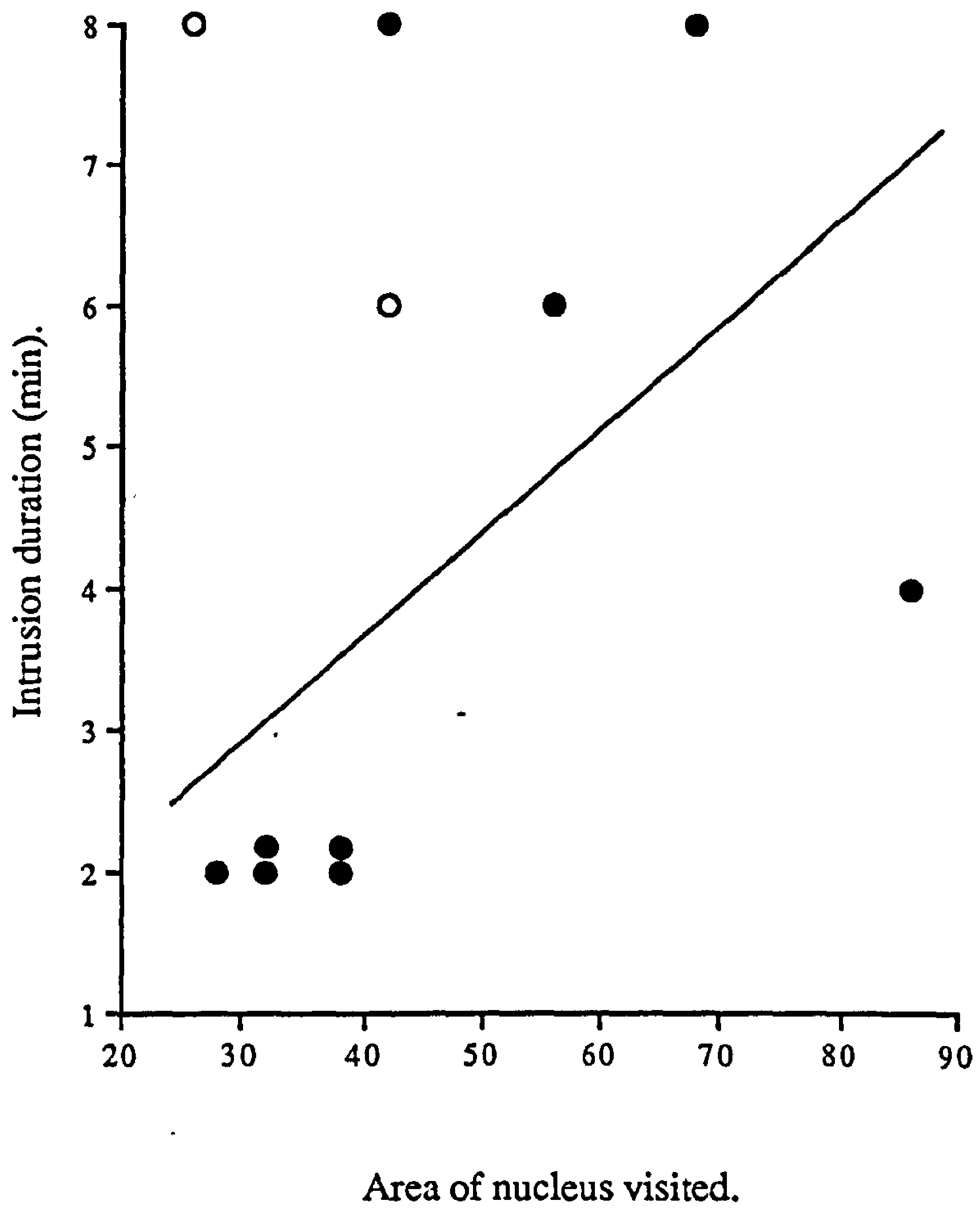


Fig.5.4.2. The duration of intrusions by robins during midday (min) plotted against the area of the core-nucleus visited ($m^2$). Robins only visited one nucleus during each intrusion. The solid symbols show intrusions that were terminated when the intruder left of its own accord ($r_s$=0.78 p<0.01 n=9). Open symbols show intruders that were encountered and evicted by owners. The line is that fitted to the equivalent data for owners (Fig.5.3.6.).

evicted from a nucleus during an intrusion was seven minutes (range 6-8 n=2).

Tic calls appeared to be particularly important for territory owners in the monitoring of movements by neighbours. An example of such tic call mediated interaction between two territorial neighbours is shown in Fig.5.4.3.

Non-territorial robins were evicted more often (0.75 $hr^{-1}$) than territorial robins (0.05 $hr^{-1}$)(Table 5.4.2.). In common with the territorial birds most evictions occurred during midday (78 %) and least at dusk (0 %)(Table 5.4.2.).

### 5.4.3. Discussion.

Compared to previous studies of the robin the levels of intrusion and eviction recorded in the present study were low. A comparison between the number of evictions recorded per eight hour winter day in Cambridge recorded by visual observation (Harper 1984) and measured by radio-tracking in the present study is shown in Table 5.4.3. Harper provided no sample sizes, so statistical comparisons were not possible. The intrusion pressure recorded using the rigorous radio-tracking technique produced values approximately half those recorded using visual observations. A possible explanation for this is that many excursions may have been misclassified by Harper as intrusions when in fact they only represented birds visiting bushes located in the neutral interstices between territories. If, however, radio-tracking recorded all intrusions while the visual observations of Harper only some, then the observed difference may be real, reflecting differences in the territorial behaviour of the two populations.

On the whole however, the results from radio-tracking showed strong similarities with those of Harper; most intrusions by territorial birds were into the territories of near neighbours; intruding robins were never tolerated on the territory of a neighbour if encountered by the owner; intruders visited only one territory before returning to their own territory; most intrusions occurred during the middle of the day with fewest at dusk; and non-territorial robins intruded and were evicted considerably more often than robins which were territorial.

The purpose of intrusions is assumed to be that initially of information gathering. Such information may include assessing prey densities or thermoregulatory costs of occupying different core-nuclei. Since dyads of neighbours can monitor each others location by listening to vocalisations, intrusions probably do not serve to determine the occupancy of neighbouring

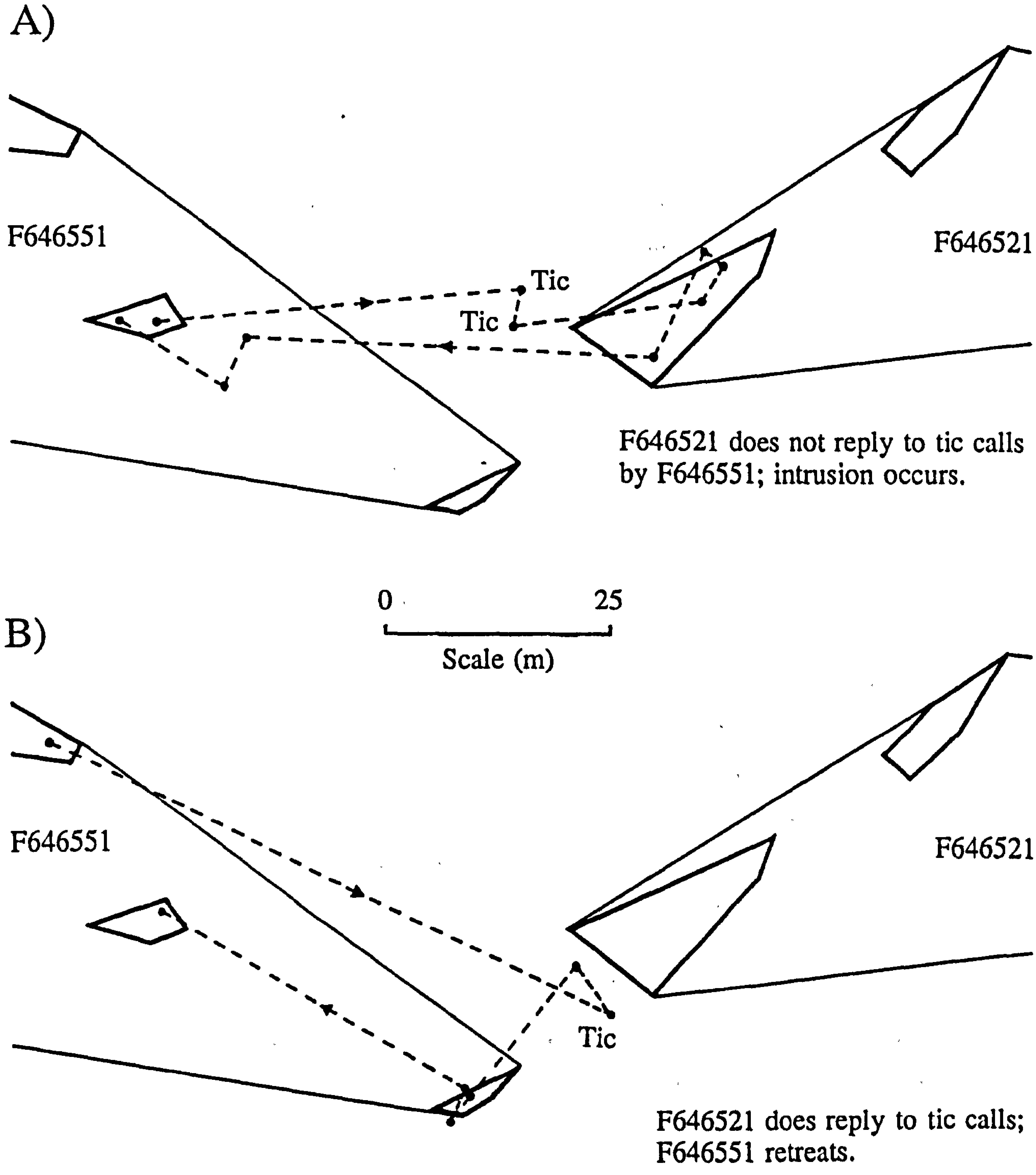


**Fig.5.4.3.** An example of the role of Tic-calls in the initiation of intrusions by territorial robins into neighbours. The behaviour of the focal robin is shown during midday on 11th January in (A) and during midday on the 14th January in (B). Thick lines indicate core-nuclei, thin lines usual-areas and dashed lines inferred movement between continuous tracking locations.

territories. The ultimate purpose of such information gathering, however, may be to increase resource holding potential (Parker 1974) during a take-over of one or all of a neighbours foraging patches by territory drift. Furthermore, some intrusions may simply be concerned with stealing food from a neighbours patches to supplement that available on a poor territory. Knowledge of which patches are food rich would then be useful.

On average, intruders visited core-nuclei of smaller area than robins visiting their own nuclei. This was because higher a number of intrusions were experienced by robins occupying territory networks containing large numbers of nuclei. These contained nuclei of small individual area (section 5.3.). For core-nuclei of the same area it would be expected that, if not located and evicted, the visit duration of intruders would be less than the visit duration of owners with no intruders. This is because the average time elapsed between nucleus visits by owners and subsequent intruders will be less than the most economic return time (Davies & Houston 1981). Intruders will experience prey densities less than the asymptotic value of each patch and therefore robins harvesting available prey should show shorter giving up times. The relationship between visit duration of owners and nucleus area (a measure of the asymptotic number of prey and therefore patch quality) is shown in Fig.5.3.6. The line extrapolated from these data is also shown in Fig.5.4.2. The visit durations of intruders were significantly shorter than the visit durations of owners (Mann-Whitney $U=13.0$ $p<0.05$; intruders median visit duration=2.0 min range 2-8 $n=9$; owners median visit duration=6.3 min range 3.4-8.6 $n=7$). Furthermore, intruders which were located and evicted had stayed in patches longer than would be expected for the area of patch visited. These individuals had perhaps intruded into patches in which prey densities were close to full recovery leading to long giving up times, but which were next in sequence to be visited by the owner.

Territory owners vocalise when arriving on and leaving their core-nuclei. Intruding robins could, therefore, monitor the locations at which territorial neighbours vocalise to synchronise their intrusions to target core-nuclei that were last visited by the owner for a period just under the optimal return time. Intruders may thus take advantage of higher prey availability than they would obtain by selecting a nucleus at random. For this reason perhaps, owners vocalised during only 30% of nucleus visits. Robins may therefore experience a tradeoff between the benefits of communicating the territorial ownership of nuclei and the costs of revealing which feeding patches have just been depleted and therefore which have fully recovered (Goldberg & Ewald 1991). In a similar way pikas have been shown to monitor neighbours and only mount intrusions when they were inactive (Smith & Ivins 1986). Intruders which stayed the longest were more likely to be encountered by owners and evicted. This would occur if intruders failed to anticipate the arrival of owners, perhaps because the latter did not reveal their position by vocalising. Although robin song has received a great deal of attention (Hoelzel 1986, Brindley 1991) there is no information available as to the behavioral ecology of tic calls. It would be advantageous for robins to respond to the tic calls of neighbours, since such calls are often used as an alarm call (Cramp 1988). In such situations tic calls are used to signal to a predator, such as a stoat, that it has been detected and an attack would be pointless. In a similar way the hare uses a visual signal when the approach of a fox has been detected (Holley 1993). Robins, therefore, may use tic calls to deceive neighbours into revealing their location prior to an intrusion. In this situation therefore, the tic call could be interpreted as meaning "here am I, where are you?"

Intruders were more likely to occur in territory networks with high numbers of core-nuclei, and therefore linear-length, even though individual feeding patches were smaller. This is because potential intruders moving through the habitat in a random direction would be more likely to encounter one of the many nuclei that are strung out in highly linear configuration in large territory networks.

The presence of an intruder may inflict a cost on owners in two ways. Intruders may gather information which may enhance their resource holding potential (Parker 1974) during subsequent territory drift or bids for territory ownership. The effect of foraging intruders is a reduction of the owners foraging efficiency, through depleting patches shortly before visited by the owner. Intruders however will also incur a cost when intruding. The feeding patches of any neighbour visited will always be at a suboptimal level of recovery if underlying patch qualities are the same, and may have just been depleted. Furthermore, the patches in the intruders own territory network will not be harvested during intrusions by them into the territories of neighbours, and so once the prey densities in such patches have fully recovered, they will represent the highest quality habitat to a simultaneous intruder.

During normal behaviour, robins spent the majority of their time out of sight in the bushes and shrubs in which their core-nuclei are sited. In such situations, the visibility of the rest of their territory is probably limited to an area within a few metres by dense vegetation. Because of this, owners may only have a high probability of detecting an intruder when it visits the nucleus that they already occupy. Conversely, the chance of an owner detecting an intruder that is visiting another nucleus within their territory network may be low. Because intruders usually visit the core nuclei of an owner for a similar or shorter period as the owner and terminate the intrusion when they leave the patch, the theoretical probability of an owner encountering an intruder within its territory network therefore will be one divided by the number of nuclei within the network.

Theoretical studies have used the concept of intruder equilibrium when modelling territory size (Schoener 1971,1987). This implies that the number of intruders that an owner evicts from its territory reaches an equilibrium with the density of intruders. The intruder density experienced by territorial robins is so low (less than two per day) that this concept does not apply. Nevertheless, the impact of patch depletion by intruders on the foraging economics of territory occupants may have important implications for the energy costs of territory maintenance during winter.

## 5.5. The defense component of territorial behaviour.

### 5.5.1. The consequences of hypothetical defense behaviours.

Animals may meet their energy requirement by adopting time-energy budgets which achieve one of a number of different foraging goals (Schoener 1971). These different time-energy regulation strategies are independent of the foraging strategy, such as perch and drop or ground hopping (East 1980, 1982), that is pursued by an individual. Many animals and small territorial birds in particular, have been considered to be energy maximisers with daylength acting as a time constraint (Schoener 1971, 1981, Hixon & Carpenter 1983, Beletsky 1986, Eason 1992). The goal of a robin which behaves as an energy maximiser and spends all of its time within its network of core-nuclei, therefore, is assumed to be the maximisation of its net rate of energy gain. This can be achieved by exploiting a number of feeding patches. Patches should only be revisited within a regular foraging route between nuclei after the prey densities have recovered from previous depletion by the owner. A hypothetical robin which follows such behaviour is here termed an ideal exploiter. An ideal exploiter invests all of its time and energy in the economic exploitation of the patches of renewing resource it uses. Such an individual invests nothing in other activities, such as predator avoidance or interactions with other robins.

Robins occupying networks containing large numbers of small patches move between nuclei more often and spend less time in patches than robins within networks containing a smaller numbers of larger patches. Furthermore, individuals using larger numbers of feeding patches experience a higher intruder pressure (section 5.4.). The expulsion of intruders by territory owners may be important for several reasons. An intruder which enters the territory of a robin without being located will deplete patches such that they will not have fully recovered when they are revisited by owners, thus reducing the average rate of energy gain of owners (Davies & Houston 1981). By terminating their visit without being evicted, intrusions may be considered successful, and therefore may return more frequently than intruders that are located and evicted (Ewald & Carpenter 1978). Finally, successful intruders may become more difficult to evict (Krebs 1982). As their knowledge of the owners territory increases, their resource holding potential also increases, perhaps leading to escalated fighting (Krebs 1982).

The goal of a robin which spends all of its time in defense of the foraging patches it uses, is to maximise its probability of encountering intruders. A hypothetical individual which follows this behaviour is here termed an ideal defender. Ideal defenders invest their time and energy only in searching for intruders. The behaviour which achieves this ideal defense has received much theoretical speculation. Dill (1978) considered animals occupying circular territories with perfect visibility. His model dictated that owners must make a return trip from the centre of the territory to the perimeter to evict an intruder. Schoener (1987) describes models of optimal territory size in which time budgets of owners contain patrol time, but the nature of this is indeterminate. An approach from the level of populations has been used by Parker & Knowlton (1980) to model evolutionary stable strategies for maintenance of territory size. Their model considers the effect of mutant strategies of defensive effort within a territorial population, although once again the nature of the different kinds of defensive effort are not described.

Field studies of territorial birds have attempted to describe such defensive investment in more detail. Frequently this has been considered to simply involve the eviction of intruders when located (Davies & Houston 1981, Ewald 1992). In hummingbirds, however, increased defense may be achieved simply by differential allocation of foraging effort over the territory (Paton & Carpenter 1984). The apparent quality of a territory to potential intruders is reduced by the owners concentrating their foraging effort at the edge of their territory in the early morning. Intruders first assess the profitability of persisting with an intrusion by foraging at the edge of a target territory. This "defense by exploitation" results in higher net energy gains to owners and lower food losses to intruders (Paton & Carpenter 1984).

Bird song has often been implicated in territorial defense (Krebs 1977). Song has been proven to play a role in territorial maintenance in the great tit (Krebs 1977), where playback of song during the breeding season in unoccupied territories delayed the settlement of pairs from adjacent poor quality habitat. Song output is also related to the energetic condition of territory owners and so may act as a reliable indicator of fighting motivation and territory quality (Strain & Mumme 1988). Birds subject to higher temperatures (Garson 1979), low parasite loads (Moller 1991), or with access to supplementary food (Strain & Mumme 1988, Cuthill & Macdonald 1990) sing more. Even if birds with access to supplementary food do not increase their background levels of song, they may still be able to increase song output during a territorial emergency, such as an attempted takeover. This has been shown to occur in the robin (Harper 1984) and suggests singing has associated costs. Playback of song from undefended feeders has been shown to attract non-territorial hummingbirds (Goldberg & Ewald 1991). Consequently territorial birds that sing may provoke either decreased or increased intrusions depending on whether intruders interpret the signal as indicating a high ability and motivation to fight, or as indicating the presence of feeding patches of high quality.

Clearly an ideal exploiter cannot maintain optimal return times for the core-nuclei within the network it occupies without experiencing resource depression by intruders, and an ideal defender would lose no food to intruders but would die from starvation. In successfully maintaining an economic territory therefore, a robin must be investing time and energy in both exploitation and defense activities. The goals of these two activities are mutually incompatible; a robin that is commuting between the core-nuclei within its territory network in a regular sequence cannot be maximising encounter rates with unseen potential intruders which can arrive anywhere in its territory. The territory owner must therefore adopt a compromise between the two conflicting goals such that the trade off in investment between the two is optimised (Fig.5.5.1.). This has been studied using captive great tits (Kacelnik *et al* 1981). The birds were considered to be vigilant for intruders while moving between patches, and not vigilant when foraging within patches, since these two activities were assumed to be incompatible. In response to the presentation of another great tit (a potential intruder) the subjects moved between feeding patches more often, increasing their vigilance time but decreasing their foraging time and therefore rate of energy gain. The degree to which

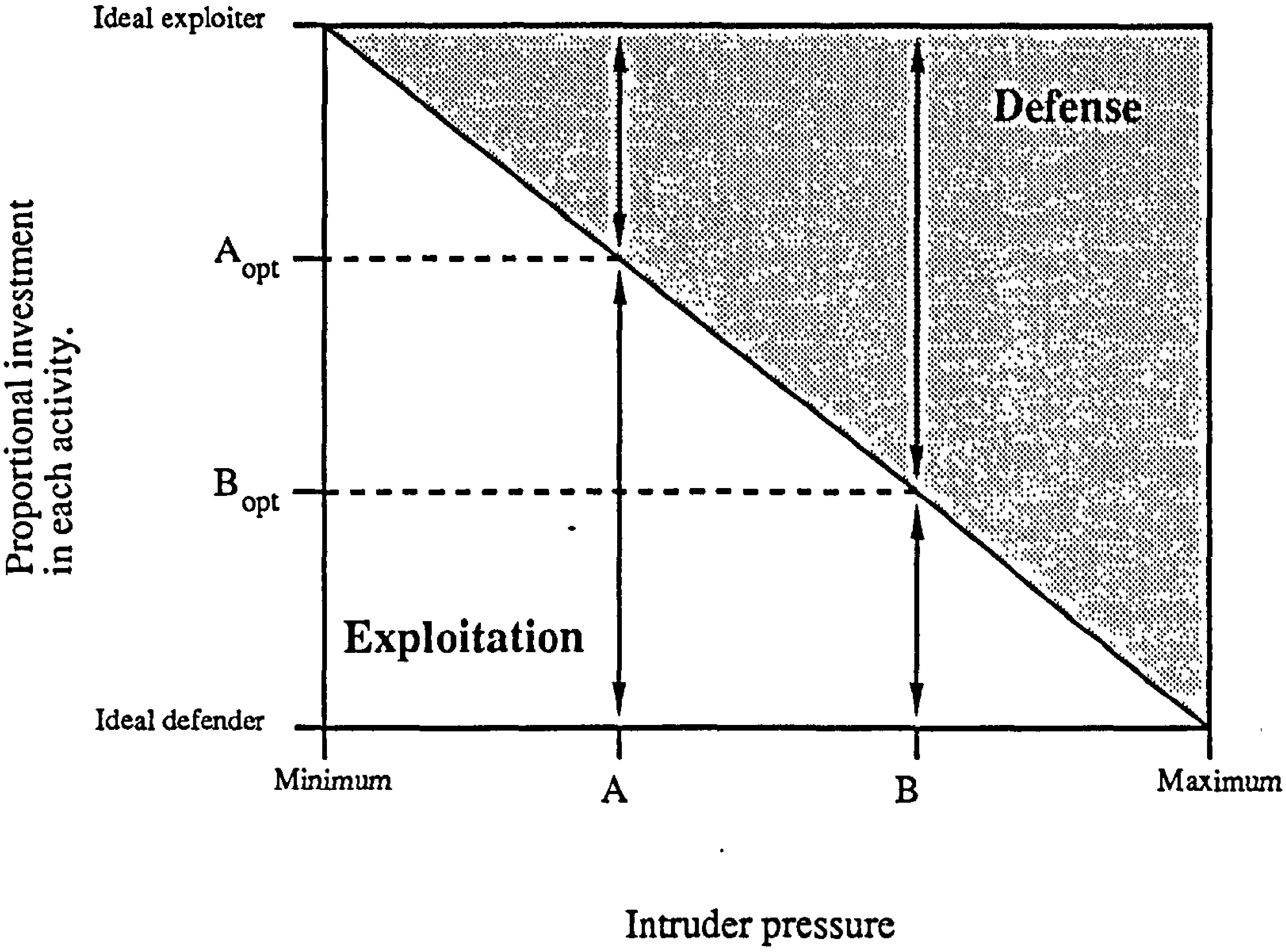


**Fig.5.5.1.** A model to illustrate the tradoff between territory exploitation and defense behaviour. Assuming the activities involved with territorial exploitation and defense are mutually incompatible, robins must find an optimal tradeoff in investment between the two, depending on the immediate importance of each activity.

In this figure, a robin which experiences intruder pressure (A) selects an optimal tradeoff ($A_{opt}$) in which two thirds of its time and energy are invested in activities associated with exploitation, and one third in territorial defense. If intruder pressure increases to (B), the robin must increase its investment in defense, the optimal tradeoff therefore changes ($B_{opt}$) to that in which one third of time and energy is invested in exploitation and two thirds in defense.

Robins which invest all their time and energy in exploitation are ideal exploiters, while robins which invest all their time and energy in defense are ideal defenders. Neither of these extremes, however, is a viable option (see text).

an individual can increase patrolling time and decrease foraging time will therefore depend on its energetic condition as demonstrated using free living territorial great tits (Ydenberg 1984, Ydenberg & Krebs 1987). Using principles of dynamic optimality, they showed that an individual will change the tradeoff between foraging (time within patches) and territorial defense (moving between patches) with changes in food deficit.

Some qualitative predictions of the effects of different defense behaviours on owners and intruders are shown in Table 5.5.1. The probability of encountering intruders can only be increased by the owner spending less time away from its territory. This represents a cost to territory occupants, if intrusions allow owners to gain valuable information on neighbours. Different changes in the pattern of network use will produce different effects on both owners and potential intruders. Increasing the commuting rate will make patches less profitable to intruders but also increase the commuting costs of owners. Increasing the randomness of patch visits will similarly make patches less profitable for intruders. Although this will cause no increase in exploitation costs, the owner will, however, experience a reduced rate of energy gain. Commuting costs will be reduced by birds using "short cuts" to decrease linearity L and increase the accessibility of the foraging patches they use. The increased individual flight distances required may however, have an associated increased predation risk. Furthermore, such behaviour will have no effect on either the probability of owners encountering intruders or the profitability of intrusions to intruders. Increase in vocalisations similarly will have no effect on the probability of owners encountering intruders or the profitability of intrusions to intruders. Owners which signal to potential intruders by vocalising may encourage intrusions by revealing their location and communicating the economic defendability of the territory and the state of recovery of individual patches.

The extent to which these effects occur will depend on the number of core-nuclei in the network used by the territory owners. Robins occupying large numbers of nuclei will initially experience a relatively low probability of encountering an intruder, assuming the visibility between core-nuclei experienced by foraging robins is low (Fig.5.5.2.). Furthermore, territory networks containing large numbers of nuclei suffer a higher intruder pressure (Fig.5.5.2.). Each territory network contained a similar total area of foraging patches. In large networks therefore, the proportion of the total prey available from the entire network, that is available per nucleus is lower (Fig.5.5.3.). Robins were only observed to visit one nucleus before terminating an intrusion (section 5.4.). Consequently the potential damage to the

**Table 5.5.1.** Some predictions of the effects of different defense behaviour on owners and intruders. P signifies probability, and arrows indicate an increase or decrease in the magnitude of predicted effects on owners and intruders due to the different behaviours.

| Defense behaviour of owner | Effect on P(encounter intruder) | Effect on owners rate of energy gain | Effect on owners commuting cost per unit time | Effect on owners foraging cost per unit time |
|---|---|---|---|---|
| None | - | - | - | - |
| Increase time on territory network | ↑<br>Increased chance of owner being on territory when intrusion occurs. | - | - | - |
| Increase commuting rate * | -<br>Assuming intruders will respond to reduction in apparent patch quality. | -<br>Patches revisited before full recovery but are visited more often. | ↑<br>Movement between patches more frequent. | -<br>Less prey to collect per patch due to reduced return but patches visited more often. |
| Increase randomness of commuting movements * | -<br>Assuming intruders respond to reduction in apparent patch quality. | ↓<br>Patches revisited before full recovery yield low gain, but patches revisited after full recovery do not provide any higher gain. | - | ↓<br>Less prey to collect averaged over all patches. |
| Use longer commuting flights between core-nuclei to decrease index of linearity L * | - | - | ↓<br>Average cost per unit time decreases due to use of "short cuts". However predation risk may increase. | - |
| Vocalise more often when arriving on and leaving patches. | ↓<br>May reveal location of owners allowing intruders to avoid encounters. | - | - | - |

* Only possible if territory network contains greater than two core-nuclei.

Table 5.5.1. continued.

| Defense behaviour of owner | Effect on patch quality that would be experienced by potential intruder | Effect on rate of energy gain experienced by intruder relative to that without defense by owner |
|---|---|---|
| None | - | - |
| Increase time on territory network | ↓<br>Patches harvested more often. | ↓<br>Less prey available per patch due to more frequent harvesting by owner. |
| Increase commuting rate * | ↓<br>Patches harvested more often. | ↓<br>Less prey available per patch due to more frequent harvesting by owner. |
| Increase randomness of commuting movements * | ↓<br>Patches harvested less regularly resulting in increased range of quality. Decrease on average since patches recently visited by owneryield low gain but, patches revisited after recovery do not yield any higher gain. | ↓<br>Less prey available per patch on average due to low gain in patches recently visited by owner but patches visited aften full recovery do not provide any higher gain. |
| Use longer commuting flights between core-nuclei to increase index of linearity L * | - | - |
| Vocalise more often when arriving on and leaving patches. | ↑<br>If intruder uses vocalisations of owners to predict which patch has most recovered from depletion. | ↑<br>If intruder uses vocalisations of owners to predict which patch has most recovered from depletion. |

* Only possible if territory network contains greater than two core-nuclei.

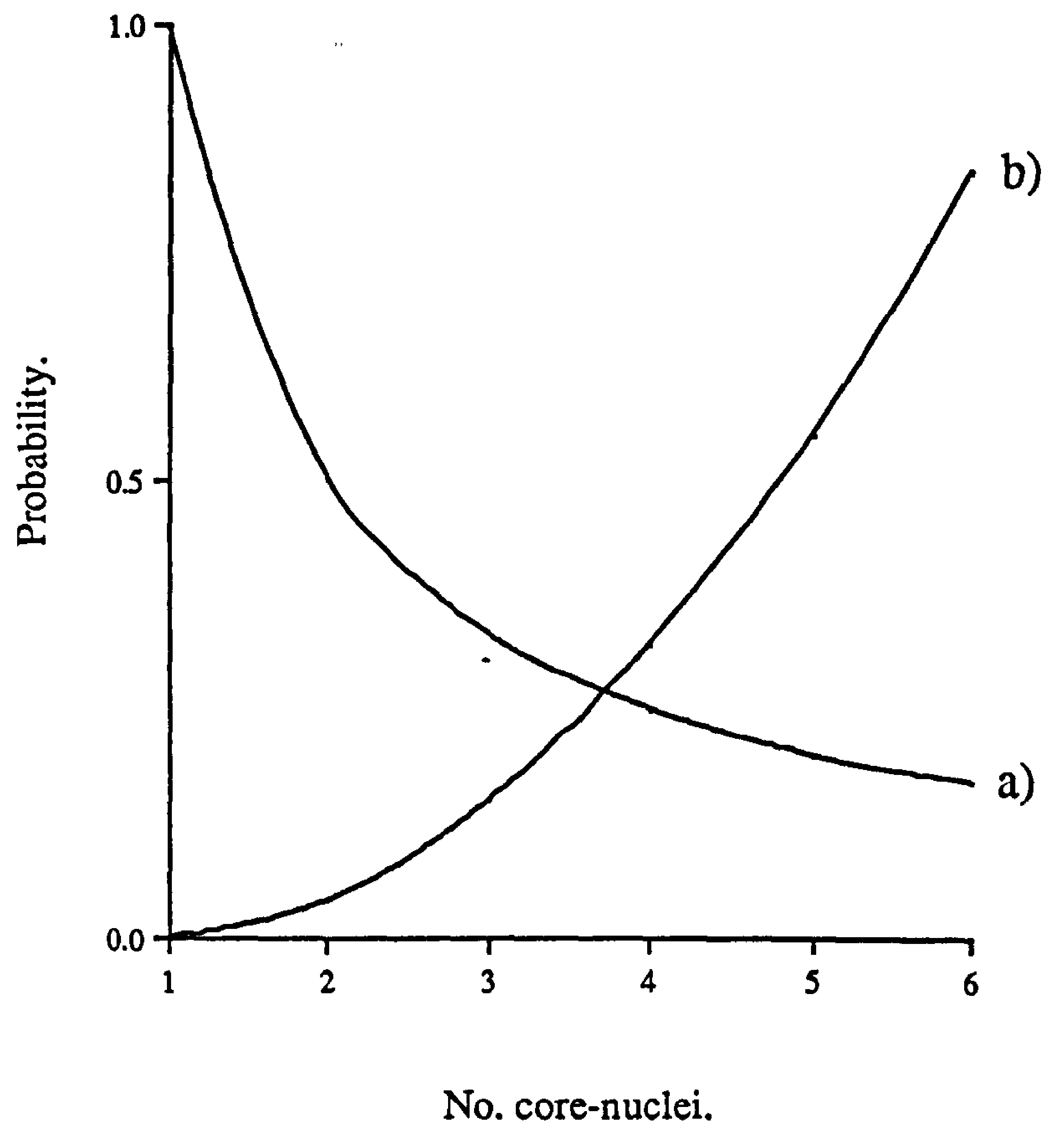


**Fig.5.5.2.** The probability of a territorial robin detecting an intruder within its network of foraging patches will decrease exponentially with the number of patches it uses (curve a), assuming visibility between nuclei is very poor and as observed intruders only visit one nucleus before leaving of their own accord.

Conversely, the probability of an intrusion occurring will increase with the number of foraging patches (curve b). The curve is the polynomial equation fitted to the observed data in Fig.5.4.1.

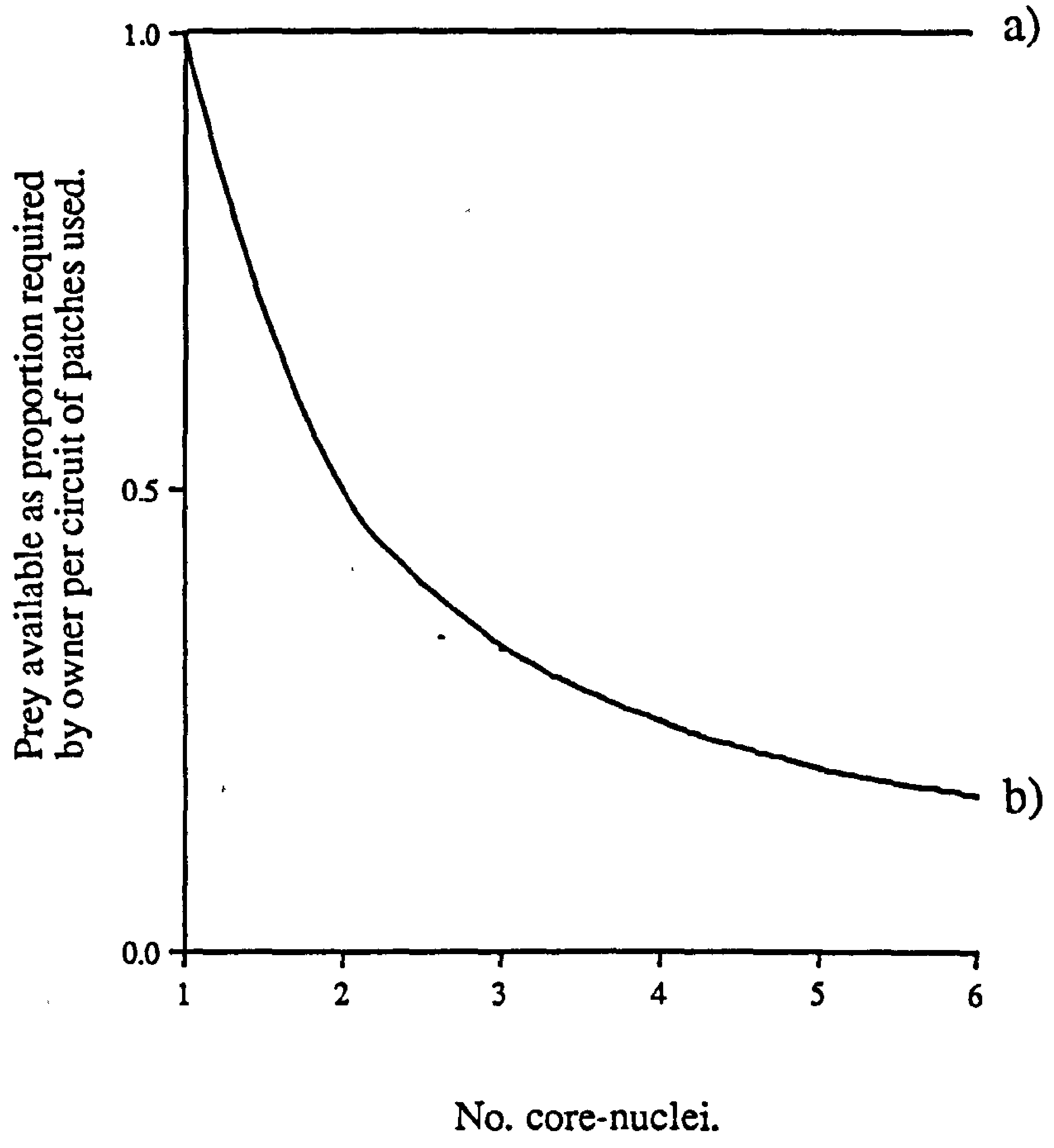


**Fig.5.5.3.** The foraging patches within a territory network contain all of the prey required by the owner per circuit of visits (line a). Territories containing different numbers of patches contain very similar total patch areas, and there is no difference in the prey densities between individual patches of different area.

As the number of such core-nuclei within territories increases therefore, their individual area decreases, and the proportion of the total prey required that is available from each nucleus, also decreases exponentially (curve b).

owners rate of energy gain by one intruder will be less in a large territory than in a small territory.

It is not possible to quantify the degree to which the overall behaviour for any particular individual is a trade off between exploitation and defense simply by observations of behaviour. The unknown defense component of the optimal compromise may only be revealed by carrying out manipulations such that the territory owner is forced to alter its allocation of effort and hence the optimal tradeoff between the two. The consequences for the overall behaviour of the individual may then be assessed (Fig.5.5.1.).

### 5.5.2. Methods.

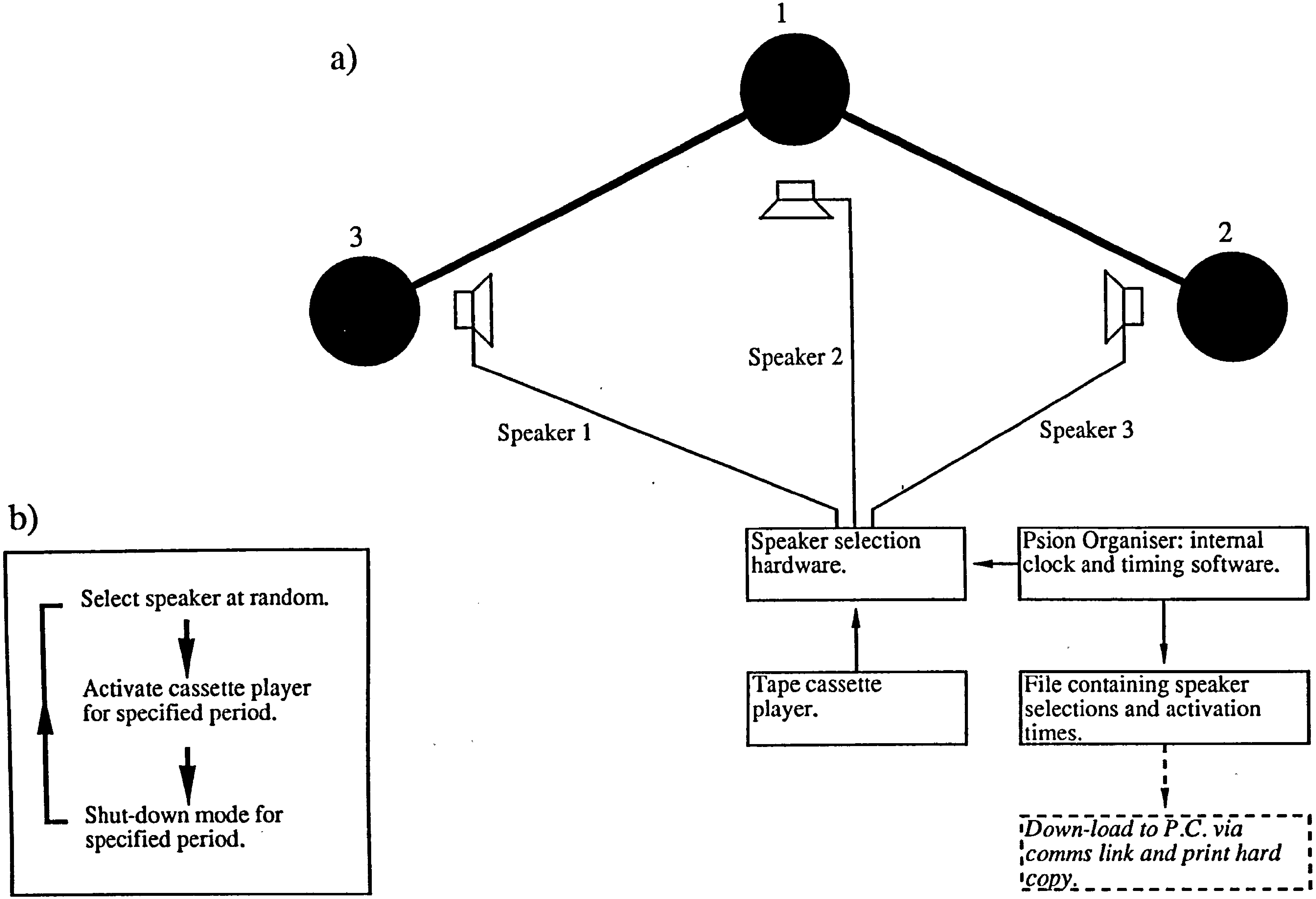
The territorial robins which were continuously tracked at different times of the day were presented with simulated territorial intrusions by conspecifics. These took the form of short periods of playback of robin song from one of up to four speakers which were placed in the estimated locations of the owners core nuclei, separated by periods of silence. Although this did not realistically replicate the behaviour of the usual furtive intrusions which were impossible to simulate, it did represent a potential threat to the territory owner. Robins frequently sing during intrusions, particularly if their intention is to usurp the owner and take over the territory (Lack 1965, Harper 1984).

A 60 min tape cassette containing three copies of a 20 min recording of Autumn and Winter robin song was obtained from the British Library of Wildlife Sounds. The tape contained song from 11 individuals recorded in England. Details of the recordings are listed in Appendix 8. Although clines in song phrase pitch and length have been described across Europe, no such differences between populations in Britain have been observed (Cramp 1988). All of the taped song was therefore considered to simulate a threat to territory owners. The taped song was played on a Sony TCM-818 cassette player and presented through Sony SRS-37 speakers with integral amplifiers via 25-50 m cables. The quality of the tape head was sufficiently high to reproduce the high frequencies in robin sing (P.Slater pers. comm.). The selection, activation and timing of song playback was controlled by software running on a Psion Organiser linked to speaker selection hardware. All of the power requirements were provided by a 12v automobile battery so the selection of owners and territories to be manipulated was not dependent on the proximity of a mains supply The Equipment was constructed by the Micro Processor Group at the University of Stirling, and is illustrated in Fig.5.5.4.

**Fig.5.5.4.** The equipment used to present playback of robin song during manipulations of territory use.

In (a) are shown the speakers placed in or near to the locations of core-nuclei (solid circles numbered one to three and linked by commuting paths), and linked to the speaker selection hardware. This was controlled by a Psion personal organiser which selected a speaker at random and activated the tape recording for specified periods.

The flow diagram for the Psion program is shown in (b).


a)
1
2
3
Speaker 1
Speaker 2
Speaker 3
Speaker selection hardware.
Psion Organiser: internal clock and timing software.
Tape cassette player.
File containing speaker selections and activation times.
*Down-load to P.C. via comms link and print hard copy.*
b)
Select speaker at random.
Activate cassette player for specified period.
Shut-down mode for specified period.

Speakers were placed in what were estimated to be the locations of core-nuclei. The discontinuous tracking data, from which the locations of the core-nuclei were determined, were analyzed after the continuous tracking was completed. This insured that the two types of data were independent. The estimated locations always proved to be correct after subsequent data analysis. Robins habitually sing from perches well above the ground (East 1982). This increases efficiency of the signal projection (Rae 1979, Brindley 1991). Speakers were therefore located two metres above the ground, attached to tree trunks or branches, and facing towards the geometric centre of the usual-area. This ensured that the song could be heard by the owner while in any of its core-nuclei. The volume of the song playback was standardised to an average of 90 dab (Brindley 1991) at one metre using a Lucus Instruments CEL-214 impulse sound level meter. There was some variation in the sound levels due to variation in the original recording levels. Preliminary trials with the recorded robin song broadcast from a single speaker showed that the study population did respond to the tape, probably because they recognised it as conspecific. For example, individuals would reply from a distance, approach and sometimes circle round the speaker.

The experimental procedure was as follows. An asymptotic sample of discontinuous tracking data was collected over four days from the focal individual. On the day before the start of the manipulation, the speakers were placed in the estimated core-nuclei of the focal individuals territory. This allowed time for the owner to habituate to their presence. The next day (set as day one) the territory owner was continuously tracked for periods of one hour at dawn, midday and dusk. Behavioural observations of territorial defense and vocalisations were recorded. This activity represented the control data. On day two, approximately 10 min before dawn the sample of continuous tracking commenced, the playback equipment was activated to present the recorded tape from a randomly selected speaker for 2.5 min, followed by 2.5 min of silence. A duration of 2.5 min was an arbitrarily selected period, but was similar to that of previous playback experiments on the robin (Hoelzel 1986, Brindley 1991). This continued until the period of radio-tracking was over, exposing the territory owner to 12 periods of playback during the period of continuous tracking period. The 20 min of recorded song from 11 birds ensured that the subjects were only exposed more than once to a very small number of song phrases. This was probably insufficient for habituation (Rae 1979, Hoelzel 1986). The equipment was similarly activated before and deactivated after the midday and dusk observation periods and represented the experimental data. The number of speakers deployed in each territory could be varied between two and four, so that as far as possible there was one speaker in or near each nuclei used by the focal bird. The continuous tracking data was quantified by applying the movement rules outlined in section 5.2. and measures of network use obtained (Table 5.3.2.) obtained. In addition, the response of experimental birds to the active speakers was scored as either movement towards, movement away from, or no change in location relative to each activated speaker in turn.

### 5.5.3. Results.

The midpoint temperatures on control and experimental playback days were not significantly different (control median=8.5°C range 5.7-10.6, playback median=10.3°C range 2.7-12.6, Wilcoxon Signed-rank Matched-pairs Z=0.00 ns n=7). Any temperature related changes in behaviour (eg East 1982) will therefore not cause responses to playback to differ significantly.

There was no relationship between the number of nuclei used by each individual and the percentage of occasions on which they approached, retreated or showed no reaction to the activation of speakers (Table 5.5.2.). The data could therefore be grouped between individuals, increasing cell frequencies sufficiently for chi-square analysis of the frequency of movement in relation to the activation speakers. There was no significant difference between the frequency of moving and not moving at different times of the day ($\chi^2$=3.96 df=2 ns n=195). Furthermore when birds did move, they were equally likely to move towards or away from speakers when activated at each time of day ($\chi^2$=0.08 df=2 ns n=151).

The continuous tracking data for the robins during the playback manipulation are presented in Appendix 9. Comparing data from the different times of day, there were no significant differences between the measures of space use on control and playback days (Table 5.5.3.). Furthermore there were no differences between the measures of space use when averaged over the control and playback days (Wilcoxon Signed-rank Matched-pairs all p>0.3 n=7). The absolute and percentage change in the measures of space use in response to the playback manipulations are shown in Table 5.5.4.

Correlations between changes in space use and territory size, measured by number of core-nuclei, are summarised in Table 5.5.5. When presented with simulated intrusions territorial robins responded by changing their commuting rate or proportion of movements that were backtracks, depending on whether they occupied networks containing small or large

**Table 5.5.2.** Correlations between the number of core-nuclei occupied by each robin and the percentage of occasions on which birds were observed to move towards, away from or show no reaction on occasions when speakers playing robin song were activated (n=7). All p>0.05.

| Time of day | Spearman correlation | | |
|---|---|---|---|
| | Move towards | No reaction | Move away |
| Dawn | -0.20 | -0.28 | 0.36 |
| Midday | 0.00 | 0.14 | -0.30 |
| Dusk | 0.33 | -0.11 | -0.58 |

**Table 5.5.3.** Nonparametric paired tests between the control and experimental values of measures of space use at different times of the day (n=7). See Appendices 7. and 9. for ranges of data.

| Measure of space use | Median values | | | | | | Wilcoxon matched-pairs signed-ranks test | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Control | | | Experimental | | | Z | | | p | | |
| | Dawn | Midday | Dusk | Dawn | Midday | Dusk | Dawn | Midday | Dusk | Dawn | Midday | Dusk |
| Proportion of time on usual-area | 1.00 | 0.93 | 0.60 | 0.90 | 1.00 | 0.73 | -0.27 | -0.40 | -0.10 | 0.79 | 0.69 | 0.92 |
| Commuting rate (movements $hr^{-1}$) | 9.0 | 6.4 | 6.7 | 8.0 | 6.0 | 10.0 | -0.59 | -0.51 | -1.18 | 0.55 | 0.61 | 0.24 |
| Time singing (sec $hr^{-1}$) | 11 | 0 | 0 | 18 | 12 | 0 | -0.40 | -1.60 | -1.60 | 0.69 | 0.11 | 0.11 |
| Proportion of locations at which birds vocalised | 0.13 | 0.10 | 0.07 | 0.17 | 0.10 | 0.07 | -1.15 | -0.67 | -0.63 | 0.25 | 0.50 | 0.53 |
| % departure from ideal-linear use[#] | 13.8 | 15.9 | 7.4 | 10.6 | 3.9 | 1.3 | -0.40 | -0.53 | 0.00 | 0.69 | 0.59 | 1.00 |
| Proportion of movements that were backtracks[#] | 0.42 | 0.45 | 0.25 | 0.57 | 0.47 | 0.48 | -1.21 | -0.73 | -1.07 | 0.22 | 0.47 | 0.29 |

[#] Robins occupying less than three core-nuclei can only use them in an ideal-linear manner and can only visit them in a regular sequence. Any such individuals were omitted from the analysis, therefore here n=6.

**Table 5.5.4.** Summary of continuous tracking data for the seven robins averaged over the control day and experimental playback day. Data for the different times of day are shown in Appendices 7. and 9.

| Ring No. | Proportion of time on usual-area | | | | Commuting rate (movements $\text{hr}^{-1}$) | | | | Time singing (sec $\text{hr}^{-1}$) | | | | Proportion of locations at which birds vocalised | | | | % departure from ideal-linear use | | | | Proportion of movements that were backtracks | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Cont. | Expt. | Δ | % Δ | Cont. | Expt. | Δ | % Δ | Cont. | Expt. | Δ | % Δ | Cont. | Expt. | Δ | % Δ | Cont. | Expt. | Δ | % Δ | Cont. | Expt. | Δ | % Δ |
| F646581 | 1.00 | 1.00 | 0.00 | 0.0 | 9.7 | 9.7 | 0.0 | 0.0 | 47 | 1 | -46 | -97.7 | 0.13 | 0.02 | -0.11 | -84.6 | 13.1 | 8.1 | -5.0 | -38.2 | 0.34 | 0.49 | 0.15 | 44.1 |
| F646569 | 0.63 | 0.87 | 0.24 | 38.1 | 7.7 | 6.5 | -1.2 | -15.6 | 4 | 47 | 43 | 1075.0 | 0.11 | 0.18 | 0.07 | 63.6 | 30.4 | 30.9 | 0.5 | 1.6 | 0.27 | 0.45 | 0.28 | 103.7 |
| F646546 | 0.90 | 0.97 | 0.07 | 7.8 | 19.5 | 20.8 | 1.3 | 6.6 | 98 | 134 | 36 | 36.7 | 0.32 | 0.42 | 0.10 | 31.3 | 8.3 | 4.5 | -3.8 | -45.8 | 0.19 | 0.41 | 0.22 | 115.8 |
| F646551 | 0.72 | 0.58 | -0.14 | -19.4 | 5.6 | 8.4 | 2.8 | 50.0 | 0 | 0 | 0 | 0 | 0.02 | 0.07 | 0.05 | 250.0 | 5.7 | 0.0 | -5.7 | -100.0 | 1.00 | 1.00 | 0.00 | 0.0 |
| F227546 | 0.75 | 0.56 | -0.19 | -25.3 | 7.8 | 3.1 | -4.7 | -60.0 | 0 | 0 | 0 | 0 | 0.08 | 0.08 | 0.00 | 0.0 | 21.3 | 30.4 | 9.1 | 42.7 | 0.55 | 0.25 | -0.30 | -60.0 |
| F646547 | 0.89 | 0.80 | -0.09 | -10.1 | 4.7 | 7.6 | 2.9 | 61.7 | 10 | 16 | 6 | 60 | 0.05 | 0.11 | 0.06 | 120.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.40 | 0.39 | -0.01 | -2.5 |
| F646590 | 0.81 | 0.91 | 0.10 | 12.3 | 2.7 | 5.6 | 2.9 | 107.4 | 5 | 41 | 36 | 720 | 0.08 | 0.17 | 0.09 | 112.5 | - | - | - | - | - | - | - | - |

| | |
|---|---|
| Δ | Absolute change in pattern of space use between control and experimental treatment. |
| % Δ | Absolute change as a percentage of the control value. |
| - | Number of core-nuclei less than 3. |

**Table 5.5.5.** Correlations between changes in measures of space use in response to experimental playback and number of core-nuclei within the territory network; a measure of territory size (n=7). Values in brackets indicate the result after removing an outlying point.

| Measure of space use | Spearman correlation | |
|---|---|---|
| | Absolute change | % change |
| Proportion of time on usual area | 0.05 | -0.16 |
| Commuting rate (movements $hr^{-1}$) | -0.74 *<br>(-0.78 *) | -0.76 *<br>(-0.81 *) |
| Time singing (sec $hr^{-1}$) | 0.17 | -0.11 |
| Proportion of locations at which birds vocalised | 0.11 | -0.60 * |
| % departure from ideal-linear use # | 0.25 | 0.26 |
| Proportion of movements that were backtracks # | 0.44<br>(0.87 *) | 0.53<br>(0.97 **) |

* p<0.05 ** p<0.005

\# Robins occupying less than three core-nuclei can only use them in an ideal-linear manner and can only visit then in a regular sequence. Any such individuals were omitted from the analysis, therefore here n=6.

numbers of core-nuclei (Fig.5.5.5., Fig.5.5.6.). In summary robins using small territories increased their rate of commuting between foraging patches, while robins using large territories increased the randomness of their sequence of patch visits. The data from one bird, indicated by a star in the figures, were clearly different to the rest of the sample. This individual was the only robin for which there was a severe ground frost on the experimental playback day, but not on the control day. None of the other birds experienced such an large difference in the environmental variables on the control and playback days.

### 5.5.4. Discussion.

In response to the playback of song to simulate intrusions into their territories, the experimental robins in the present study did not respond by approaching active speakers or by increasing their vocalisations. Several studies have assessed the effect of experimental playback of song on territorial robins (Rae 1979, Chantrey & Workman 1984, Hoelzel 1986, Brindley 1991), although their conclusions were confined to the nature of communication and aggression between individuals. In these earlier studies, trials lasted no longer than 35 min (Rae 1979), and were usually less than 10 min (Hoelzel 1986, Brindley 1991), and presented playback from a single speaker placed either in the centre of territories or in locations defined as territory boundaries. All studies recorded approach behaviour, vocalisations and display for the time that the focal birds were visible. The two studies carried out at the same time of year as the present study concluded that robins can determine the sex, distance and identity of other singing robins, frequently recording aggressive approaches to the speakers when birds were presented with the song of strangers (Hoelzel 1986, Brindley 1991). In the present study therefore, a robin apparently could have identified the simulated intruders as strangers, and approached in order to evict them from its territory. The reasons why the birds did not respond by approaching speakers in this way are unclear. Possibly the two-minute sample interval necessary for continuous tracking resulted in any rapid dashes to the speakers, in response to a series of song phrases, being missed. This is unlikely however, since for much of the monitoring periods, the location of focal birds was known continually but only recorded at two minute intervals. Alternatively, the random locations at which playback was presented, more closely simulated the natural behaviour of intruders rather than the much more threatening apparent challenges for territory ownership represented by stationary playback presentations. The latter may elicit a much stronger reaction by owners in response to the

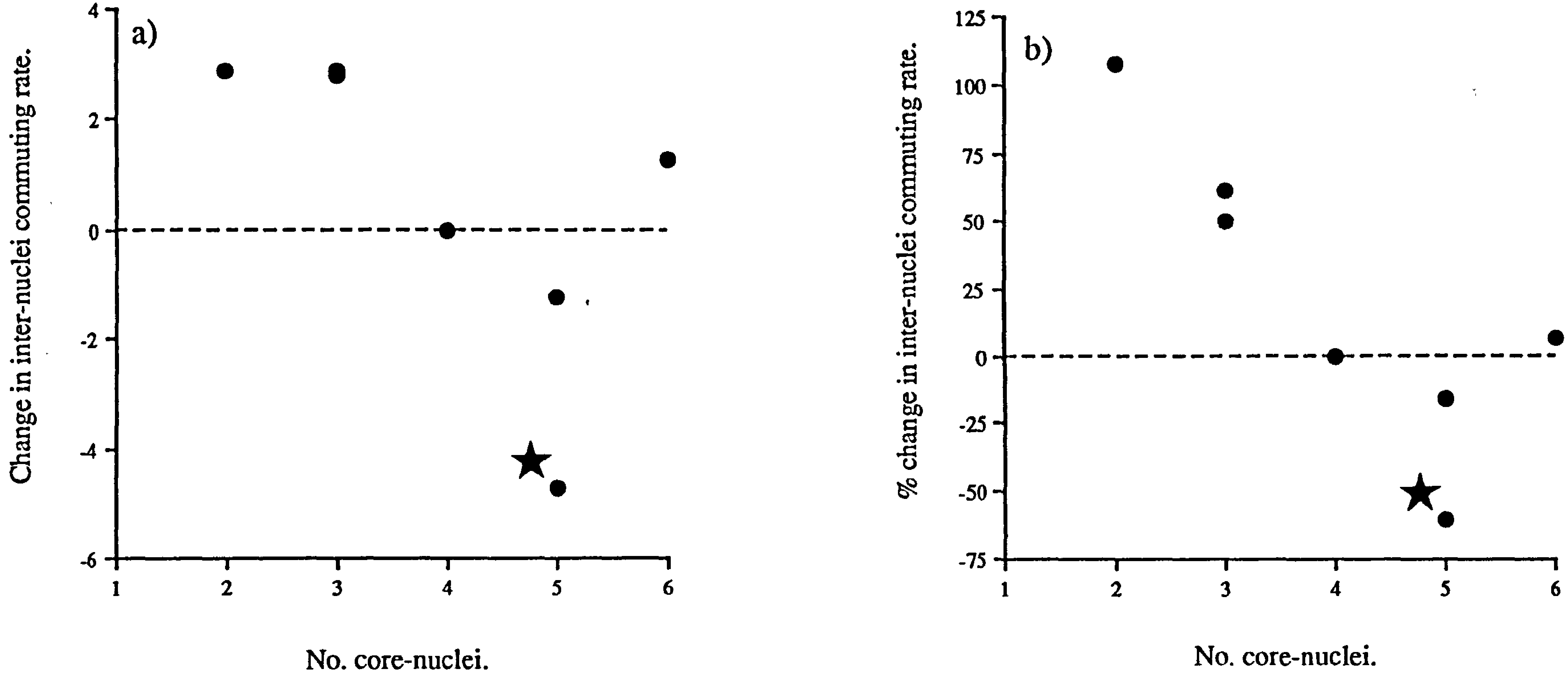


**Fig.5.5.5.** The change in inter-nuclei commuting rate (movements $hr^{-1}$) in response to the simulated territorial intrusions; (a) absolute change $r_s$=-0.74 $p<0.05$ n=7, (b) % change $r_s$=-0.76 $p<0.05$ n=7. Exclusion of the outlier indicated by a star had little effect on these correlations (absolute change $r_s$=-0.78 $p<0.05$ n=6, % change $r_s$=-0.81 $p<0.05$ n=6).

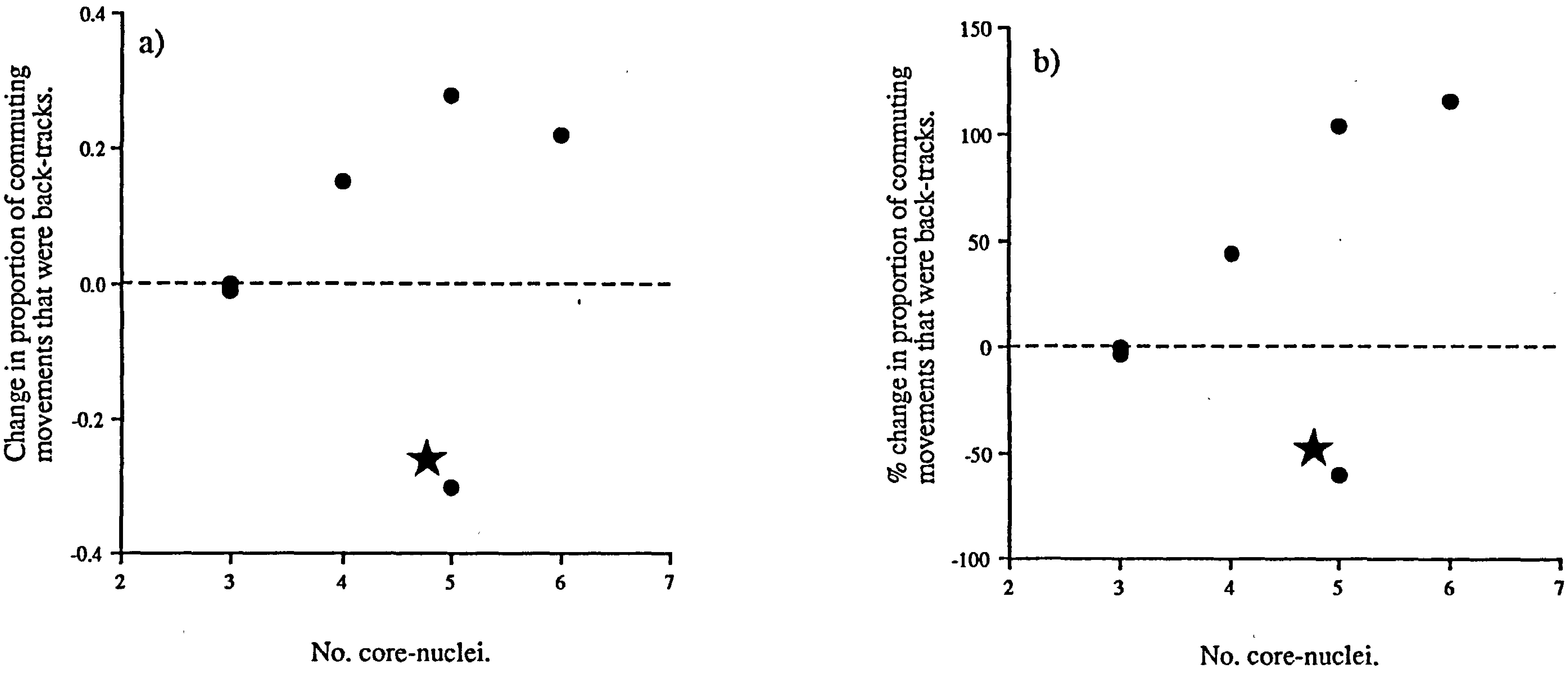


**Fig.5.5.6.** Change in the proportion of commuting movements that were back-tracks in response to the simulated territorial intrusions; (a) absolute change $r_s$=-0.44 ns n=6, (b) % change $r_s$=-0.53 ns n=6. Exclusion of the outlier indicated by a star considerably increased the correlations (absolute change $r_s$=-0.87 $p<0.05$ n=5, % change $r_s$=-0.97 $p<0.005$ n=5).

perceived territorial emergency. Lack (1965) observed frequent intrusions by neighbours to forage. These intruders were not aggressively evicted by owners. Furthermore, the large number of individuals on the recording, their random temporal scheduling and the multiple locations at which song was presented may have better simulated multiple intrusions and a higher intruder pressure, rather than a single territorial challenge.

It remains possible that the experimental birds simply did not recognise the recording as a potential territorial threat. The significant results from analysis of the measures of space use and casual observations of approach behaviour to the speakers by some individuals some of the time, however, showed that the robins did react to the simulated intrusions, but generally in a more subtle way than previous playback experiments have considered.

Robins may increase their probability of encountering intruders by increasing the time they spend on their territory. The birds that were subjected to playback already spent over 80% of their time associated with their usual-areas (median 81 range 63-100 n=7), slightly greater than the 79% predicted from the probabilistic model of territory use in chapter 3. The robins therefore had little scope for increasing their time on territory without compromising their own information gathering excursive (but not necessarily intrusive) activity. Nevertheless, the robins did change their space use in response to simulated intrusions. Only the robins occupying smaller numbers of core-nuclei increased their commuting rate. By doing this, the birds decreased the quality of the feeding patches within their territory by revisiting them before the full recovery time had elapsed. Potential intruders would therefore experience lower prey densities than if owners continued to forage as they had before. Flight is the most energy costly activity of the robin (Tatner & Bryant 1986). This increased commuting activity will, therefore, result in an increased energy expenditure by the owner, but with no decrease in the owners rate of energy gain since patches were visited more often.

Robins occupying larger numbers of core-nuclei did not increase their commuting rate. Such individuals were perhaps already working at close to some maximum sustainable rate merely to maintain such large territories, and so could not incur additional costs. These birds increased the randomness of their visits to core-nuclei. This resulted in a similar decrease in the apparent quality of patches as perceived by potential intruders. Increased randomness of movements will not increase energy expenditure, but owners may incur a decrease in their own rate of energy gain, since patches visited too often will be at an early stage of prey recovery and yield a low rate of energy gain, while patches visited less often than the full recovery time will not any yield higher energy gains. There was no tendency for robins to increase their departure from ideal-linear network use when commuting between foraging patches. Possibly the risk of predation is too great a potential cost for a trade off to be made with the benefits of increased accessibility of foraging patches.

Robins appear to increase their territorial defense by decreasing the apparent quality of the feeding patches they use. The reduced average prey densities within patches will discourage any intruders from remaining to forage or returning at another time. This "defense by resource depression" shows strong similarities with the defense by depletion of pied wagtails (Davies & Houston 1981) and defense by exploitation of the rufus hummingbird (Paton & Carpenter 1984). This nectivorous bird depletes the periphery of its territory early in the morning. Intruders, which will encounter this part of the territory first, experience low rates of energy gain and so are discouraged from remaining on the territory. Owners would be able to detect and monitor the effect of intruders by comparing the actual prey densities in patches with that anticipated if there were no intruders. Owners can consequently modify their pattern of network use accordingly. The highly patchy structure and absence of discrete territory boundaries in the robin means that in order to discourage intruders from staying, owners must keep all of their feeding patches at a low level of prey recovery. The robin may therefore show two types of territorial defense. Firstly, the eviction of challengers for territory ownership, which requires intruders to be aggressively dominated and expelled; and secondly, the discouragement of information gathering intruders by an increased degree of resource depression. This latter mechanism of territory defense does not require owners to locate intruders at all. Since temporary or long-term injury may compromise fitness (Arcese 1987), this pattern of interference competition may be a less risky strategy.

The evidence from pitfall traps and observed patterns of network use in the robin, and previous studies of other small birds, suggests that the maintenance of a renewing food supply is frequently the economic basis for territorial behaviour during the non-breeding season. Nevertheless, since overwinter survival is the goal of such birds, the effects of long term prey depletion may also be of economic importance. Although active during the winter, small leaf litter invertebrates do not undergo reproduction. Over the winter, therefore, the asymptotic prey densities within patches will decline as robins successively remove visible prey. Consequently, in addition to short term exploitation and defense behaviours, a third as yet unidentified component of the temporal scheduling of patch visits may be the prevention of gross losses of prey to intruders.

# Chapter 6.

# 6. The energy costs of territory use.

## 6.1. Introduction.

In previous studies, it has been assumed that the costs of territorial behaviour in birds are related to the area of the territory they occupy (Stephens & Dunbar 1993). In chapter 5 a new model of territory structure was developed for the robin that was based on the concept of a territory as a number of defended foraging patches linked by a network of preferred flight paths. The size of a territory can therefore be measured in terms of number of patches and flight distances, in addition to the simple estimate of total area. The main points concerning the structure and use of such territory networks are summarised below.

Robins concentrated their time in a varying number of patches. These were located in bushes and shrubs, in which they foraged. Individual foraging patches were termed core-nuclei. As the number of core-nuclei increased, the core-area was fragmented into foraging patches of decreasing individual size. The total area of the patches used by each individual was similar, although there was a consistent small increase in total area for each additional patch used. No territory contained more than six core-nuclei. The individual commuting movements that minimised the distance between patches were on average 20 m in length. This distance was similar for territories containing different numbers of patches. Large territories, therefore, contained many small foraging patches and a long total distance of commuting flights. Small territories contained few large patches and a short total flight distance. The total flight distance was termed the linear length.

Robins tended to visit the core-nuclei within their territory in a regular sequence; termed a foraging circuit. The return time for visiting patches was approximately 30 min for all territories, regardless of the number of foraging patches they contained. This was because robins exhibited shorter giving-up times in small patches. The length of a foraging circuit depends on the configuration of the nuclei within the territory. Foraging circuits are at their shortest when the nuclei are in an circuit-polygonal or ideal-polygonal configuration, and at their longest when in an ideal-linear configuration. Results suggest that robins select foraging patches which together produce territory shapes of high eccentricity. Furthermore, individuals move between patches in a highly linear manner. The parameters which quantify the structure of territory networks of different size for the observed range of territory sizes, are shown in Table 6.1. The values and relationships were derived from information on the space use of

**Table 6.1.** Specifications for territories of different size from the network model of territory structure in non-breeding robins. Large territories were those with large numbers of core-nuclei and large linear-lengths. Note total perimeter length increases at 1.7 times the rate of increase in total core area as territory size increased.

| No. core-nuclei | Linear length (m)[†] | Total core area ($m^2$)[*] | Total edge length of core area (m)[#] | Circuit length during ideal-linear use (m)[$] | Circuit length during ideal- polygonal use (m)[§] |
|---|---|---|---|---|---|
| 1 | 0 | 178 | 47.3 | 0 | 0 |
| 2 | 20 | 204 | 71.6 | 40 | 40 |
| 3 | 40 | 230 | 93.3 | 80 | 60 |
| 4 | 60 | 256 | 113.4 | 120 | 80 |
| 5 | 80 | 282 | 133.1 | 160 | 100 |
| 6 | 100 | 308 | 152.4 | 200 | 120 |

† Linear length = (n-1)d
* Total core area = A+(n-1)a
\# Total edge length; see Appendix to Table 6.1.
$ Circuit length during ideal-linear use = 2(n-1)d
§ Circuit length during ideal-polygonal use = nd

Where:
d = 20 m (slope of equation in Fig.5.3.1.
n = No. core-nuclei
A = 178 $m^2$ (from equation in Fig.5.3.3.)
a = 26 $m^2$ (slope of equation in Fig.5.3.3.)

**Appendix to Table 6.1.** Derivation of the expression for the total edge length of the core-nuclei within a territory network.

For a circle of radius r, circumference C, and area A;

$$C = 2\pi r$$

$$A = \pi r^2$$

$$\therefore \quad r = \sqrt{\frac{A}{\pi}}$$

So, assuming the core-nuclei comprising each territory network are circular and of similar individual areas;

$$\text{Total core area} = A+(n-1)a$$

$$\therefore \text{ Area of individual nuclei} = \frac{A+(n-1)a}{n}$$

$$\therefore \text{ Radius of individual nuclei} = \sqrt{\frac{A+(n-1)a}{n\pi}}$$

$$\therefore \text{ Edge length of individual nuclei} = 2\pi\sqrt{\frac{A+(n-1)a}{n\pi}}$$

$$\therefore \text{ Total edge length for all nuclei} = n\left(2\pi\sqrt{\frac{A+(n-1)a}{n\pi}}\right)$$

*Where;*

*A = Total core area when number of core-nuclei equals one (Fig.5.3.3.).*

*a = Incremental increase in total core area for each successive increase in number of core-nuclei (slope of line in Fig.5.3.3.).*

*n = Number of core-nuclei in territory network.*

43 non-breeding territorial robins.

Territorial robins showed a differential response to simulated intrusions, depending on the size of the territory they occupied. Birds using small territories increased their rate of commuting between foraging patches; an activity with an associated increased energy expenditure. Birds using large territories increased the randomness with which they visited their foraging patches; an activity which requires no increase in energy expenditure, but which has an associated decrease in foraging success.

These observations provide a basis for the prediction of time/activity budgets for robins using territory networks of different size and configuration. From this the form of the energy cost constraint on territory size can be determined, and compared with direct measurements of energy expenditure.

## 6.2. Modelling the time/activity budgets for territorial robins.

### 6.2.1. Time/activity budgets and network size.

Detailed time/activity budgets for the behaviour of non-breeding territorial robins have been published by East (1980, 1982) for individuals under similar environmental conditions to those experienced by robins in the present study. These studies were carried out at the University of Sussex in a 6.75 ha copse of deciduous woodland, within which the shrub layer was dominated by bramble and hawthorn bushes (Hoelzel 1989). This was of similar spatial structure to that occupied by robins in the present study (Table 2.1.). The categories into which activities were divided are summarised in Table 6.2. Time/activity budgets for robins occupying territory networks of different size and configuration may vary. East (1980, 1982) however, did not consider differences between robins defending small or large territories. The assumptions associated with three possible sources of variation in time/activity budgets with territory size are presented in Table 6.3. and form the basis for the models developed in this chapter.

In Model I the only element of owners time budgets to vary is the total time spent commuting between core-nuclei. Robins occupying large territory networks have to move between many small foraging patches more often than those occupying small territories containing large patches. As commuting time increases, the time available for perching quietly must correspondingly be reduced to balance the time budget. This assumption is also made for Models II and III. The robin uses two main foraging strategies; perch & drop and ground

**Table 6.2.** Definitions of activities recorded in the time/activity budgets of non-breeding territorial robins (after East 1980 & 1982).

| | |
|---|---|
| **Perched quietly;** | Not engaged in any other identifiable activity. Includes resting and scanning for prey since these were indistinguishable. |
| **Perch & drop foraging;** | If a bird dropped to the ground and returned to a perch without moving while on the ground. |
| **Ground hop foraging;** | If while on the ground the bird hopped about in search of prey. |
| **Vocalisation;** | Full song and subsong. |
| **Other;** | Activities of very short duration were grouped and included; agonistic encounters; flight; alert perching; preening and vocalisations other than song. |

**Table 6.3.** Assumptions associated with the three models of changes in time/activity budgets with territory size for territorial robins.

| Model | Assumptions |
|---|---|
| I | Commuting costs vary with number of core-nuclei.<br>Foraging costs constant. |
| II | Commuting costs vary with number of core-nuclei.<br>Ground hopping and perch & drop foraging behaviours used in the same ratio throughout patch areas; total foraging costs vary with number of core-nuclei in proportion to total patch area. |
| III | Commuting costs vary with number of core-nuclei.<br>Ground hopping used over patch areas, perch & drop concentrated at patch edges. Each varies with number of core-nuclei in proportion to total patch area and total patch edge length. |

hopping (Table 6.2.). In Model II the foraging behaviour is assumed to vary in proportion to the total patch area, for example a 10 % increase in patch area will require a 10 % increase in time spent foraging to collect all available prey. Within patches robins are assumed to use both foraging strategies over the whole area of each patch, such that the ratio of time spent in each foraging strategy is constant. Perch & drop foraging behaviour involves scanning for small prey items from a perch some distance above the ground (East 1980). This increases the range over which prey can be detected and reduces prey disturbance (Grajetsky 1993). In order to detect prey, however, light levels must be high and there must be sufficient space for unimpaired flight from the perch to the ground and back. This imposes a constraint upon where the perch & drop foraging strategy can be employed within the territory. In Model III this constraint is assumed to confine perch & drop foraging to the perimeters of patches, where illumination is good and flight unrestricted. Ground hopping is therefore the dominant foraging strategy when birds are moving in the dense vegetation typical of the centre of core-nuclei. Consequently, in Model III the time invested in perch & drop behaviour is assumed to vary in proportion to the total patch perimeter length, and the time invested in ground hopping is assumed to vary with the total core area. The rate of change in total core area and total core perimeter, due to changes in the number of core-nuclei, were not equal. As core areas fragmented into increasing numbers of nuclei, the total perimeter length increased at 1.7 times the rate of increase in total core area (Table 6.1.). Following this, the proportion of the active period spent in different activities by non-breeding territorial robins are shown as percentages in Table 6.4. following the assumptions for each of the three models. Values were derived from average time/activity budgets from East (1980, 1982). In these studies, focal individuals were generally observed continuously for between 15 min and one hour, any observations of less then 10 min being excluded from the analysis (East 1982). This 15 min period is longer than the longest visits by robins to foraging patches within multinuclear territories (Fig.5.3.5.). Furthermore, the robins in these studies were sometimes observed to spend up to 20 min perched quietly within bushes (M.East pers.comm.), suggesting that any bias in the published time/activity budgets towards individuals that were more active and visible was minimal. Robins with average time/activity budgets were assumed to occupy territories of average size and configuration. In the present study the median number of core-nuclei occupied by territorial robins was 4 (range 1-6, n=43). Time budgets could have been predicted for robins occupying territory networks containing more than six foraging patches,

**Table 6.4.** Proportion of time during active period spent in each activity for robins occupying territories of different numbers of core-nuclei used in an ideal linear manner (shown here as percentages). When used in an ideal polygonal manner the only parameters to change are commuting time (decreases by 66.7 and 60.0 % for 4 nuclei and 6 nuclei respectively) and time perched quietly (which increases by the same amounts).

| Activity | **Model I** | | | | **Model II** | | | | **Model III** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. core-nuclei | | | | No. core-nuclei | | | | No. core-nuclei | | | |
| | 1 | 2 | 4* | 6 | 1 | 2 | 4* | 6 | 1 | 2 | 4* | 6 |
| Perched quietly | 56.03 | 56.02 | 56.00 | 55.78 | 63.34 | 60.90 | 56.00 | 50.91 | 66.40 | 62.71 | 56.00 | 49.36 |
| Perch & drop | 11.00 | 11.00 | 11.00 | 11.00 | 7.64 | 8.76 | 11.00 | 13.23 | 4.59 | 6.95 | 11.00 | 14.78 |
| Ground hop | 13.00 | 13.00 | 13.00 | 13.00 | 9.05 | 10.37 | 13.00 | 15.65 | 9.04 | 10.36 | 13.00 | 15.64 |
| Vocalisation | 15.00 | 15.00 | 15.00 | 15.00 | 15.00 | 15.00 | 15.00 | 15.00 | 15.00 | 15.00 | 15.00 | 15.00 |
| Commuting # | 0 | 0.01 | 0.03 | 0.25 | 0 | 0.01 | 0.03 | 0.25 | 0 | 0.01 | 0.03 | 0.25 |
| Other | 4.97 | 4.97 | 4.97 | 4.97 | 4.97 | 4.97 | 4.97 | 4.97 | 4.97 | 4.97 | 4.97 | 4.97 |
| Total | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |

* From East (1982) averaged over temperature ranges 0-5°C and 6-10°C (see text).

\# Commuting time forms part of "other" behaviour for an average territory which is assumed to contain four core-nuclei, with a linear length of 60m (Table 6.1.). Increase in commuting time was deducted from time resting quietly. Commuting time is proportion of time spent flying between core-nuclei at a speed of 3.85 msec$^{-1}$ reflecting a series of brief flights between intermediate perches (Tatner & Bryant 1986).

although this was never observed in the field.

The eviction of intruding robins by territory owners was rare in the present study. In chapter 5. intruders were shown to occur more often in large territories (section 5.4.2. Fig.5.4.1.). Due to the skulking nature of intruders, and the impracticality of radio-monitoring all potential intruders, it was not possible to measure the intrusion rate into a particular territory. If the number of intrusions initiated by a focal bird is assumed to equal the number of intrusions experienced by it, however, it is possible to estimate the percentage of the active period that territory owners were estimated to have been engaged in the eviction of intruders for territory networks of different size (Table 6.5.). All intruders were assumed to be encountered and evicted, and based on observations of evictions during both radio-tracking and qualitative observations (n>10), each was assumed to require a 40 m flight at 3.85 $msec^{-1}$ (Tatner & Bryant 1986). Even if all intruders were evicted, which is unlikely, and evictions required considerably more time than this, however, the proportion of the active period that owners were engaged in evicting intruders would have been extremely small (Table 6.5.). Consequently this activity could not justifiably be included in the time activity budgets constructed using the assumptions of the three models.

### 6.2.2. The effects of network shape.

The predicted time/activity budgets in Table 6.4. are for territory networks that are used in an ideal-linear manner. That is, the owners only use the commuting paths that make up the linear length when visiting patches. The length of the foraging circuit for this pattern of use will therefore equal twice the linear length. It is possible for some configurations of core-nuclei to be visited using a circuit-polygonal or ideal-polygonal network of flight paths (section 5.2.2.). Such configurations are characterised by a linearity (L) of equal or less than 0.25 . This will result in a considerable reduction in the flight distance required to complete a sequence of patch visits (Table 6.1.). The angles between commuting paths in ideal-linear configurations will be 180°. As the linearity decreases and the configuration becomes progressively more polygonal these angles will become smaller, increasing the benefit of using short cuts (section 5.2.2.).

Clearly by definition, only territory networks containing three or more core-nuclei may be used in a polygonal manner. The only parameters to change when time/activity budgets are constructed for robins following a pattern of polygonal rather than linear use are the time

**Table 6.5.** Predicted numbers of intrusions occurring per day in the territories of owners occupying networks containing different numbers of core-nuclei, and the percentage of their active period engaged in evictions if all intruders were encountered. Since some will inevitably be missed, this represents an over-estimate of the true time spent evicting intruders.

| No. core-nuclei | P(intruding $hr^{-1}$) * | No. intruders evicted per 8 hr winter day if all intruders encountered | % active period engaged in evicting intruders # |
|---|---|---|---|
| 1 | 0.00 | 0 | 0 |
| 2 | 0.04 | 0.32 | $1.8 \times 10^{-6}$ |
| 3 | 0.15 | 1.20 | $7.2 \times 10^{-6}$ |
| 4 | 0.32 | 2.56 | $1.6 \times 10^{-5}$ |
| 5 | 0.55 | 4.40 | $2.6 \times 10^{-5}$ |
| 6 | 0.84 | 6.72 | $4.0 \times 10^{-5}$ |

* From equation fitted to data in Fig.5.4.1. Assumes P(focal territorial robin intruding into a neighbour) equals P(neighbours intruding into focal territory).

\# Assuming each eviction requires 40m of flight at a speed of 3.85 $msec^{-1}$ (Tatner & Bryant 1986).

spent commuting between nuclei and the time spent perching quietly, assuming foraging requirements do not change. For networks containing four nuclei commuting time decreases by 66.7 %, and for six nuclei commuting time decreases by 60.0 %, when used in a circuit-polygonal rather than linear manner. The time perched quietly increases by equivalent amounts.

## 6.3. Direct measurements of energy expenditure.

### 6.3.1. Methods.

Measurements of energy expenditure were carried out using the doubly labelled water technique. The field protocol and analysis for this technique are fully described in chapter 2. Over the four days preceding stable isotope loading, a standardised sample of radio-location estimates was collected following the protocol described in chapter 3. During the measurement period, isotope loaded individuals were also continuously tracked for an hour at dawn, midday and dusk if possible, and behavioral observations recorded following the methodology of chapter 5.

### 6.3.2. Results.

Over the course of the study 20 robins were loaded with doubly labelled water. Of these 13 (65 %) were subsequently recaptured and an estimate of energy expenditure obtained (section 2.2.1.3.). Since two of these were un-tagged control individuals, detailed information on the energy expenditure and space use was available from 11 radio-tagged robins. Measurements of energy expenditure were assumed accurate to ±10% (Tatner & Bryant 1989).

The morphological, energetic, space use and environmental data relating to these individuals are presented as a series of tables. The individual attributes and energy expenditures are shown in Table 6.6. The discontinuous radio-tracking data were analyzed using sequential cluster analysis to determine the utilization distribution statistics, following the methods developed in chapters 3. & 5. The results are shown in Table 6.7. Following the definition in chapter 3, three of the robins were classified as non-territorial. Measures of space use were derived from the continuous tracking data (Table 6.8.), methodology and definitions following those in chapter 5. The environmental variables experienced by the robins during the period of measurement of energy expenditure are summarised in Table 6.9.

**Table 6.6.** Measurements of the size, mass and energy expenditure of free-living robins (n=11).

| Ring No. | Date stable isotope loaded | Predicted mass (g) * | Wing span (mm) # | Mean mass (g) | Mass change (g $day^{-1}$) | $rCO_2$ $ ($cm^3CO_2hr^{-1}$) | ADMR $ ($cm^3CO_2g^{-1}$ $hr^{-1}$) | DEE $ (kJ $day^{-1}$) | BMR $ (kJ $hr^{-1}$) | M $ |
|---|---|---|---|---|---|---|---|---|---|---|
| F646727 | 28th January 91 | 19.2 | 230 | 20.4 | -0.7 | 3.45 | 4.89 | 63.21 | 1.19 | 2.22 |
| H227556 | 28th November 91 | 20.2 | 227 | 20.2 | -2.0 | 4.63 | 5.13 | 65.81 | 1.18 | 2.33 |
| F646592 | 28th November 91 | 19.4 | 231 | 18.3 | -0.6 | 3.97 | 4.86 | 56.49 | 1.10 | 2.14 |
| F646583 | 28th November 91 | 18.8 | 226 | 18.6 | -2.4 | 3.42 | 4.11 | 48.55 | 1.11 | 1.82 |
| F646591 | 1st December 91 | 18.7 | 228 | 20.6 | -0.8 | 5.10 | 5.55 | 72.55 | 1.20 | 2.53 |
| F646546 | 1st December 91 | 19.3 | 228 | 20.1 | -1.1 | 4.53 | 5.05 | 64.35 | 1.17 | 2.28 |
| F646590 | 21st January 92 | 19.3 | 228 | 18.7 | -0.8 | 5.00 | 5.88 | 71.07 | 1.13 | 2.62 |
| F646594 | 24st January 92 | 20.2 | 232 | 21.5 | 0 | 5.48 | 5.70 | 77.83 | 1.23 | 2.63 |
| H227546 | 4th February 92 | 18.0 | 225 | 18.6 | -0.4 | 4.34 | 5.23 | 61.72 | 1.11 | 2.32 |
| F646582 | 4th February 92 | 18.8 | 225 | 18.8 | -0.3 | 3.62 | 4.31 | 51.40 | 1.12 | 1.91 |
| F646569 | 6th February 92 | 19.5 | 228 | 19.2 | -0.8 | 4.43 | 5.17 | 62.94 | 1.14 | 2.31 |
| Mean |  | 19.2 | 228 | 19.5 | -0.9 | 4.36 | 5.08 | 63.27 | 1.15 | 2.28 |
| (SD) |  | (0.6) | (2.3) | (1.05) | (0.7) | (0.69) | (0.54) | (8.79) | (0.04) | (0.26) |

* Predicted from keel length and bill depth, and represents a measure of structural size.

\# Predicted from wing chord length.

$ $rCO_2$ = rate of $CO_2$ production; ADMR = average daily metabolic rate; DEE = daily energy expenditure; BMR = basal metabolic rate, from the equation 0.503 $Mass^{0.726}$ (Aschoff & Pohl 1970); M = metabolic intensity, where M = DEE/(BMRx24).

**Table 6.7.** Utilization distribution statistics for robins at the same time as their energy expenditure was measured.

| Ring No | Territorial status* | No. nuclei | Usual-area ($m^2$) | Linear length (m) | Eccentricity $\in$ | Angles between commuting paths (degrees)# | |
|---|---|---|---|---|---|---|---|
| | | | | | | Mean | Range |
| F646727 | NT | 5 | 3037 | 136 | 0.71 | 93 | 70-130 |
| H227556 | T | 3 | 276 | 39 | 0.15 | 162 | 145-180 |
| F646592 | T | 2 | 165 | 15 | 0.26 | - | - |
| F646583 | T | 2 | 277 | 14 | 0.80 | - | - |
| F646591 | T | 4 | 532 | 55 | 0.57 | 120 | 80-150 |
| F646546 | T | 3 | 513 | 45 | 0.18 | 160 | 160 |
| F646590 | T | 4 | 996 | 62 | 0.65 | 108 | 65-160 |
| F646594 | T | 5 | 456 | 51 | 0.24 | 112 | 90-135 |
| H227546 | NT | 5 | 5322 | 138 | 0.53 | 100 | 90-120 |
| F646582 | NT | 5 | 6765 | 231 | 0.21 | 105 | 85-140 |
| F646569 | T | 5 | 1102 | 77 | 0.58 | 100 | 90-130 |

* T = territorial and NT = non-territorial, following the definition developed in chapter 3.

\# A territory network of two core-nuclei only contains one commuting path. Sample size of mean equals number of core-nuclei minus one.

**Table 6.8.** Rates of space use and singing by robins for which free-living energy expenditure was measured. Values are based on an hour of continuous tracking carried out at dawn, midday and dusk during the period over which energy expenditure was measured. Dashes show non-territorial individuals for which commuting rate between core-nuclei cannot be measured.

| Ring No. | Speed (m min$^{-1}$) | Commuting rate (movements hr$^{-1}$) | Time singing (sec min$^{-1}$) |
|---|---|---|---|
| F646727 | 7.78 | - | 0 |
| F646583 | 5.71 | 3.6 | 0.27 |
| F646590 | 5.40 | 6.3 | 0 |
| F646594 | 4.27 | 10.0 | 0 |
| H227546 | 6.50 | - | 0 |
| F646582 | 5.10 | - | 0 |
| F646569 | 4.75 | 5.0 | 0 |

**Table 6.9.** Environmental variables during the 24 hr period over which energy expenditure was measured.

| Date | Temperature (°C) | | Wind speed (knots) | Rainfall (mm) | Daylength (hrs) |
|---|---|---|---|---|---|
| | Minimum | Maximum | | | |
| 28th January 91 | 0.2 | 2.1 | 2.0 | 0 | 8.3 |
| 28th November 91 | 3.0 | 10.1 | 5.0 | 1 | 7.5 |
| 1st December 91 | 4.6 | 8.2 | 2.0 | 0 | 7.5 |
| 21st January 92 | -4.0 | 3.7 | 0.0 | 0 | 8.0 |
| 24th January 92 | 0.4 | 5.9 | 2.0 | 0 | 8.3 |
| 4th February 92 | 1.9 | 11.7 | 7.0 | 0 | 8.8 |
| 6th February 92 | 6.8 | 9.3 | 3.5 | 1 | 9.0 |

The relationships between energy expenditure and territory size and shape; individual attributes; activity and environment for territorial robins are presented as a correlation matrix in Table 6.10. In summary, measures of territory size were most closely correlated with ADMR, although usual-area was not correlated with any measure of energy expenditure. Territory shape, estimated by eccentricity ($\epsilon$) and mean angle between commuting paths, was not significantly correlated with energy expenditure. The correlations between individual attributes and energy expenditure were strongest for DEE, specifically body mass and wingdisc loading. Of the measures of activity, only commuting rate was correlated with energy expenditure, although the sample size was very small. The environmental variables showed most significant correlations with ADMR.

Taking all the individuals for which doubly labelled water measurements were made, there was a significant loss of body mass between the initial and final captures of isotope loaded birds (Wilcoxon Matched-pairs Signed-ranks test $Z=-2.85$ $p<0.005$ $n=13$). Mass change was however not significantly correlated with energy expenditure (all individuals $r_s<0.16$ for ADMR, DEE and M, all ns $n=13$; territorial only Table 6.10.). One individual died 16 hrs after isotope loading. The weather conditions at the time were severe frost and freezing fog, conditions under which resident robins were most likely to disappear, presumably having died.

## 6.4. A test of the models.

### 6.4.1. Predicting energy budgets from their component costs.

The total energy expenditure of a bird engaged in a particular activity varies with the ambient temperature due to changing thermoregulatory requirements. The measures of temperature used in the present study were the minimum and maximum for each day (Table 6.9.). In constructing energy budgets for robins, the ambient temperature during the active period was assumed to equal the upper quartile of the observed mean temperature range, and the ambient temperature for the roosting period the lower quartile. Although this only estimates ambient temperatures, simply using the midpoint temperature for both would fail to allow for the fact that daytime is always warmer than nighttime, an important consideration considering the imbalance in the duration of each period during short winter days. The use of 75 % and 25 % of the temperature range respectively, however, approaches the values used by Ward (1992) in adjusting minimum and maximum temperatures to mean temperature for daytime and nighttime periods experienced by the same dipper population observed in chapter

**Table 6.10.** Spearman correlations between measures of energy expenditure and other variables for non-breeding territorial robins (n=8). See Tables 6.7-6.9 for definitions and units.

| | Territory size | | Individual atributes | | Activity | | Environment | |
|---|---|---|---|---|---|---|---|---|
| **A.D.M.R.** | No. core-nuclei | 0.83 *** | Predicted mass | 0.17 | Speed | -0.29 | Midpoint temperature | -0.65 * |
| | Usual-area | 0.62 | Wingspan | 0.41 | Commuting rate (n=4) | 0.80 | Wind | -0.80 ** |
| | Linear-length | 0.81 ** | Body mass | 0.55 | Time singing | -0.61 | Rain | -0.65 * |
| | Eccentricity | 0.02 | Wingdisc loading [#] | 0.12 | | | Active period [$] | 0.63 * |
| | Mean angle(n=6) | -0.60 | Mass change | 0.51 | | | | |
| **D.E.E.** | No. core-nuclei | 0.68 * | Predicted mass | 0.18 | Speed | -0.32 | Midpoint temperature | -0.72 * |
| | Usual-area | 0.31 | Wingspan | 0.43 | Commuting rate (n=4) | 0.99 *** | Wind | -0.70 * |
| | Linear-length | 0.52 | Body mass | 0.83 *** | Time singing | -0.61 | Rain | -0.76 * |
| | Eccentricity | -0.33 | Wingdisc loading [#] | 0.53 | | | Active period [$] | 0.30 |
| | Mean angle(n-6) | 0.09 | Mass change | 0.46 | | | | |
| **M** | No. core-nuclei | 0.78 ** | Predicted mass | 0.30 | Speed | -0.39 | Midpoint temperature | -0.68 * |
| | Usual-area | 0.40 | Wing span | 0.43 | Commuting rate (n=4) | 0.99 *** | Wind | -0.70 * |
| | Linear-length | 0.64 * | Body mass | 0.71 * | Time singing | -0.61 | Rain | -0.65 * |
| | Eccentricity | -0.19 | Wingdisc loading [#] | 0.28 | | | Active period [$] | 0.52 |
| | Mean angle(n=6) | -0.26 | Mass change | 0.51 | | | | |

* $p<0.05$ ** $p<0.01$ *** $p<0.005$

[#] Wingdisc loading equals body mass divided by wingdisc area (g $mm^{-2}$)(Feinsinger & Chaplin 1975).

[$] Active period equals day length plus 22 min before sunrise and 18 min after sunset (Cramp 1988).

4. during springtime.

The energy costs for robins engaged in each of the daytime activities from which time budgets were constructed, could be calculated for different ambient temperatures, using published equations (Tatner & Bryant 1986). The costs of vocalisation and other-activities (preening and defecating) were assumed to equal 1.1 times the cost of perching quietly (Ettinger & King 1980). Based on the minimum and maximum temperature averaged over the days that energy expenditure was measured (Table 6.9.), the temperature during the active period was taken to equal 6.8°C and during the roosting period 3.8°C. The energy costs of robins engaged in the different activities were calculated for individuals operating at these temperatures, along with predicted values of B.M.R. from the equation of Aschoff & Pohl (1970)(Table 6.11.). The values shown correspond to the minimum, mean and maximum body mass of robins for which estimates of energy expenditure were made.

Although the energy cost of night time resting will be the lowest of the different activity costs due to inactivity during the roosting period, it nevertheless is one of the most important, since this period represents approximately two thirds of the daylength during winter. Radio-tracking results show that the robin will readily return to previously used roost sites on subsequent nights (chapter 3). One of the potential advantages of repeatedly using a particular site would be the presence of a favourable microclimate (Webb & Rogers 1988). In such a location, the energy expended during nocturnal roosting will be less than that expended at the same level of activity outside the roost, because of reductions in the energy lost from the inactive bird via various routes (Webb & Rogers 1988). The routes of heat loss for a roosting robin are summarised in Fig 6.1. after Webb & Rogers (1988). The magnitude of these, mediated by the temperature in the roost microhabitat will have a direct effect on the thermoregulatory requirements of the roosting bird. Since roosting birds are not foraging, this energy is obtained by the assimilation of gut contents and the mobilisation of energy deposits, such as fat, laid down during the active period. Birds should select sites which minimise the use of these stores, within the constraint imposed by the risk of being predated while roosting. Furthermore, ambient temperature inside the roost is likely to be slightly higher than the open site at which the temperature data was recorded. Based on previous studies of the energetics of roosting in small birds (Walsberg 1986, Webb & Rogers 1988), therefore, the cost of roosting was taken to equal 85 % of the cost of night resting at the mean ambient temperature outside the roost (Table 6.11). This represents the mean of two

**Table 6.11.** The energy expenditure of robins engaged in different activities for minimum, mean and maximum body mass, at 75% and 25% of the mean temperature range over the active period and roosting period respectively (6.8°C and 3.8°C respectively). Also shown is the cost of existance per gram of body mass.

| Activity | **Cost (kJ hr$^{-1}$)** | | | **Cost per gram of body mass (kJ hr$^{-1}$)** |
|---|---|---|---|---|
| | Body mass 18.3g | Body mass 19.5g | Body mass 21.5g | |
| Perched quietly (day resting) * | 2.20 | 2.35 | 2.59 | 0.12 |
| Perch & drop (flight) * | 25.30 | 26.45 | 28.29 | 1.35 |
| Ground hop (hopping) * | 3.05 | 3.99 | 4.40 | 0.20 |
| Vocalisation # | 2.42 | 2.59 | 2.85 | 0.13 |
| Commuting (flight) * | 25.30 | 26.45 | 28.29 | 1.36 |
| Other (preening, defacating) # | 2.42 | 2.59 | 2.85 | 0.13 |
| Roosting (85% night resting at ambient temperature) *† | 1.49 | 1.58 | 1.74 | 0.08 |
| B.M.R. $ | 1.10 | 1.15 | 1.23 | 0.06 |

* Using data or equations in Tatner & Bryant (1986)

\# 1.1 times the cost of perching quietly (Ettinger & King 1980)

† Mean of values in Walsberg (1986) and Webb & Rogers (1988) for small passerines with similar roosting habits and similar temperature range (10.0°C and 0.6°C respectively).

$ 0.503 Mass$^{0.726}$ (Aschoff & Pohl 1970)

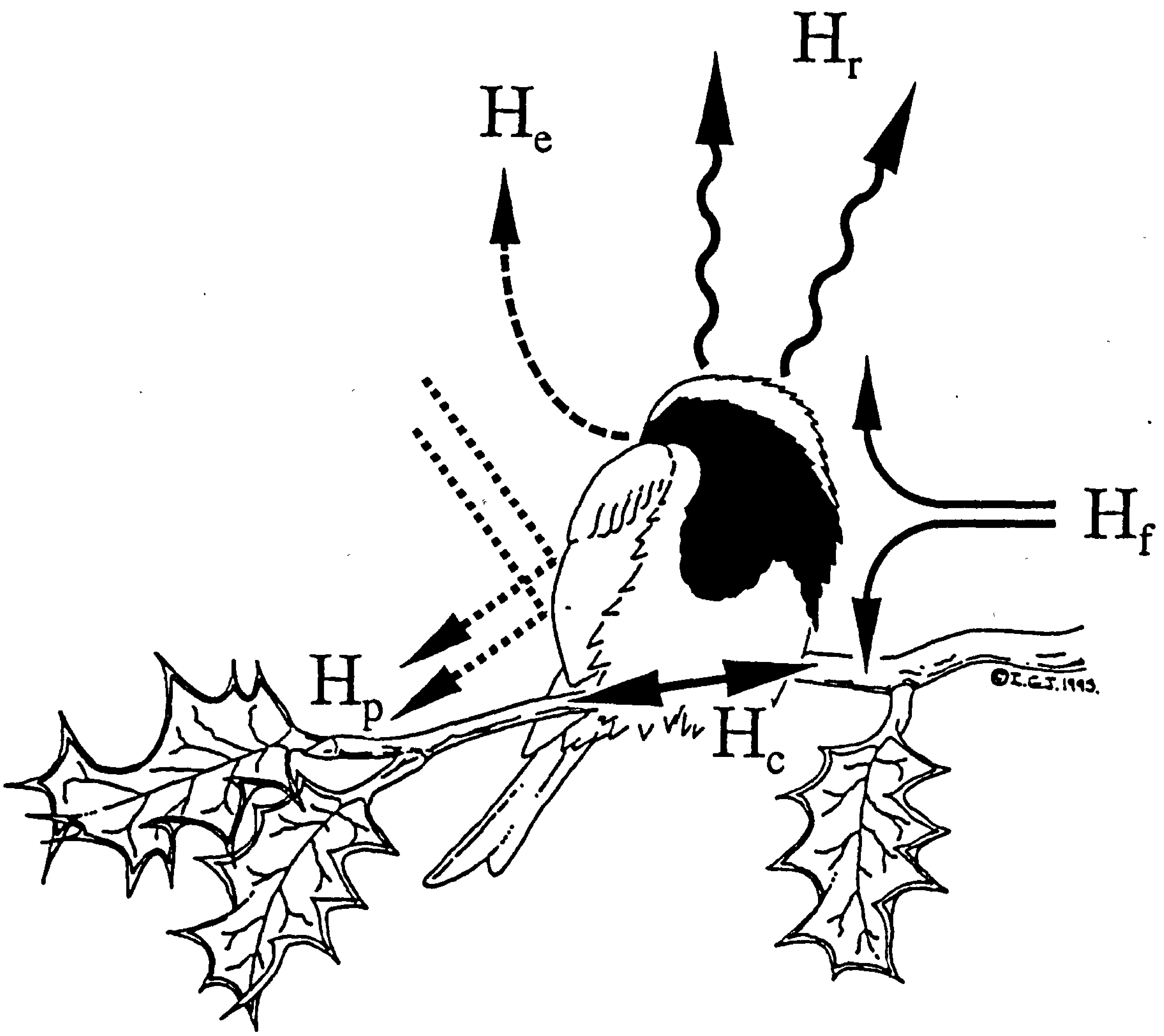


**Fig.6.1.** The routes of heat loss experienced by a roosting passerine such as the robin, ranked in approximate in order of decreasing importance (after Webb & Rogers 1988). Since birds such as the robin are immobile for up to two thirds of the day during winter, the selection of roost sites which minimises their effects could realise considerable reductions in thermoregulatory costs.

$H_f$ = Forced convective loss due to wind penetration through roost site.
$H_e$ = Evaporative heat loss down vapour density gradient between the birds surface and the environment.
$H_r$ = Long-wave radiative heat loss; surrounding vegetation acts to shield the bird from the sky, to some extent reducing long-wave flux.
$H_p$ = Effect of precipitation through plumage wetting; heat lost is due to the high specific heat capacity of water and reduction in insulating properties.
$H_c$ = Conductive loss; heat lost through contact with branch negligible.

values for small passerines which roosted alone in similar sites and under similar temperature ranges (9 % saving at 0.6°C; Walsberg 1986, 20 % saving at 10°C; Webb & Rogers (1988).

Using the values of energy expenditure during different activities (Table 6.11.), the energy budget for a 19.5 g robin was predicted under the assumptions inherent in each of the three models. Energy expenditure per hour was calculated by multiplying the proportion of time spent in each activity (Table 6.4.) by the energy cost per hour (Table 6.11.). The results are shown in Table 6.12. Daylength was set to the mean value for the days on which energy expenditure was measured, and was taken to be typical of the mid-winter period.

### 6.4.2. Energy expenditure and territory size.

For the territorial robins, energy expenditure was correlated with two out of the three measures of territory size (Table 6.10.). Of these, the closest correlations were with ADMR; a measure independent of body size. The median value of ADMR for robins using the largest territories (5 core-nuclei) was 21 % higher than the ADMR for robins using the smallest territories (2 core-nuclei). Gram for gram therefore, robins using large territories expended more energy than those using small territories. Energy expenditure was not correlated with territory size as estimated by the usual-area (Fig.6.2.). Energy expenditure was, however, highly correlated with the number of core-nuclei within the territory network (Fig.6.3.) and the linear length of the territory network (Fig.6.4.). In Figs.6.3.- 6.4. are also shown the lines representing the minimum ADMR required for robins to use ranges of different size, predicted by the three models of time/activity budgets. Also indicated are the linear regressions fitted to the observed values of ADMR in each case. For comparison, the data for robins which were classified as non-territorial are also shown. Range size for these individuals are of uncertain value however, due to the characteristic rapid rate of range drift. Hence instantaneous range sizes may have been smaller. Nevertheless the measures of range size for territorial and non-territorial robins were comparable, since they are all based on a standardised sample size. The statistics for the lines predicted by the three models and the fitted regressions are shown in Table 6.13. for the two measures of territory size. Probability levels are given despite some degree of violation of the assumptions concerning the parametric regression technique. In addition is shown the percentage departure of the predicted lines from the fitted regression equations. Although the median ADMR of non-territorial birds was 7 % lower than that for territorial birds, this difference was non-significant (Mann-Whitney U-test Z=-1.0 ns, territorial median=5.18 $cm^3CO_2g^{-1}hr^{-1}$ range 4.11-

**Table 6.12.** Energy expended while engaged in different activities per hour during active period, and total energy expenditures for robins of body mass 19.5g occupying territories of different numbers of core-nuclei. Energy expended while engaged in each activity per hour was calculated by multiplying the proportion of time spent in each activity (Table 6.4.) by the energy cost per hour (Table 6.11.).

| | **Model I** | | | | **Model II** | | | | **Model III** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. core-nuclei | | | | No. core-nuclei | | | | No. core-nuclei | | | |
| | 1 | 2 | 4 | 6 | 1 | 2 | 4 | 6 | 1 | 2 | 4 | 6 |
| **Activity** | | | | | | | | | | | | |
| Perched quietly | 1.316 | 1.316 | 1.316 | 1.316 | 1.488 | 1.431 | 1.316 | 1.196 | 1.560 | 1.474 | 1.316 | 1.160 |
| Perch & drop | 2.910 | 2.910 | 2.910 | 2.910 | 2.021 | 2.317 | 2.910 | 3.499 | 1.214 | 1.838 | 2.910 | 3.909 |
| Ground hop | 0.519 | 0.519 | 0.519 | 0.519 | 0.361 | 0.414 | 0.519 | 0.624 | 0.361 | 0.413 | 0.519 | 0.624 |
| Vocalisation * | 0.353 | 0.353 | 0.353 | 0.353 | 0.353 | 0.353 | 0.353 | 0.353 | 0.353 | 0.353 | 0.353 | 0.353 |
| Commuting | 0 | 0.003 | 0.008 | 0.066 | 0 | 0.003 | 0.008 | 0.066 | 0 | 0.003 | 0.008 | 0.066 |
| Other | 0.129 | 0.129 | 0.129 | 0.129 | 0.129 | 0.129 | 0.129 | 0.129 | 0.129 | 0.129 | 0.129 | 0.129 |
| **Total** | 5.227 | 5.230 | 5.235 | 5.293 | 4.352 | 4.647 | 5.235 | 5.867 | 3.617 | 4.211 | 5.235 | 6.241 |
| E.E.$_{active}$ (kJ)# | 45.789 | 45.815 | 45.850 | 46.367 | 38.124 | 40.708 | 45.850 | 51.395 | 31.685 | 36.888 | 45.850 | 54.671 |
| E.E.$_{roost}$ (kJ)$ | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 |
| D.E.E. (kJ day$^{-1}$)† | 69.929 | 69.955 | 69.990 | 70.507 | 62.264 | 64.848 | 69.990 | 75.535 | 55.825 | 61.028 | 69.990 | 78.811 |
| A.D.M.R. (cm$^3$CO$_2$g$^{-1}$hr$^{-1}$)† | 5.651 | 5.653 | 5.656 | 5.698 | 5.032 | 5.241 | 5.656 | 6.104 | 4.512 | 4.932 | 5.656 | 6.369 |
| M † | 2.534 | 2.535 | 2.536 | 2.555 | 2.256 | 2.350 | 2.536 | 2.737 | 2.023 | 2.211 | 2.536 | 2.855 |

* The birds in this study did not vocalise during the period of measurement so cost was set to that of perched quietly.

\# Energy expended during an active period of 8.76 hrs (daylength plus 40 min (Cramp & Simmons 1989) based on mean of days on which DLW measurements were carried out.

$ Energy expended at roost, assuming a roosting period of 15.24 hrs.

† Metabolic intensity. See Table 6.11 for value of BMR for a robin of 19.5 g.

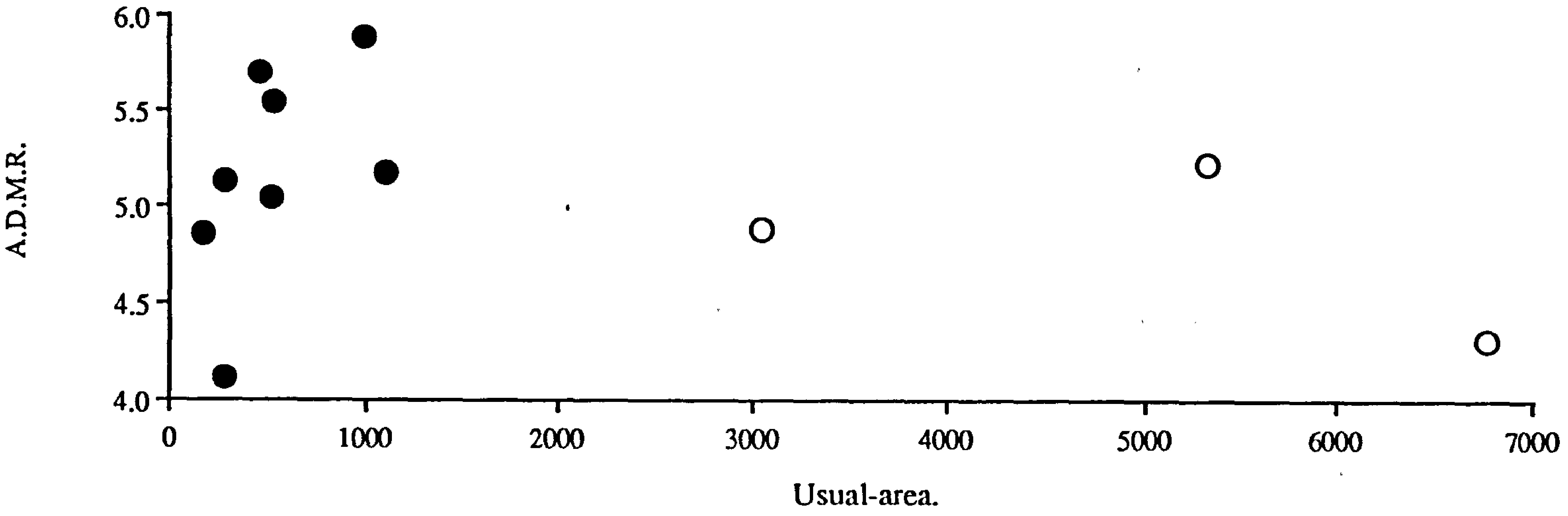


**Fig.6.2.** The relationship between average daily metabolic rate ($cm^3CO_2g^{-1}hr^{-1}$) and usual-area ($m^2$), for non-breeding territorial robins ($r_s$=0.62 ns n=8). Solid symbols indicate territorial; open symbols non-territorial, following the definition in chapter 3.

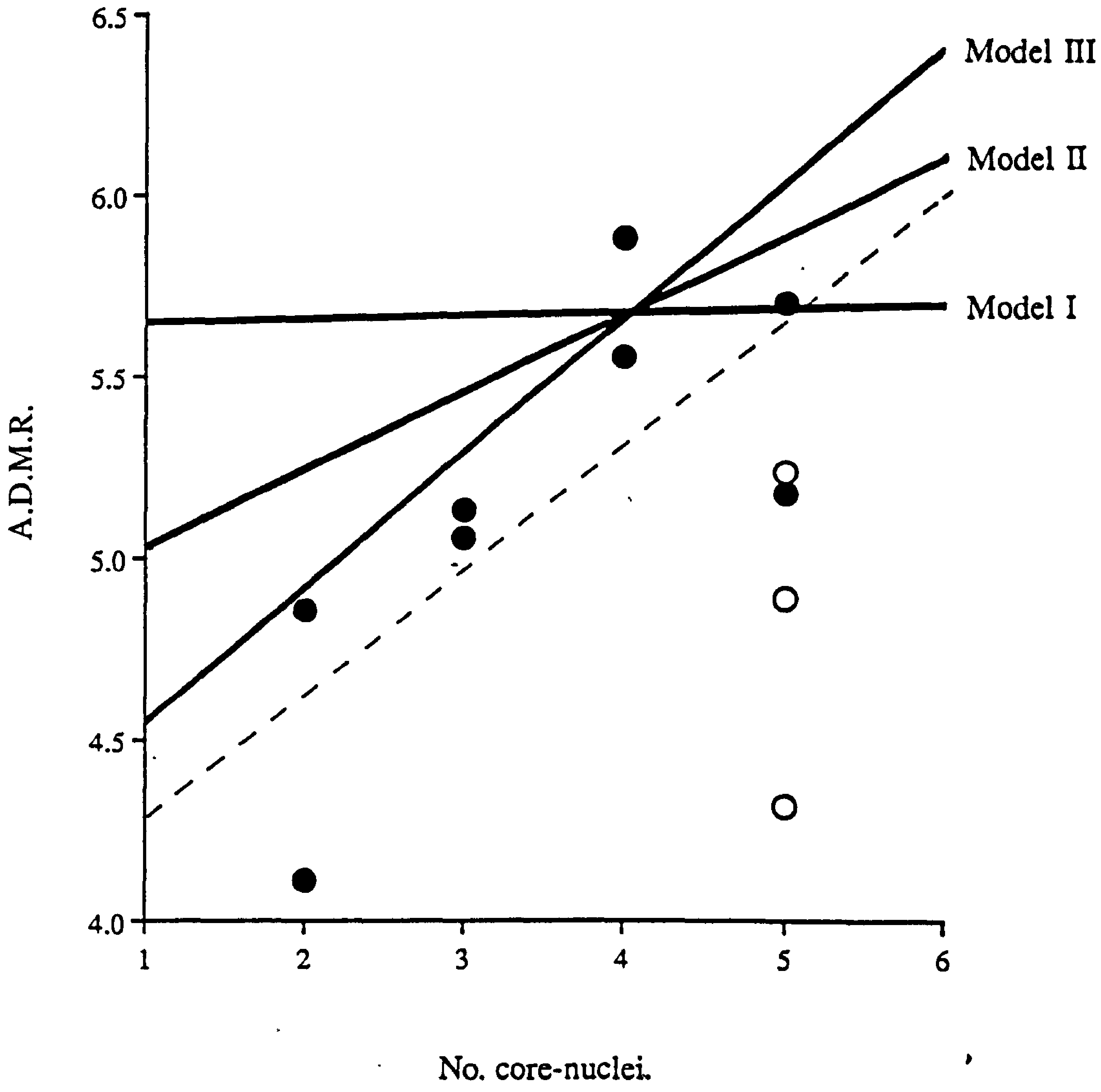


**Fig.6.3.** The relationship between average daily metabolic rate ($cm^3CO_2g^{-1}hr^{-1}$) and the number of core-nuclei used by non-breeding territorial robins ($r_s$=0.83 p<0.005 n=8). Solid symbols indicate territorial; open symbols non-territorial, following the definition in chapter 3. The solid lines show the constraint on energy expenditure predicted by each of the three models, and the dashed line shows the fitted linear regression. The equations and statistics are shown in Table 6.13.

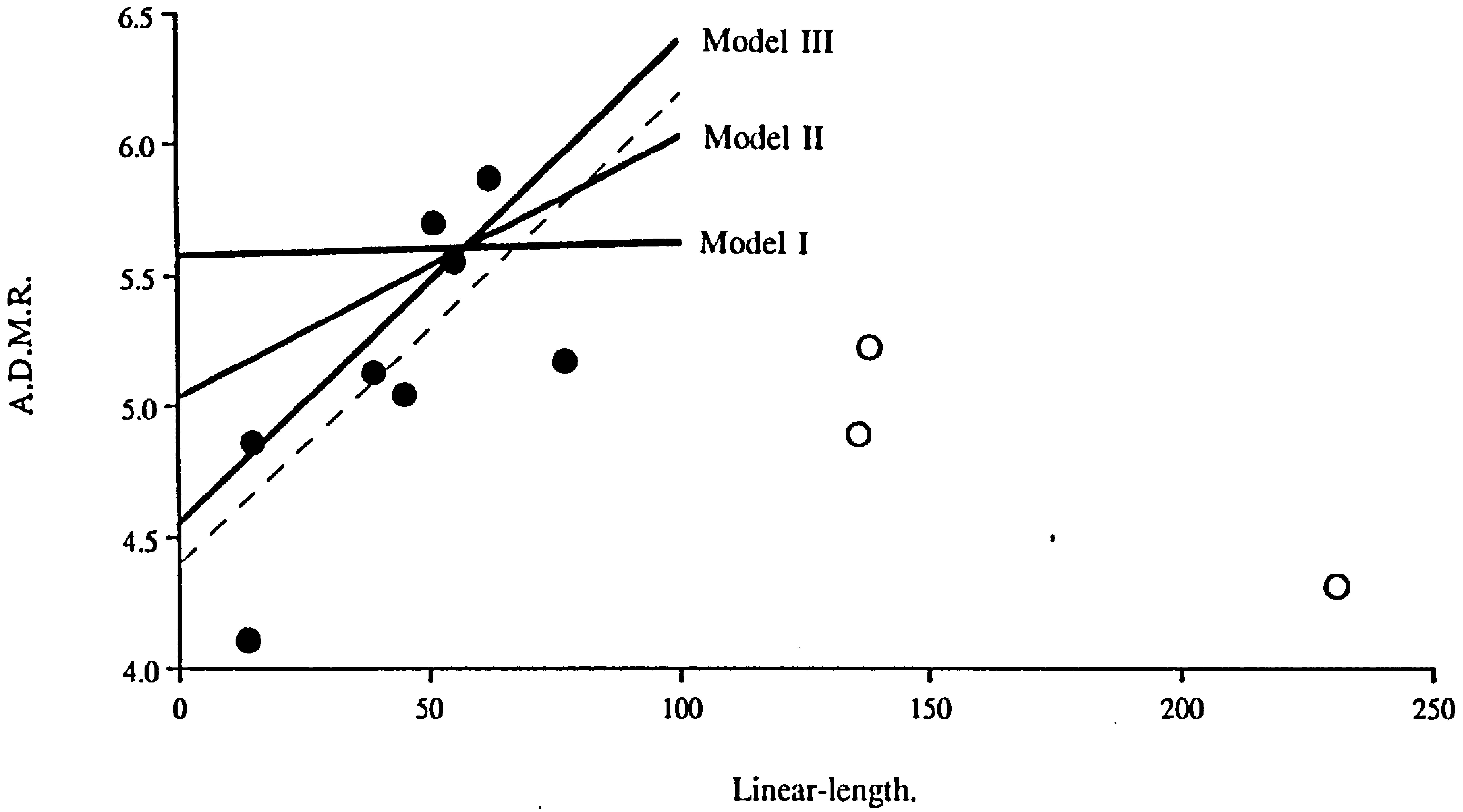


**Fig.6.4.** The relationship between average daily metabolic rate ($cm^3CO_2g^{-1}hr^{-1}$) and the linear-length (m) of ranges used by non-breeding territorial robins ($r_s$=0.81 $p<0.01$ n=8). Solid symbols indicate territorial; open symbols non-territorial, following the definition in chapter 3. The solid lines show the constraint on energy expenditure predicted by each of the three models, and the dashed line shows the fitted linear regression. The equations and statistics are shown in Table 6.13.

**Table 6.13.** Comparison of the lines predicted by the three models of energy costs of ideal linear network use and the observed linear regressions of ADMR on number of core-nuclei and linear-length. Equation parameters predict ADMR for each of the two measures of territory size.

| | **Model I** | | **Model II** | | **Model III** | | Fitted linear regressions (n=8) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | β | α | β | α | β | α | β | α | $r^2$ | F |
| **No. core-nuclei** | | | | | | | | | | |
| Equation parameters | 0.009 | 5.636 | 0.214 | 4.813 | 0.369 | 4.169 | 0.346 | 3.965 | 0.48 | 7.58 * |
| % departure from fitted regression | -98 | +42 | -39 | +21 | +6 | +5 | | | | |
| **Linear-length** | | | | | | | | | | |
| Equation parameters | 0.000 | 5.645 | 0.010 | 5.027 | 0.018 | 4.538 | 0.018 | 4.359 | 0.44 | 6.55 * |
| % departure from fitted regression | -78 | +30 | -39 | +15 | 0 | +4 | | | | |

| | |
|---|---|
| β | Slope of line. |
| α | Elevation of line. |
| * | $p<0.05$ |

5.88 n=8, non-territorial median=4.81 $cm^3CO_2g^{-1}hr^{-1}$ range 4.31-5.23 n=3).

The fit of the models to the observed data was assessed using paired T-tests between observed values of ADMR, and predicted values from the models matched by territory size (Table 6.14.). At the 10 % probability level, there was no significant difference between the observed data and Model III using number of core-nuclei as the measure of territory size. There was no significant difference between the observed data and Models II and III at the 10 % level if linear-length was used as the measure of territory size (Table 6.14.). Therefore although the assumptions associated with Model III produced the best predictions of the energy costs of territory use in the non-breeding robin, Model II could not on the basis of this evidence be rejected with confidence.

A sensitivity analysis was carried out on the predictions of Model III to assess the degree to which the relationship between energy expenditure and territory size was influenced by the cost of each component activity included in the energy budgets. This was done by decreasing the cost of each of the activities in turn by 10 % and assessing the effect on the slope and elevation of the predicted energy cost constraint (Table 6.15.). On examining the percentage change in the equation parameters for each activity, it was clear that for both measures of territory size, a reduction in the cost of perch & drop foraging and commuting (i.e. flight) produced the largest decrease in the slope of the line (-12%), while a reduction in the cost of roosting produced the largest decrease in the elevation of the line (-4%). In no other case did the effect on calculated energy costs exceed 4%.

Any territorial robin is able to move outside its territory at dusk in order to find locations in which microhabitat characteristics produce the largest reduction in the energy costs of roosting overnight. The energy cost of activities involving flight, such as perch & drop foraging and commuting between core-nuclei, however, may only be reduced by a reduction in the wing loading; a fixed attribute of the territory owner. In the robin, the wing span and body mass vary between individuals (this study). An individual of proportionally lower body mass or longer wings will experience a lower wing loading and consequently incur a reduced flight cost (Pennycuick 1989). During most flights involved in perch & drop foraging and inter-patch commuting, the bird is moving at speeds below $V_{mp}$ (Tatner & Bryant 1986). It was not possible, therefore, to evaluate the effects of variation in wingspan on flight costs directly, since the software of Pennycuick (1989) can only estimate flight parameters for speeds between $V_{mp}$ and $V_{mr}$. Using the equation in Tatner & Bryant (1986), it was possible, however, to model the effects of variation in body mass on flight costs at such low

**Table 6.14.** T-values and probability levels for paired T-tests between observed values of A.D.M.R. and predicted values from each model matched by territory size (n=8).

| | **Model I** | **Model II** | **Model III** |
|---|---|---|---|
| No. core-nuclei | -2.51 ** | -2.67 ** | -2.13 * |
| Linear-length | -2.36 ** | -1.95 * | -1.19 |

* p<0.1 ** p<0.05

**Table 6.15**. Sensitivity analysis of Model III. The costs of each activity included in the time budgets were decreased in turn by 10 % and the consequences for the slope and elevation of the line predicting ADMR assessed.

| Activity whose cost was decreased by 10% * | No. core-nuclei | | | | Linear-length | | | |
|---|---|---|---|---|---|---|---|---|
| | β | %Δ | α | %Δ | β | %Δ | α | %Δ |
| Roosting | 0.359 | -3 | 4.012 | -4 | 0.018 | 0 | 4.371 | -4 |
| Perched quietly | 0.365 | -1 | 4.076 | -2 | 0.018 | 0 | 4.440 | -2 |
| Other | 0.359 | -3 | 4.164 | 0 | 0.018 | 0 | 4.534 | 0 |
| Ground hopping | 0.365 | -4 | 4.162 | 0 | 0.018 | 0 | 4.538 | 0 |
| Perch & drop and commuting (flight) | 0.323 | -12 | 4.156 | 0 | 0.016 | -11 | 4.478 | -1 |

| | |
|---|---|
| * | Activities ranked in order of increasing cost. |
| β | Slope of line. |
| α | Elevation of line. |
| %Δ | Percentage departure from standard model III. |

speeds, by assuming wing span is constant and assessing flight cost of birds of different mass. The effects of differences in body mass on total free-living energy expenditure, when occupying territories of different size, are shown in Table 6.16. and Fig 6.5. Lines show the cost constraint for each value of body mass, predicted by the time/activity budgets under the assumptions of Model III. These differences are best illustrated by differences in DEE, since birds of different mass experience different component costs. The statistics for the predicted lines representing the energy cost constraints on territory size are shown in Table 6.17. Decrease in body mass decreases wingloading. Intuitively therefore, decreasing wingspan increases wingloading, and the effect on energy expenditure of variation in wingspan may be inferred. The predicted effects of body mass on energy expenditure will also hold if individuals are assumed to follow the assumptions of Model II.

### 6.4.3. Discussion.

Differences in territory size, individual attributes, activity and environmental conditions accounted for some of the variation in energy expenditure experienced by territorial robins. Territory size, as estimated by number of core-nuclei and linear-length, was most closely correlated with ADMR, as would be expected if differences in activity were the underlying cause of variation rather than differences in body size. In accord with this, the individual attributes, specifically body mass and wingloading, were most closely correlated with DEE; large birds having a higher energy expenditure because of their greater mass of metabolizing tissue and higher BMR, and birds with high wingloading experiencing higher flight costs. Territory area was not significantly correlated with energy expenditure, either for ADMR or DEE. The number of foraging patches used and the total length of the flight paths between nuclei was, however, highly correlated. This is consistent with the concept of territories as forging patches linked by a network of commuting paths, rather than a simple defended area within which birds are equally likely to move between and use any locations. Environmental variables were most closely correlated with ADMR, implying that the energy expenditure by individuals of different size was similarly subject to the effects of weather and season.

Radio-tracking indicated that all robins classified as territorial during the period that they were monitored, were occupying exclusive ranges, from which intruders were always evicted when encountered. The proportion of energy budget devoted to specific territory defence activities such as vocalisations and evicting intruders was negligible for all sizes of

**Table 6.16.** Energy expenditure by territorial robins of different body mass and occupying networks of different numbers of core-nuclei, predicted by Model III. The values of body mass modelled represent the minimum, mean and maximum of the individuals for which energy expenditure was measured.

| | **Energy expenditure (kJ)** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. core-nuclei; body mass 18.3g | | | | No. core-nuclei; body mass 19.5g | | | | No. core-nuclei; body mass 21.5g | | | |
| | 1 | 2 | 4 | 6 | 1 | 2 | 4 | 6 | 1 | 2 | 4 | 6 |
| E.E.$_{\text{active}}$* (kJ) | 29.328 | 34.225 | 42.661 | 50.939 | 31.685 | 36.888 | 45.850 | 54.671 | 34.584 | 39.928 | 49.695 | 63.063 |
| E.E.$_{\text{roost}}$# (kJ) | 22.708 | 22.708 | 22.708 | 22.708 | 24.140 | 24.140 | 24.140 | 24.140 | 26.518 | 26.518 | 26.518 | 26.518 |
| D.E.E.$ (kJ day$^{-1}$) | 52.036 | 56.933 | 65.369 | 73.647 | 55.825 | 61.028 | 69.990 | 78.811 | 61.102 | 66.446 | 76.213 | 89.581 |

* Energy expenditure during active period of 8.76 hrs.
\# Energy expenditure during roosting period of 15.24 hrs.
$ Daily energy expenditure.

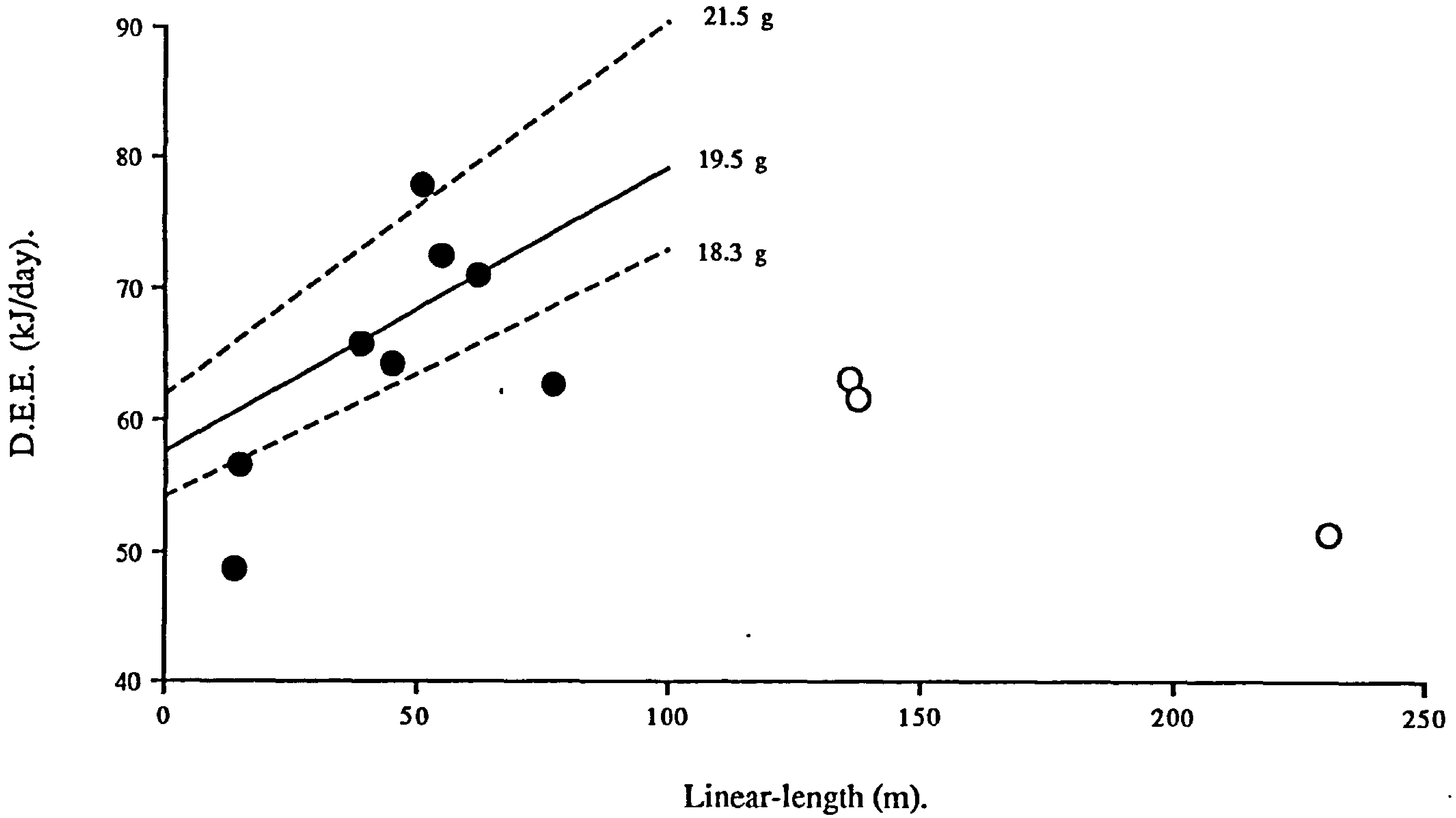


**Fig.6.5.** The relationship between daily energy expenditure and linear length used by non-breeding territorial robins. Solid symbols indicate territorial; open symbols non-territorial, following the definition in chapter 3. The lines are based on the assumptions of Model III, and show the effect of variation in body mass on energy expenditure by robins using territories of different size. The equations for the lines are shown in Table 6.17.

**Table 6.17.** Comparison of the lines predicted by Model III for robins of different body mass. The values of mass modelled represent the minimum, mean and maximum of the individuals for which energey expnditure was measured. Equation parameters predict D.E.E. for each of the two measures of territory size.

| | Body mass set to 18.3g | | Body mass set to 19.5g | | Body mass set to 21.5g | |
|---|---|---|---|---|---|---|
| | β | α | β | α | β | α |
| **No. core-nuclei** | | | | | | |
| Equation parameters | 4.18 | 48.58 | 4.45 | 52.14 | 5.78 | 54.88 |
| % departure from equation for mean mass of 19.5g | -6 | -7 | | | 30 | 5 |
| **Linear-length** | | | | | | |
| Equation parameters | 0.21 | 52.75 | 0.22 | 56.58 | 0.29 | 60.66 |
| % departure from equation for mean mass of 19.5g | -5 | -7 | | | 32 | 7 |

| | |
|---|---|
| β | Slope of line. |
| α | Elevation of line. |

territory occupied. In a review of energy allocation to resource defense, Walsberg (1983) found an average of 11 % of DEE invested in advertisement and defense activities by birds at all stages of the annual cycle, although in five out of eight studies (63 %) this was less than 8 %. As shown in chapter 5, increased investment in territory defense, involves changes in the trade off between ideal patch harvesting behaviour and ideal intruder location behaviour rather than increased investment in some discrete and costly boundary patrolling behaviour. Consequently the energy costs of defense are inextricably bound up with the costs of exploitation, and should not be considered as separate activities in time/activity/energy budgets.

The results suggest that the assumptions of Model III most closely represent the differences in time/activity budgets of robins using territories of different size, although the assumptions of Model II could not be rejected. The energy costs of commuting between core-nuclei, in whatever configuration and over any distances consistent with observed territory sizes, represent less than one percent of the total time/activity and energy budgets predicted by all three models of variation with territory size. Therefore the effect of territory shape and actual commuting distances on the energy costs of network use are negligible. The sensitivity analysis indicated the most important factor affecting the increase in energy expenditure with territory size was the degree of fragmentation of the foraging patches. Use of a larger number of foraging patches requires owners to spend a greater proportion of their time in perch & drop foraging, because of the greater length of total patch perimeter relative to total patch area. The assumptions about foraging behaviour upon which Model III was based could be tested by equipping robins with radio-tags containing mercury droplet activity sensors, from which instantaneous behaviour could be determined (Exo *et al* 1992).

Bryant & Prys-Jones (1985) showed that change in body mass was positively correlated with DEE in non-breeding dippers. This was because increased body mass represents an increase in the amount of metabolizing tissue in an individual. Although there was a significant loss of mass during the period of doubly labelled water measurement in robins, there was no associated relationship with energy expenditure. This was possibly due to the small range of the mass changes involved, or the fact that the mass changes were due to the assimilation or evacuation of gut contents rather than change in the amount of metabolizing tissue. The cause of the mass loss was probably the enforced fasting period of one hour during which the injected isotopes were allowed to equilibrate with the body water pool. If so, a second measurement of body mass just prior to release may have reduced the apparent mass loss. Any loss of mass as a result of blood sampling was considered negligible. Another source of this mass loss may have been the use of baited traps for initial captures and mist nets for final captures. The initial mass measurement could have been raised by recently ingested food.

Several studies have proposed the existence of an upper limit to the rate of energy assimilation (Kirkwood 1983) and maximum sustainable rate of energy expenditure by homeotherms (Drent & Dann 1980, Bryant 1989, Bryant & Tatner 1991). Work in excess of this apparent threshold is possible however, although individuals may incur loss of condition as energy reserves are used, or associated increased predation risk (Drent & Dann 1980). The frequency distribution of daily energy expenditures suggest that this metabolic ceiling lays near a metabolic intensity equal to 4xBMR or even 5xBMR, although the value will vary between species (Bryant 1989). A comparison of the frequencies of M measured in the present study with values for robins at stages of the annual cycle excluding nestling provisioning (a very costly activity) from Bryant & Tatner (1991) is shown in Fig.6.6. The data show that few individuals expended energy at a rate greater than 3xBMR. Previous results have suggested that, unlike those using small territories, robins using large territories are unable to increase their energy expenditure in response to simulated intrusions (section 5.5.). Although valid energy expenditures for using territory networks containing more than six foraging patches could be calculated using the assumptions of Model III, robins were never observed defending more than six foraging patches as a territory in the field. This may suggest an upper limit to territory size set by a constraint on M, above which the energy expenditure required for harvesting the foraging patches cannot be sustained. The metabolic intensity required for using a territory of the maximum six core-nuclei was predicted by Model III to equal 2.855xBMR (Table 6.12.). This is close to the 3xBMR suggested by Fig.6.6.

The observed values of M, the constraint on minimum energy expenditure required for territory use as predicted from Model III, and the proposed upper constraint on the sustainable energy cost of territory use are shown in Fig.6.7. Also indicated is the difference between the predicted energy expenditure for robins using small and large territories, and the proposed upper constraint on energy expenditure. This illustrates how robins using large territories are already working close to this upper limit, and so can only increase their level of territory

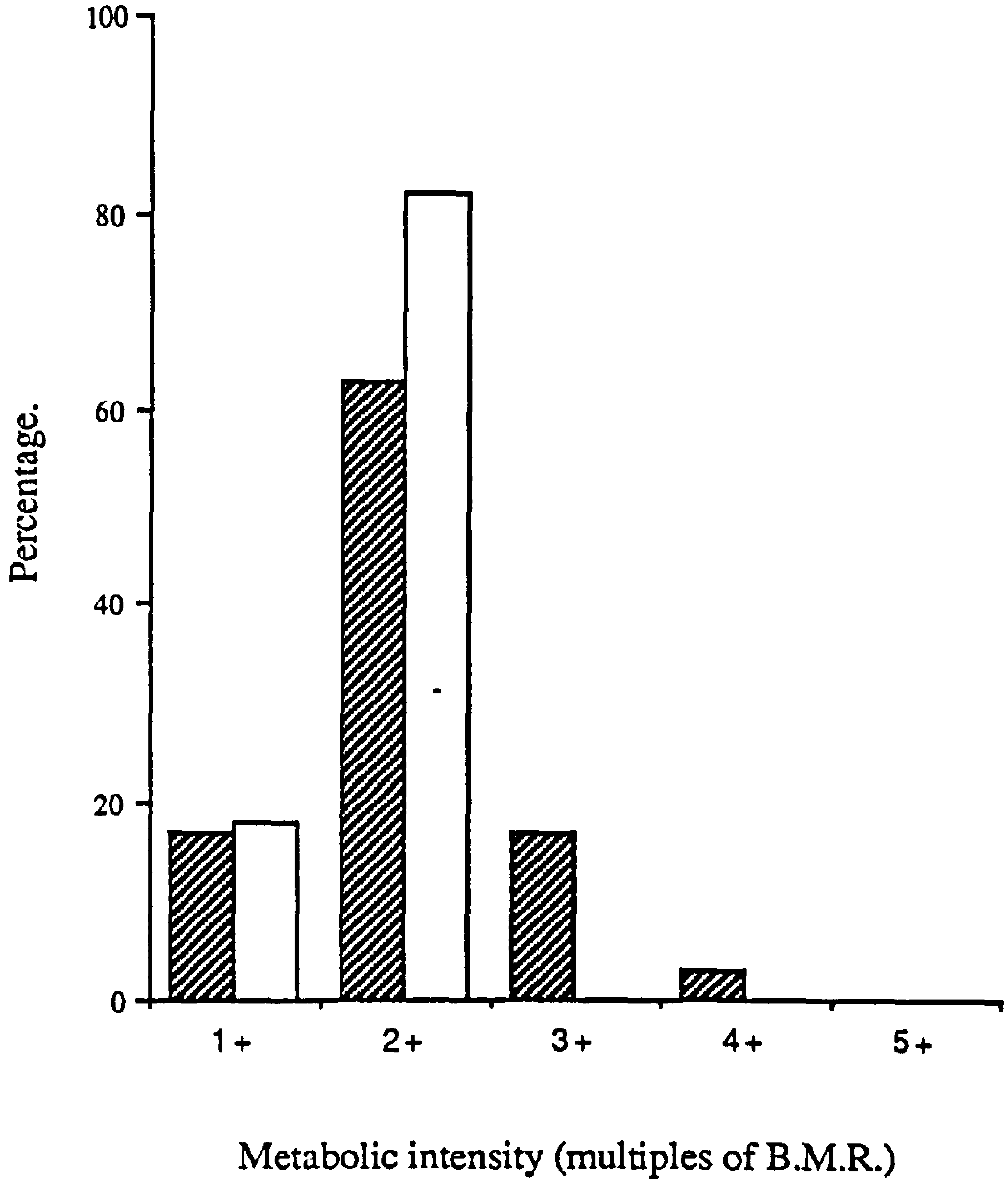


**Fig.6.6.** A histogram comparing the distribution for values of metabolic intensity in the non-breeding robin. Hatched bars show data for stages of the annual cycle excluding nestling provisioning (n=42) (after Bryant & Tatner 1991). Open bars shown the data from the present study (n=11).

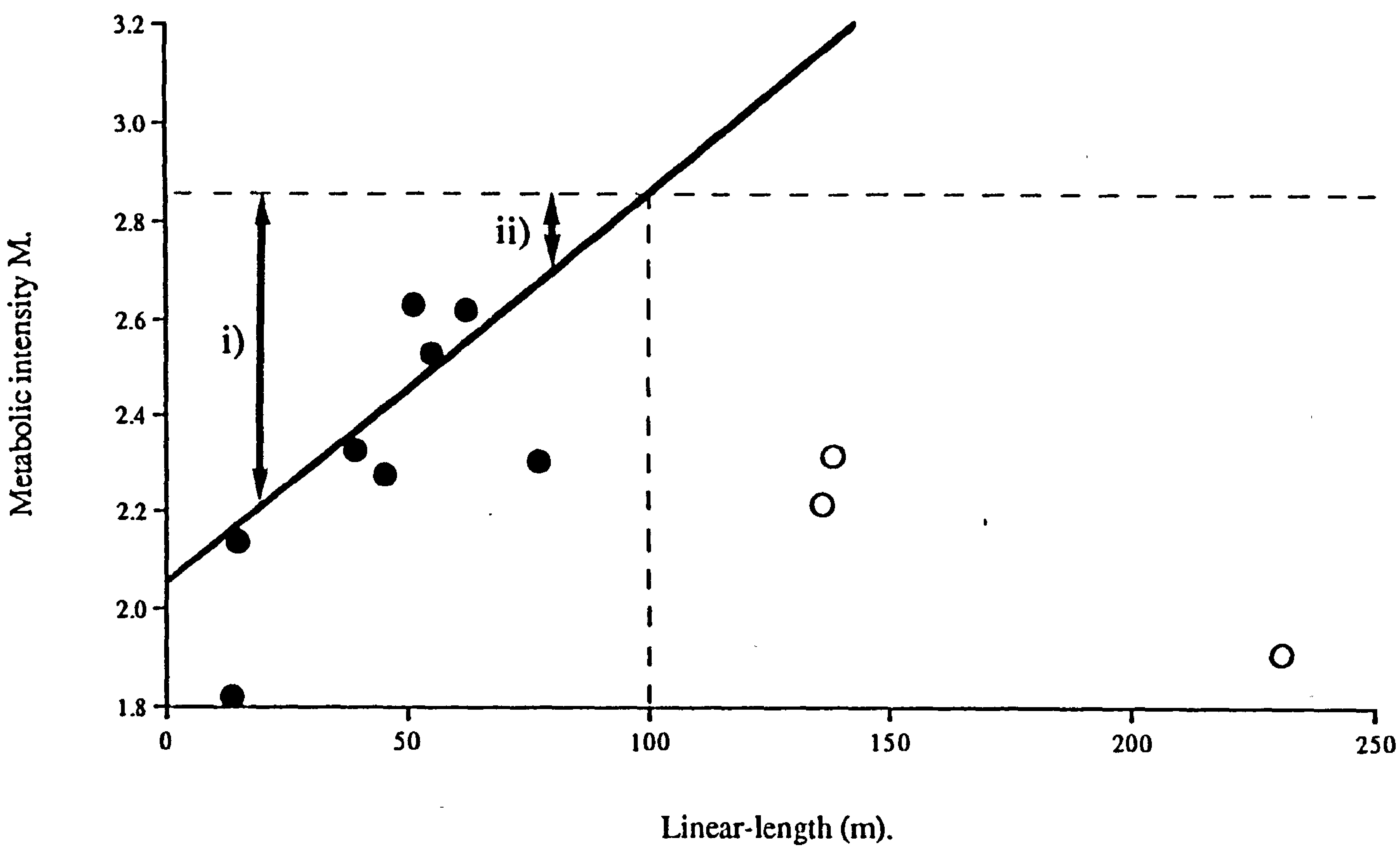


**Fig.6.7.** The relationship between the metabolic intensity M and the linear length of ranges used by non-breeding territorial robins (solid symbols)($r_s$=0.64 $p<0.05$ n=8). Robins using small territories respond to simulated intrusions by increasing their commuting rate; an energetically costly behaviour (section 5.5.). This is possible because of the large difference in energy expenditure (i) between that for territory exploitation predicted by Model III (solid line), and the proposed maximum sustainable energy expenditure (horizontal dashed line), suggested by the absence of territories of linear-length greater than 100 m (equivalent to 6 core-nuclei, Table 6.1.). Robins using large territories are already working near this limit (ii) and so cannot increase defense by investing in a energetically costly activity (section 5.5.). The vertical dashed line shows the threshold territory size beyond robins become non-territorial. This is because the energy expenditure required for territory exploitation is greater than the maximum sustainable energy expenditure.

defense by using an activity that has no additional cost (section 5.5). The two constraints on energy expenditure intersect to predict a threshold level of territory size above which robins cannot maintain territorial behaviour. This is supported by the presence of only non-territorial individuals with range sizes above this limit (Fig.6.7.).

Differences in the morphology of the robin affects the wingloading, and in turn the flight cost. Heavy birds or birds with short wing spans will experience a higher wingloading and energy cost of territory use (Table 6.16.). Robins of different morphology may therefore show differences in behaviour. For robins using a certain size of territory, some individuals of low wingloading may be able to economically exploit the renewing food supply in the constituent foraging patches, while other individuals of higher wingloading are forced by their higher energy expenditure to use space in an energetically less costly non-territorial manner. By becoming non-territorial, however, they may incur an associated reduction in fitness, due to for example increased risk of predation. The result of this would be the development of an association between wingloading and territory size.

Another factor that may affect associations between morphology and territory size is differences in dominance status between robins. Dominance has been defined as a relationship between individuals in agonistic encounters that has a predictable outcome; a dominant individual regularly defeating or displacing a subordinate. Dominant status often confers priority of access to key resources such as food (Hogstad 1988) and territories (Smith 1976, Arcese & Smith 1985). Following this, dominant individuals have been shown to be more likely to survive overwinter than subordinates (Arcese & Smith 1976). Furthermore, individuals of high body mass have previously been shown to be more dominant over low mass conspecifics (Petrie 1984, Newton 1990). In the robin, small territory networks, with their associated low energy costs of use, should be perceived as of the highest quality by all members of the population. If the dominance of individual robins over conspecifics is correlated with structural size or body mass, then dominant birds would be expected to obtain priority access to these small high quality territories. Individuals of lower mass would be excluded and must occupy larger lower quality territories. The predicted effects on the association between morphology and territory size for both of these factors is similar, and is illustrated as the modified Model III in Fig.6.8. Furthermore, if polygonal territories have shorter foraging circuits (Table 6.1.), dominant robins of large structural size or high body mass might be expected to acquire such networks. The proportion of time in costly perch &

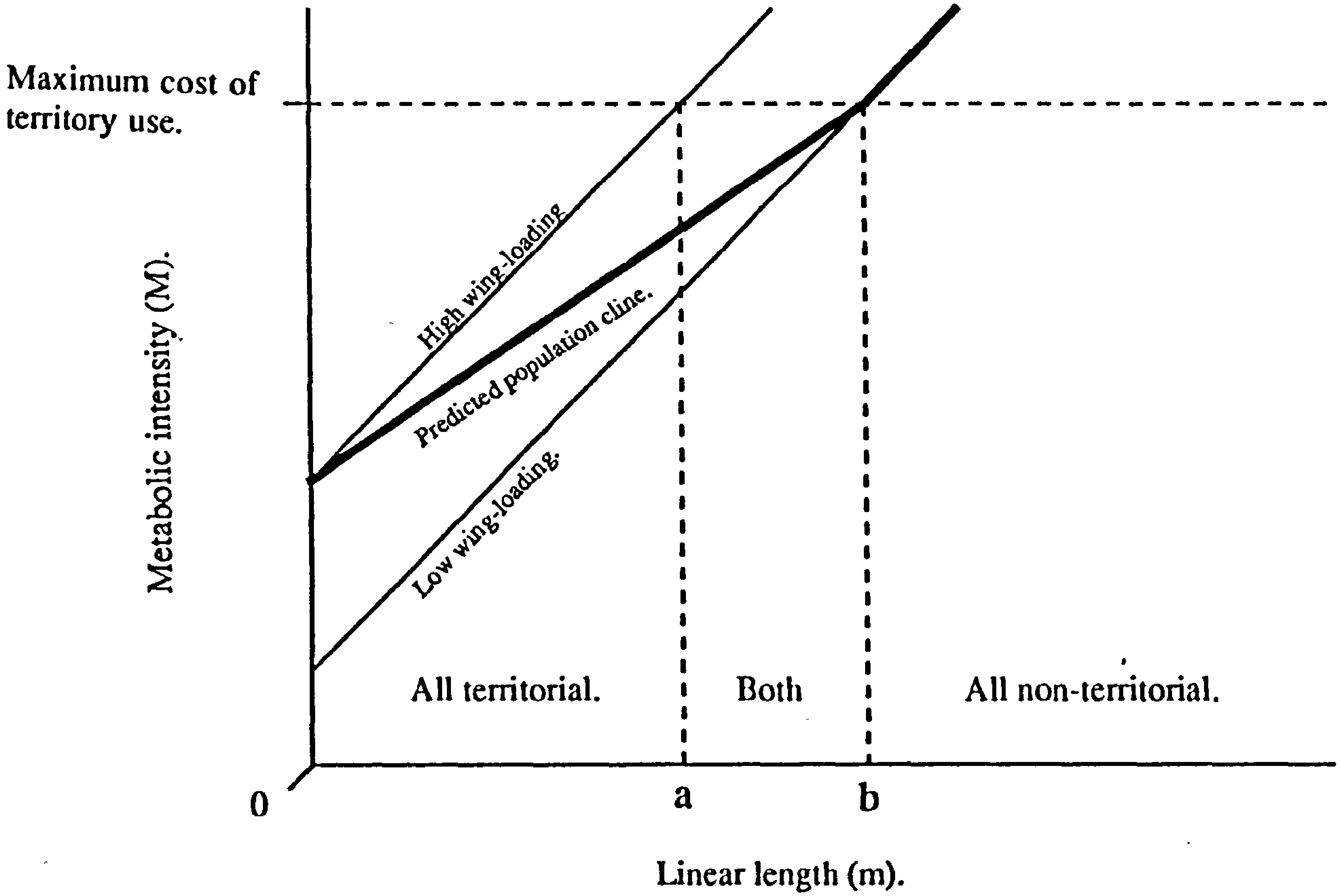


**Fig.6.8.** The modified Model III which takes into account differences in the morphology and dominance of territorial robins. The upper limit of territory size for birds of high wingloading (a) is less than the upper limit for birds of low wingloading (b). All robins using networks of core-nuclei of a linear-length (a measure of territory size) less than (a) will be able to use them a territories. All robins using networks of linear-length greater than (b) must be non-territorial. Between these lays a range of linear-lengths which may be used as territories or in a non-territorial manner, depending on the morphology of the individual.

drop foraging may not differ from that in linear networks, however, so the reduction in flight costs of using polygonal networks may be negligible and confer little energetic benefit on robins occupying polygonal territories.

Non-territorial robins were characterised by their rapid rate of range drift. Because of this, their pattern of space use could not be measured in terms of use of core-nuclei, as it was with territorial birds. Consequently a model of the time/activity budget for non-territorial birds could not be developed for comparison. Nevertheless, the extremely large ranges observed in addition to their low energy expenditure suggests that short term patterns of space use were considerably different from that of territorial birds. Perhaps non-territorial robins reduce the proportion of their time spent in high cost perch & drop foraging in favour of cheaper ground hopping. The microhabitat resource depression associated with hopping (Grajetsky 1993) may be less important if individuals are less reliant on regular sequences of visits to harvest prey in the same patches.

## 6.5. A test of the modified Model III.

### 6.5.1. Territory size and the quality of owners.

If the assumptions of Model III do correctly represent the energy cost constraint on territory size, then some relationship between individual attributes and territory size must also apply. Correlative results already suggest a positive, although non-significant, relationship between energy expenditure and wingloading (Table 6.10), however the sample size was small. By correlating territory size with individual attributes directly, the sample size can be considerably increased and the assumptions of the modified Model III tested.

Wingloading was measured in two ways; the structure dependent wingdisc loading was calculated from the body mass predicted from the individuals structural size measurements reflecting phenotypic flying ability, while the condition-dependent wingdisc loading was calculated from the observed body mass during the period that the territory size was measured, and reflects flying ability at this time. Significant relationships existed for structural size, wingloading and fat score (Table 6.18.). The results of tests between territorial and non-territorial robins for the above parameters are shown in Table 6.19. The relationships between linear length and predicted mass and structure-dependent wingdisc loading; and number of core-nuclei with fat score are shown in Figs.6.9.-11. The predicted mass, wing span, wingdisc loading, observed mass, condition and fat score are presented in Appendix 10 for the sample of radio-tracked robins whose range structure was analyzed in chapter 3.

**Table 6.18.** Spearman correlation coefficients between measures of territory size, structural size, wing size, wing loading and energetic condition for territorial and non-territorial robins.

| | Predicted mass (g) (n=30 & 36) | Wing span (mm) [#] (n=42 & 50) | Structure dependent wingdisc-loading (g mm$^{-2}$) [\$] (n=30 & 36) | Body mass (g) (n=38 & 46) | Mass dependent wingdisc-loading (g mm$^{-2}$) [†] (n=38 & 46) | Condition (g) [‡] (n=32 & 40) | Total fat score (n=28 & 36) |
|---|---|---|---|---|---|---|---|
| **No. core-nuclei** | | | | | | | |
| Territorial only | -0.17 | 0 | -0.29 * | 0.02 | 0.02 | 0.02 | 0.43 * |
| Territorial and non-territorial | -0.26 * | -0.11 | -0.27 | -0.04 | -0.03 | 0.08 | 0.42 *** |
| **Linear-length** | | | | | | | |
| Territorial only | -0.37 * | 0.04 | -0.48 *** | -0.30 * | -0.27 * | -0.10 | 0.36 * |
| Territorial and non-territorial | -0.48 *** | -0.07 | -0.52 *** | -0.20 | -0.16 | 0.13 | 0.29 * |
| **Usual-area** | | | | | | | |
| Territorial only | -0.35 * | 0.11 | -0.43 ** | -0.35 * | -0.32 * | -0.12 | 0.28 |
| Territorial and non-territorial | -0.46 *** | -0.03 | -0.50 *** | -0.22 | -0.18 | 0.16 | 0.22 |

* $p<0.05$ ** $p<0.01$ *** $p<0.005$

\# From equation in chapter 2, section 2.2.2.2.2.

\$ Predicted body mass divided by wing wingdisc area (Feinsinger & Chaplin 1975).

† Observed body mass divided by wingdisc area (Fiensinger & Chaplin 1975).

‡ Observed minus predicted body mass.

**Table 6.19.** Median and range for various parameters of robins which were classified as territorial or non-territorial. Statistics refer to Mann-Whitney tests between classes. Definitions and units as for Table 6.18.

| | Predicted mass (g) (n=30 & 6) | Wing span (mm) (n=42 & 8) | Structure dependent wingdisc-loading (g mm$^{-2}$) (n=30 & 6) | Body mass (g) (n=38 & 8) | Mass dependent wingdisc-loading (g mm$^{-2}$) (n=38 & 8) | Condition (g) (n=27 & 5) | Total fat score (n=28 & 8) |
|---|---|---|---|---|---|---|---|
| **Territorial** | | | | | | | |
| Median | 19.3 | 228.5 | 0.00047 | 19.4 | 0.00047 | -0.23 | 0 |
| Range | (18.4-20.3) | (223.9-231.9) | (0.00045-0.00049) | (17.1-22.1) | (0.00041-0.00056) | (-1.97-3.47) | (0-4) |
| **Non-territorial** | | | | | | | |
| Median | 19.0 | 227.3 | 0.00045 | 19.1 | 0.00048 | 0.98 | 0 |
| Range | (18.0-19.5) | (225.0-230.8) | (0.00045-0.00048) | (16.7-21.2) | (0.00041-0.00052) | (0.26-2.05) | (0-5) |
| W | 68 * | 166 | 51 * | 204 | 208 | 121 ** | 158 |

* $p<0.1$    ** $p<0.05$

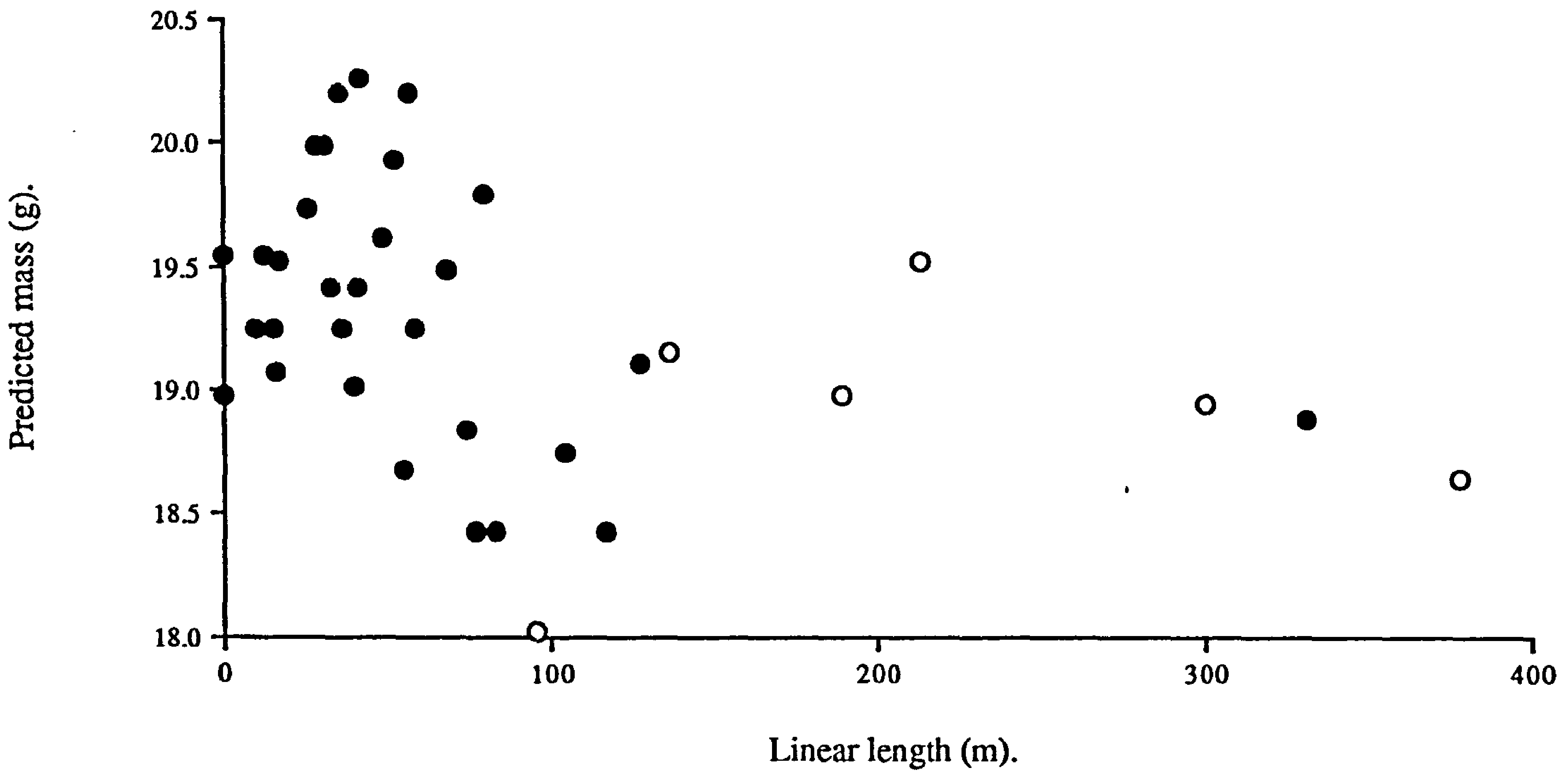


**Fig.6.9.** The relationship between structural size, in terms of mass predicted by several structural measures, and range size, measured as linear-length. Solid symbols indicate territorial; open symbols non-territorial, following the definition in chapter 3. Territorial; $r_s$=-0.37 p<0.05 n=30, all; $r_s$=-0.46 p<0.005 n=36.

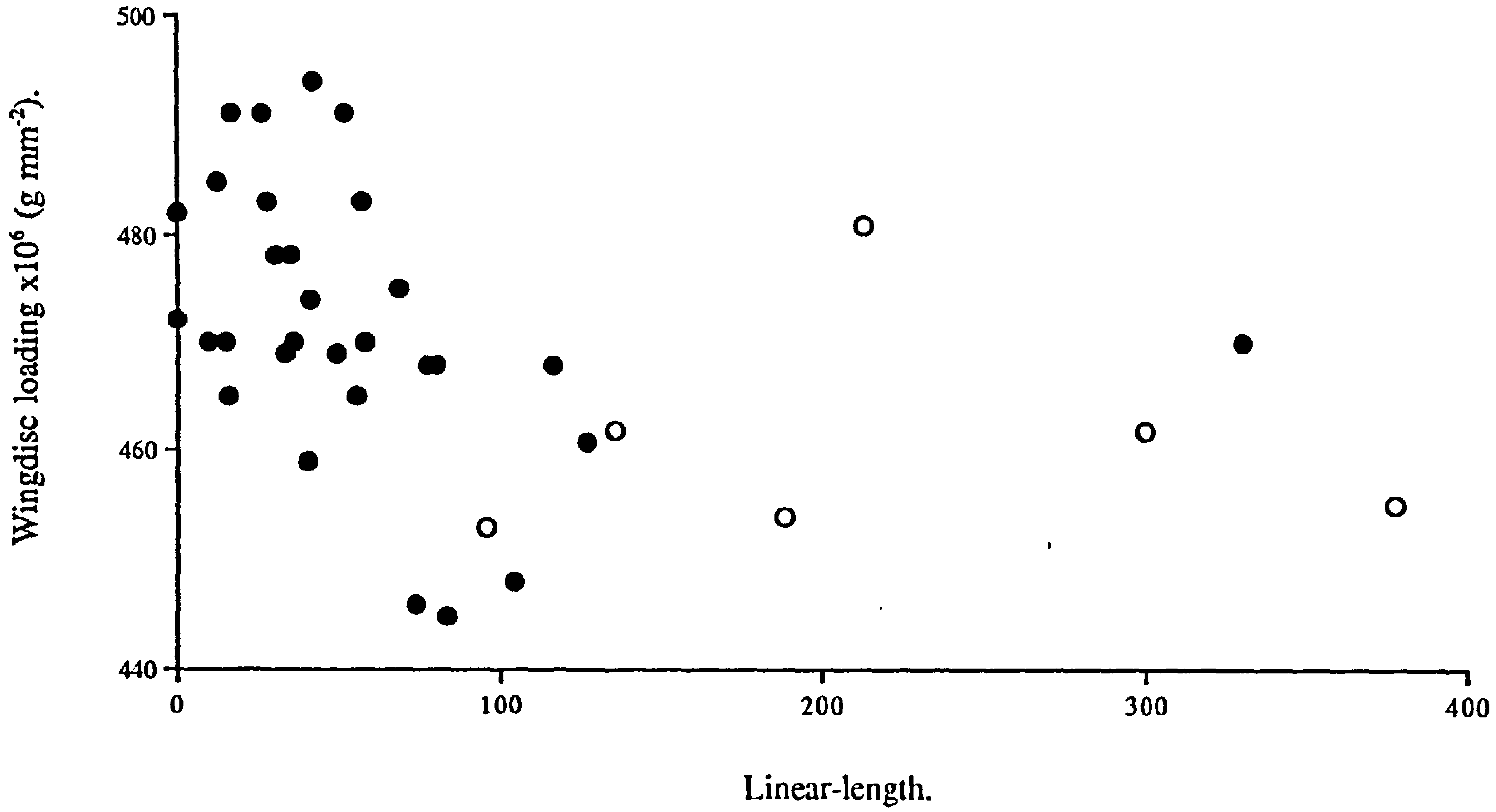
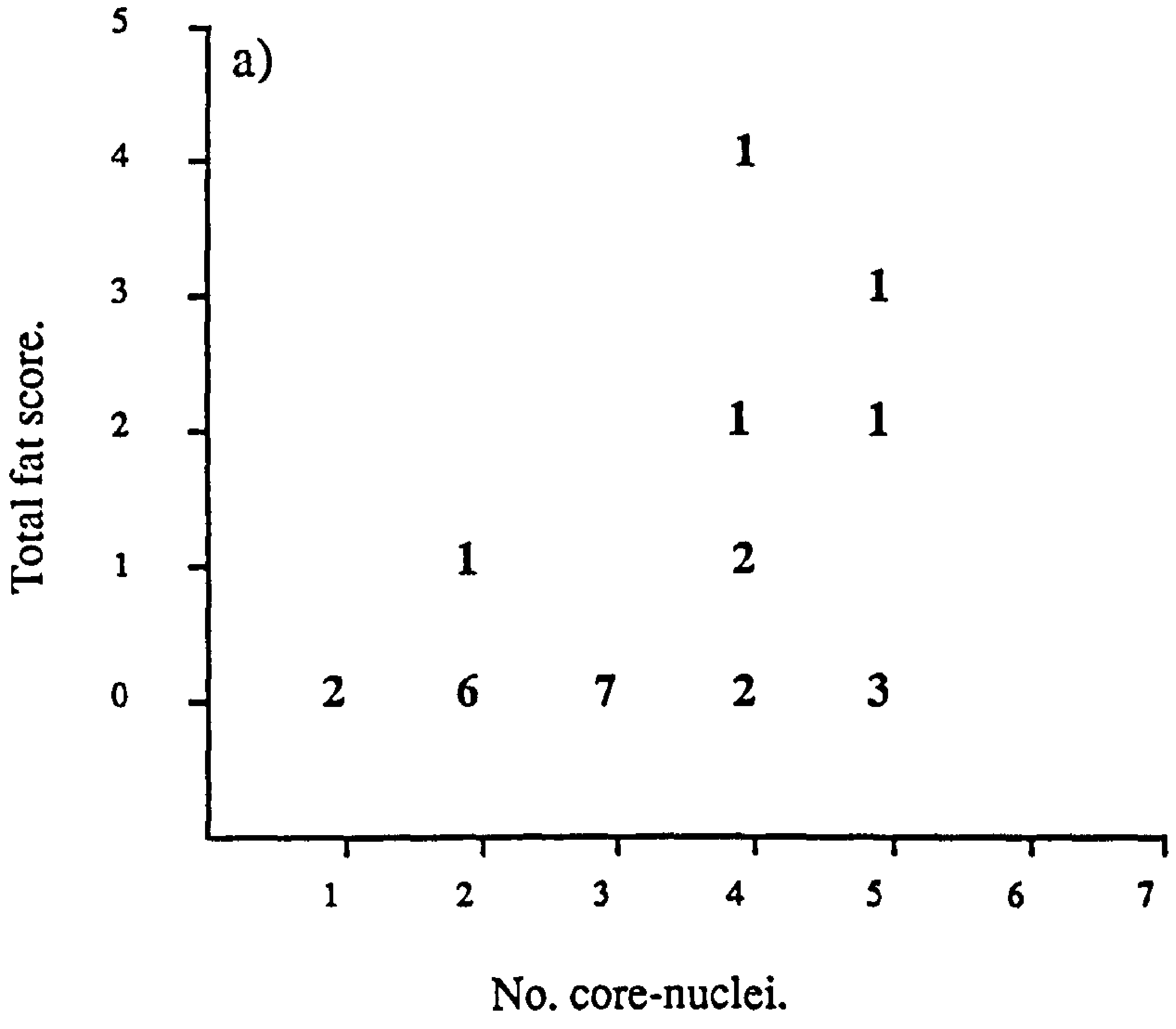


**Fig.6.10.** The relationship between structure-dependent wingdisc-loading, and range size, measured as linear-length. Solid symbols indicate territorial; open symbols non-territorial, following the definition in chapter 3. Territorial; $r_s=-0.48$ $p<0.005$ $n=30$, all; $r_s=-0.52$ $p<0.005$ $n=36$.



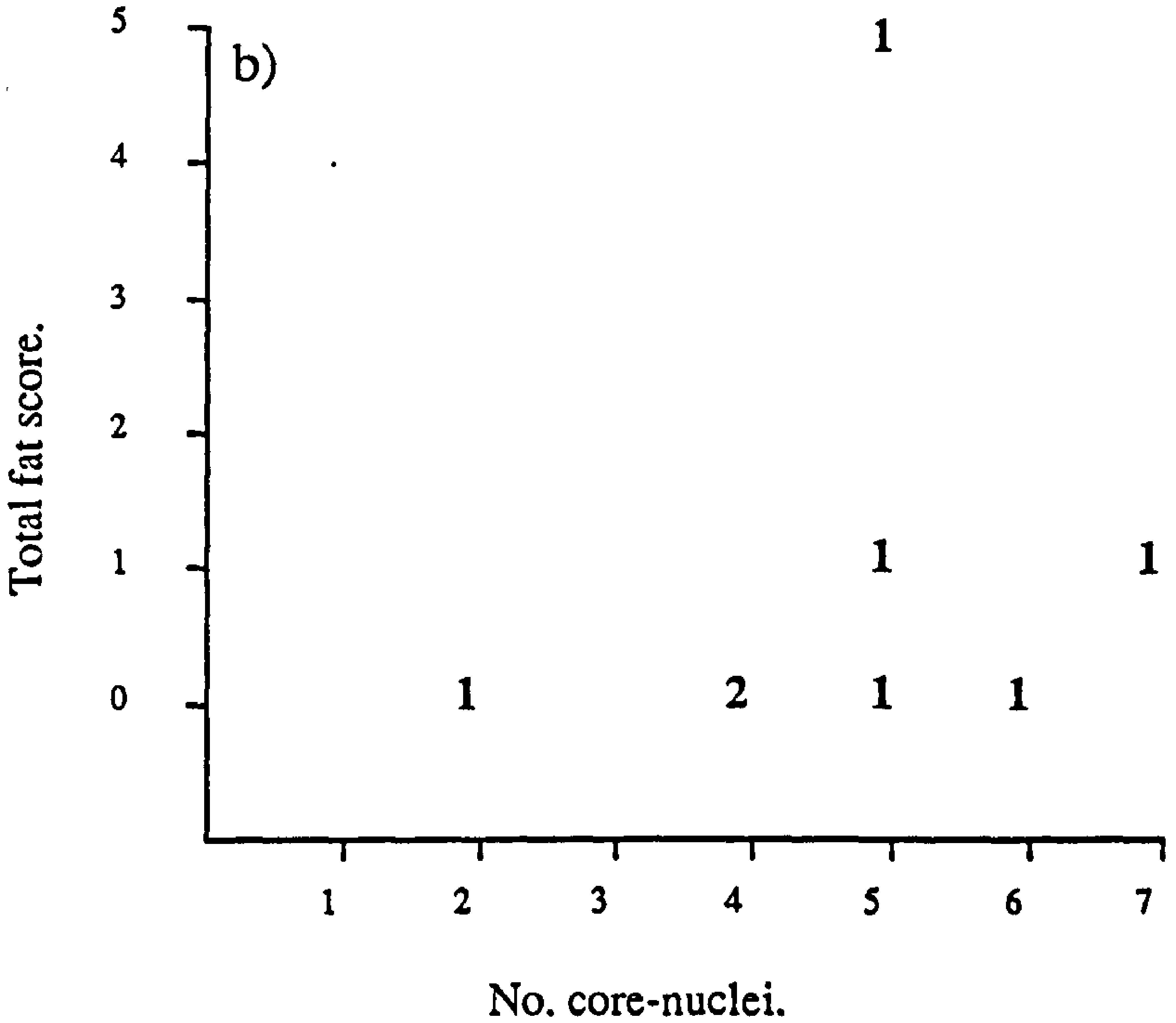


**Fig.6.11.** The relationship between total fat score, a measure independent of structural size, and range size, measured as linear-length. Territorial individuals are shown in (a) and non-territorial in (b), following the definition in chapter 3. Values indicate the number of data at each point. Territorial; $r_s=0.43$ $p<0.05$ $n=28$, all; $r_s=0.42$ $p<0.005$ $n=36$.

### 6.5.2. Discussion.

In general, the evidence supports the prediction of the modified Model III, that robins of low mass and wingloading should be excluded from small territory networks, with their associated low energy cost of use. Reasons for this may include a dominance hierarchy in the population based on body size; large birds being more likely to gain exclusive access to patches which make up a small territory networks. In addition, for a particular territory size, an individual of low wingloading may be able to economically exploit the foraging patches, while a bird of high wingloading with its' increased flight costs, cannot.

Correlations of the three measures of territory size with energy expenditure suggested that the number of core-nuclei and linear-length were the most accurate measures of territory size, if it is assumed that birds using large territories have a high energy expenditure. Of these measures of territory size, linear-length was also most closely correlated with individual attributes. The number of core-nuclei, however, were least correlated. Correlations with usual-area were of intermediate value. The reasons for this difference are unclear. The sample of 46 ranges used by territorial robins was compiled between August and February, encompassing the whole non-breeding season. It is possible that some unidentified seasonal variation in prey availability or recovery; habitat selection; or range drift reduces the accuracy with which the true number of foraging patches within territories can be identified. This would however, be expected to effect estimates of linear-length, if the model of territory structure does not also vary.

Structure-dependent wingloading was more correlated with territory size than condition-dependent wingloading. This seem likely to represent selection of territories by robins that allow optimal use over the long term (months), rather than the period over which range size was measured (days). During this short period the observed mass and therefore condition-dependent wingloading, would be subject to weather related variation. It may be more important for a territorial robin to optimise its body condition rather than its wingloading, over the short term. An example of this would be the need to lay down additional energy reserves in order to survive long winter nights during a cold snap.

Robins occupying large territories, containing many core-nuclei and a large total commuting distance, were in better energetic condition than birds occupying small territories estimated by total fat score, a measure independent of size differences, despite being structurally smaller, indicated by predicted mass, and of lower observed body mass. Robins occupying large territories change their activity in a different way to birds on small territories when increasing their level of territory defense (section 5.5.). Because of this it may be beneficial for them to maintain higher levels of energy storage, to offset decreased foraging success when intruder pressure is high. Furthermore, despite being significantly smaller and of lower wingloading at the 10 % probability level, non-territorial robins showed a significantly higher index of condition than territorial birds (5% level). The condition measure does not fully allow for size differences. Further correcting for size would, however, amplify the existing difference. The higher energetic condition of non-territorial robins relative to their territorial counterparts may be due to them requiring a larger buffer against adverse conditions, since their nomadic use of space means they cannot exploit a predictable renewing food supply. The cost of carrying additional reserves may be offset by a low wingloading and associated flight cost. The superior condition of non-territorial birds in the present study is contrary to the usual view of non-territorial birds being the poorest quality individuals in a population in terms of mass loss during cold weather in winter (Harper 1984) and while wandering prior to pairing in spring (Harper 1985).

After the analysis for the present study was carried out, Carpenter *et al* (1993a,b) published results for hummingbirds defending territories during migratory stopovers. Patterns of territory acquisition and quality were positively related to dominance, as indicated by wingloading. Adult males had the highest wingloadings, were dominant over females and immatures which had lower wingloadings, and were more likely to gain territories and occupy territories of high quality (Carpenter *et al* 1993a). Some birds at the lower end of the dominance hierarchy were forced to follow a non-territorial existence. Despite their subordinate status, however, like robins, they were able to accumulate energy reserves at a comparable or higher rate than that of territory owners. This energetic compensation was achieved due to the low wingloading and therefore flight costs of non-territorial individuals (Carpenter *et al* 1993b).

The phenotype of an individual is the product of its genotype and its environment (Boag 1983). The morphological characteristics of small birds have been shown to have high indices of heritability (Boag 1983). If the phenotype of individual robins is similarly predominately dictated by its genes rather than its environment, then these results suggest a genetic predisposition to particular patterns of territory occupancy.

# Chapter 7.

# 7. General discussion.

## 7.1. Radio-tracking small birds.

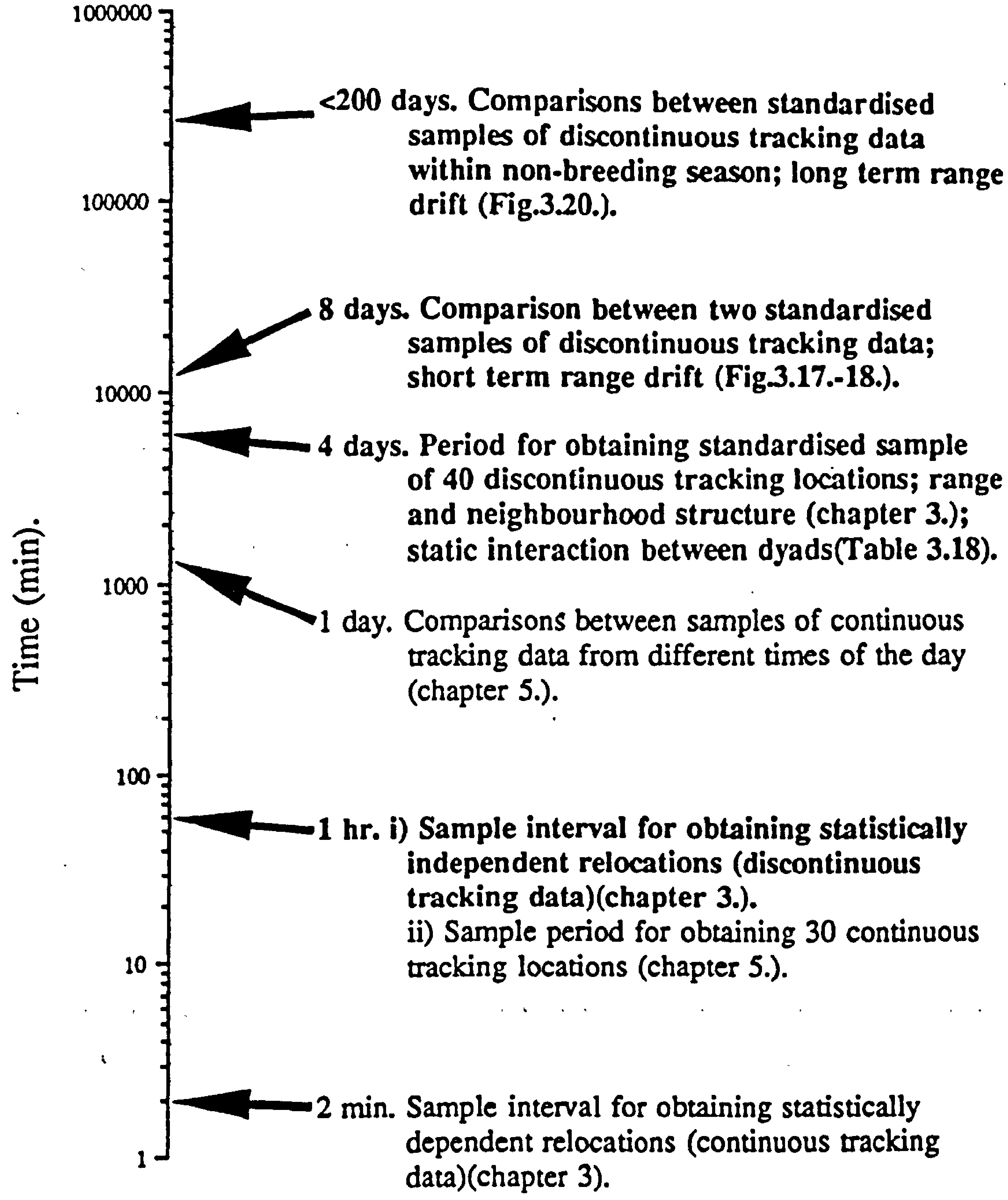
### 7.1.1. Temporal scale of observations.

A territory is a space, and a given territory must be defined in spatial terms (Kaufmann 1983). Furthermore, territories may vary in the length of time they exist on any one site, thus a territory must be described with reference to both space and time (Kaufmann 1983). In many previous studies of space use, the period over which radio-locations were collected, the sample size and the effects of autocorrelation have often not been considered important (Harris *et al* 1990). Thus differences in space use over a range of time scales have rarely been addressed. The space use of the robin and the dipper were intentionally sampled and analyzed over a variety of time scales; from as little as two minutes to as long as 200 days, requiring both autocorrelated continuous tracking data and asymptotic samples of discontinuous tracking data (Fig.7.1.). This enabled both very short and very long term changes in the territorial behaviour of a small passerine bird to be quantified over the non-breeding season in unprecedented detail.

The results from the present study demonstrate how inappropriate radio-tracking protocols could provide misleading data. For example, due to the effects of range drift, estimates of territory area based on sampling period of several weeks could severely overestimate the "instantaneous" area; that is the area used over a period of only a few days. It is suggested, therefore, that the most appropriate base-line measure of range size is that determined from an asymptotic sample size using a sample interval just sufficient to ensure statistical independence between successive location estimates, and the patterns of range use and changes in range structure over time should then be quantified relative to this, using shorter or longer sample intervals as required.

### 7.1.2. The analysis of radio-tracking data; difficulties and solutions.

In the present study the most appropriate technique for determining internal range structure was non-parametric sequential cluster analysis (Kenward 1987, 1990, 1992). This was because of its effectiveness in identifying a number of much used patches in a non-uniform multi-nuclear range, without being influenced by other locations or an arbitrary grid



**<200 days. Comparisons between standardised samples of discontinuous tracking data within non-breeding season; long term range drift (Fig.3.20.).**

**8 days. Comparison between two standardised samples of discontinuous tracking data; short term range drift (Fig.3.17.-18.).**

**4 days. Period for obtaining standardised sample of 40 discontinuous tracking locations; range and neighbourhood structure (chapter 3.); static interaction between dyads(Table 3.18).**

**1 day.** Comparisons between samples of continuous tracking data from different times of the day (chapter 5.).

**1 hr. i) Sample interval for obtaining statistically independent relocations (discontinuous tracking data)(chapter 3.).**
ii) Sample period for obtaining 30 continuous tracking locations (chapter 5.).

2 min. Sample interval for obtaining statistically dependent relocations (continuous tracking data)(chapter 3).

Fig.7.1. The temporal scale of observations available using radio-tracking data from the robin. Bold indicates use of range statistics based on discontinuous tracking data, and normal text indicates use of range statistics based on continuous tracking data.

(Kenward 1992). The number and size of core-nuclei identified by this technique depends only on the analysis algorithm; for example the number of locations required to initiate a cluster. In the Ranges IV software used to analyze the discontinuous tracking data, the minimum number of locations for cluster formation was three (Kenward 1992). Although this number is arbitrary, it represents the minimum number required to form an area (a triangle) if all three locations occur in different resolution cells. Nevertheless, using this technique the core-nuclei apparently occupied by some robins were only one resolution cell in area (1 $m^2$). This was because the bird made three or more visits to a single perch at a sufficiently large distance from other clusters. The existence of such small outlying clusters in the robin prompts the question are they used as part of the territory, or are they simply regularly visited excursive or even intrusive locations? These difficult to categorise outlying core-nuclei could be excluded from estimates of range structure by using a higher minimum number of locations for cluster initiation, although an objective criteria for determining such a minimum number is at present not available.

Once the appropriate percentage of locations was assigned to the clusters, their area was determined by constructing convex polygons around each one (Kenward 1990). Although these generally produced a tight-fitting outline, they were inevitably subject to some of the disadvantages inherent in any convex polygon measure of range area, such as the inclusion of unused areas (White & Garrot 1990). An example of this is found in core-nucleus number 2 in Fig.3.10. where the true distribution of location estimates resembles a crescent. Estimates of nucleus area which more closely follow the distribution of the locations could be obtained using concave polygons (Harris *et al* 1990), although the rules for their construction often lack objectivity.

A new non-parametric approach for identifying core-regions within ranges has been described by Wray *et al* (1992b). The use of dirichlet tessellations has the advantages of cluster analysis when applied to non-uniform multinuclear ranges, but makes no assumptions of convexity in defining core-areas. Instead, internal range structure may be described in terms of the summed area of the tiles constructed around each location (Wray *et al* 1992). Consequently, a form of cluster analysis could be developed based on the clustering of tiles of different area (tiles are smallest where the locations are densest), rather than distances between points based on sophisticated joining rules (Wray *et al* 1992).

In order for the continuous tracking information to be interpreted in terms of the use of different foraging patches, it was necessary to develop a series of movement rules. This was to remove the effect of brief anomalous movements which would otherwise disrupt the quantification of movement sequences. The precise effect of the rules were not important, since patterns of range use were compared between individuals using the same analysis protocol. The rules were deemed suitable if they enabled the duration of individual visits to foraging patches and the sequence of visits to patches, to be determined.

On superimposing continuous tracking data on the range structure determined from discontinuous tracking data, it was necessary to add a two metre boundary strip to all core-nucleus polygons, in order to assign peripheral locations to appropriate nuclei. This increased their area and in some cases caused neighbouring nuclei to fuse, reducing the number of core-nuclei in the range. Core-nucleus polygons were derived by a mathematical algorithm which was independent of the real activity of robins. Because of this the addition of a boundary strip produced range statistics that were no less representative of the behaviour of real robins.

## 7.2. Territory and neighbourhood structure.

### 7.2.1. Comparison with previous studies.

A comparison between the conclusions drawn from the present study, and those of previous studies have been discussed in detail in the previous chapters. However, the more important differences for the robin are summarised in Table 7.1. and drawn together below.

### 7.2.2. Territory structure.

The most important difference was in the approach to describing territory structure. In previous studies, both breeding and non-breeding territories have been viewed as areas of utilized habitat surrounded by a defended boundary (Lack 1940, Harper 1984, Adriaensen & Dhondt 1990). The locations of these were determined by visual observations of territorial and other behaviour, and plotted on maps as precise lines (Table 3.1.). The highly quantitative methods of measuring space use used in the present study produced no evidence for such territory boundaries. Instead, territory structure was much closer to the network concept developed in chapter 5. Robins defended a number of foraging patches located in bushes and shrubs. In order to use the territory, birds commuted between patches using a network of preferred flight paths, each of which minimised individual commuting distances.

**Table 7.1.** Comparison between previous studies of non-breeding robins and the conclusions of the present study.

| **Subject** | **Summarised conclusions of previous studies** | **Conclusions from the present study** |
|---|---|---|
| Territory shape | Most studies fail to mention territory shape specifically, although associated maps suggest highly polygonal territories.<br>Burkit (1924), however, described robins as requiring 90 yds of hedgerow, suggesting linear territories. | Usual-area polygons frequently of high eccentricity (section 3.4.1.). |
| Territory structure | Vegetation density within territories important for survival (Adriaensen & Dhondt 1990) and later reproductive success (Hoelzel 1988). Adriaensen & Dhondt (1990) describe some individuals as limiting the area they used to one bush of *Rhododendron*. | Robins defended varying numbers of core-nuclei which were of similar total area. Core-nuclei were located in bushes and shrubs, within which birds foraged. Birds were located in core-nuclei on an average of 78 % of occasions. Owners commuted between these foraging patches by using preferred flight paths which minimised the individual distances between core-nuclei. Sections 3.4.1.& 5.2.1. |
| Non-territoriality | Harper (1986) classified any widely ranging individual as non-territorial. | It was not possible to develop a universally applicable definition by which non-territorial individuals could be identified. Evidence suggested that they occupied ranges considerably larger than those of territorial robins. The ranges of non-territorial robins overlapped very little with the ranges of those that were territorial.<br>Sections 3.4.1.-3.4.3. |
| Territory fidelity | Lack (1940) describes territory boundaries as changing most often just prior to breeding.<br>Adriaensen & Dhondt (1984) qualitatively describe changes in the locations of territories as winter began. | Over short periods (days) territorial robins showed a high degree of fidelity to the core-nuclei they occupied, relative to the rapid range drift of nomadic non-territorial individuals. Over longer periods (months), some territorial robins showed a high degree of fidelity to the core-nuclei they occupied, while others displayed gradual directional territory drift. Section 3.4.2. |

Table 7.1. Continued.

| Subject | Summarised conclusions of previous studies | Conclusions from the present study |
|---|---|---|
| Neighbourhood structure | Territory boundaries usually depicted as being close-packed (Lack 1965; Fig.3.1.). | Usual-areas of neighbours separated by neutral interstices, in which birds were rarely located despite containing habitat features indistinguishable from those occupied by core-nuclei (section 3.4.3.). |
| Pattern of territory use | Only Burkit (1924) mentions the pattern of use of territories, describing it as follows;<br>"Where the habitat is a piece of hedge or hedges, the bird normally spends its day doing regular go from end to end of its estate". | The foraging patches in territories were visited in a regular sequence, following the predictions for an animal exploiting a renewing food supply. Robins commuted between their foraging patches by using preferred flight paths. Since the robins experienced shorter "giving-up" times in territories containing many small patches of a similar total area, the "return times" of all individuals were similar. Section 5.3. |
| Excursive activity and intruder pressure | Territory owners regularly intrude into the territories of immediate neighbours (Harper 1984). Intrusions by non-territorial individuals, however, represent the greatest threat to territory owners (Harper 1986). | Excursive activity was usually located in the neutral interstices between territories. Intrusions that did occur were targeted into the core-nuclei of near neighbours. Large territories experienced higher intruder pressure than small territories, although the duration of such intrusions were less. Sections 3.4.4.& 5.4. |
| Territory defense | Advertisement by song, ritualised display postures followed by aggressive evictions (Lack 1965), sometimes leading to death (Harper 1984).<br>Burkit (1924) and Adriaensen & Dhondt (1990) saw very little fighting during the winter. | Levels of territory advertisement and defense low compared to data in Harper (1986). Mutual display with no physical contact took place in the neutral interstices between territories. Playback results suggested territory owners were able to increase the effectiveness of territory defense by changing the temporal scheduling of visits to the foraging patches they used. Section 5.5. |
| A measure of territory size | Territory area, determined by a range of different definitions (Table 3.1.). Area was overestimated by 6-8 times due to the inclusion of neutral interstices between territories and the effects of territory drift not being considered. | The number of core-nuclei and linear-length were highly significantly correlated with energy expenditure while usual-area polygon was not, suggesting the concept of territories as a number of foraging patches linked by networks of preferred flight paths may be a better model of territory size than simple estimates of territory area. Section 6.4. |

### 7.2.3. Changes in territory over time.

During the non-breeding season, all territorial robins showed high fidelity to the grid-cells they occupied over the short term (days), compared to the nomadic space use of individuals classified as non-territorial. Over longer periods of time (months), however, some territorial robins appeared to show directional range drift; new core-nuclei being established and old ones abandoned, resulting in a constant prevailing range size. This behaviour may be a response to changes in the quality of foraging patches. For example, after the loss of leaves during October, the shelter from wind and rain provided by deciduous vegetation will decrease. The robins using them will therefore experience increased thermoregulatory costs. In such situations, robins would benefit from moving their defended foraging patches to habitat features which provide more shelter, such as dense evergreen bushes. It was unclear from the present study whether such behaviour involved the aggressive takeover of individual foraging patches used by other robins, or more passive responses to the movement or disappearance of neighbours.

The ability to establish and maintain a territory will have a profound influence on an individuals fitness (Howard 1983). Robins first establish territories during August (Lack 1965, present study). At this time juvenile robins, unlike adults which have already successfully over-wintered at least once, can have no knowledge of how the quality of foraging patches will change during the subsequent Autumn and Winter. It may be expected, therefore, that adults would be likely to establish territory networks containing evergreen vegetation, which will, based on previous experience, maximise their chances of surviving the next winter without further territory drift, even if such configurations are initially suboptimal. Juvenile robins, on the other hand, may be expected to select patches on a short term economic basis, such that the configurations of patches used are optimal only for current conditions. The consequences of such habitat selection by juveniles is that may need to modify their territory networks later in the Autumn as some of their foraging patches become uneconomic.

At the onset of the breeding season, signalled by the increase in vocalisations by males, females and some males adopt a nomadic non-territorial pattern of space use. In females this has been interpreted as facilitating mate selection (Harper 1985). Most males maintain normal territorial behaviour during this period, attracting females by virtue of their song (Hoelzel 1986). Some resident male robins, however, go through a brief period of pre-territorial behaviour characterised by frequent song, but with the nomadic behaviour similar to that of non-territorial birds during the Autumn and Winter. Such behaviour perhaps represents a final attempt, by rapid range drift, to increase territory quality sufficiently to support a female and attempt to rear a brood. Such pre-territorial wandering is also shown by migrant male robins which must search for a suitable location in which to establish a territory on returning to the breeding habitat.

Usual-areas occupied during breeding were not significantly different in size from those occupied during non-breeding, despite being used by both a male and female. The work described here represents the most northerly study of the robin to date. In more southerly populations in Britain, the spring song surge and establishment of pair territories takes place in early January (Lack 1965, Harper 1984), some six weeks earlier than in the present study. In such a situation, the pair members have been observed to use separate halves of the enlarged joint territory (Harper 1984). This suggests that each bird makes exclusive use of a number of foraging patches within the enlarged territory, perhaps cooperating in the eviction of challengers for territory occupancy. The delayed onset of breeding behaviour in the central Scottish population is possibly due to harsher weather in the early spring. Robins cannot manage to establish and maintain a joint territory before the onset of growth in vegetation and invertebrates, which occurs several weeks later in central Scotland than southern England (pers. obs.). It is perhaps this increase in quality of territories which allows males and females to both occupy a territory which could previously only support one bird.

Changes in the location of territories between years has been shown to be adaptive, leading to increases in area (Patersen & Best 1987), and/or reproductive success (Beletsky & Orians 1987). It would be useful to analyze the data relating to changes in territory networks obtained during the present study, to test the above hypotheses and to determine how territory drift within years contributes to increased fitness, in terms of over-winter survival and reproductive success.

### 7.2.4. A measure of territory size.

The values of territory area observed in the present study, as estimated by the usual-area, were considerably smaller than values suggested by previous studies. This was because the neutral interstices were previously included within territory boundaries, and the effects of territory drift were not considered. The network concept of territory structure, however, suggests that territory size viewed in terms of an area surrounded by a defended boundary may not be appropriate for the non-breeding robin. Furthermore, correlations between the three measures of territory size and energy expenditure suggest that the number of foraging patches defended and the total flight distance between patches, are better indicators of territory size. This provides further support for the idea of a territory as a number of defended foraging patches, between which owners commute by following a network of preferred flight paths which minimise individual distances. Many previous studies have tested hypotheses about territorial behaviour based on territory areas (eg Smith & Shugart 1987, Cave & Perdeck 1989). If this network concept of territory structure is universal among small birds occupying patchy habitats, then these results should be reconsidered in light of the findings of the present study.

Based on the network concept of territory structure and size, it may be possible, given details of a particular habitat, to predict the over-winter carrying capacity by measuring the number and area of individual bushes and shrubs, and the commuting distances required to exploit and defend different configurations. Furthermore, knowledge of a territorial individuals' specific requirements, in terms of habitat fragmentation and the quality of individual patches, may allow the manipulation of habitats to maximise the population size, survival or reproductive success.

## 7.3. The form of the energy cost constraint on territory size.

### 7.3.1. Predicted exploitation and defense costs.

The relationship between energy costs and territory size was best predicted by the assumptions of Model III, although Model II could not be rejected at the 10% level. For both models, the predicted line had an elevation of positive value. This indicated the existence of a maintenance cost incurred by all birds, similar to the cost constraint envisaged by Kodric-Brown & Brown (1978). The size of this maintenance cost was most sensitive to the cost of roosting overnight, reflecting the large proportion of the day spent at roost during mid-winter.

The energy cost of territory use in the robin was predicted to increase linearly with territory size, since investment in the component activities increased in a stepwise manner as the size of the territory network increased. The costs of evicting intruders were estimated to be negligible (section 6.2.1.). Even though the intruder pressure was observed to increase with network size (section 5.4.), at their greatest intensity intrusions were not sufficiently frequent to warrant inclusion in time/activity budgets. Consequently the energy cost constraint on territory use predicted by Model III may be considered to represent only the costs of territory exploitation.

If the time and/or energy costs of evicting intruders were larger, however, the form of the cost constraint would accelerate, following the cost constraint envisaged by Myers *et al* (1981). To illustrate this, eviction costs were modelled using literature values of the proportion of energy expenditure spent in defense. The E.E.$_{active}$ of a robin using a territory network of median size (four core-nuclei and a linear length of 60m) was increased by the mean and maximum values in table I of Walsberg (1983). The defense costs were adjusted for territories of larger and smaller size using the observed values of intruder pressure (section 5.4.). The results are presented in Table 7.2. and Fig.7.2. showing the two cost constraints are clearly accelerating. The effect of this would be to reduce the maximum territory size for which the energy costs of use are less then the energy benefits.

The results of the playback manipulations suggested, however, that robins could increase their investment in territory defense by changing the pattern in which they visit their core-nuclei (section 5.5.). Robins using small territories increased their commuting rate and therefore energy costs, while robins using large territories increased the randomness of the sequence in which they visited their foraging patches. The latter, therefore, may increase their level of territory defense without increasing their energy expenditure. This has similarities with the owner/satellite scenario in pied wagtails (Davies & Houston 1981), in which the response of territory owners to high intruder pressure is allow a temporary satellite individual to exploit the renewing food supply and contribute to territory defense. The owner incurs an energy cost in terms of reduced return times, but requires no increase in its own energy expenditure. Robins are perhaps unable to similarly share territory defense because low visibility prevents cooperating individuals from maintaining the same sequence of patch visits. Consequently, in response to very high intrusion rates, the cost constraint may maintain its linear form although the slope may decrease and the elevation increase. The reality of an accelerating cost function as territory size increases is therefore unconfirmed and may be unfounded.

It has been suggested that song in the robin plays a role in territory defense (Lack 1865). The robins for which measurements of energy expenditure were made did not vocalise. If vocalisation in the form of song formed a large part of the time/activity budget and song was a more costly activity than published estimates suggest (1.1 times cost of perched quietly; Ettinger & King 1980), then this may affect the parameters of the cost constraint. Since the

**Table 7.2.** The effect of an increased cost of evicting intruders on the from of the energy cost constraint, predicted by Model III, for non-breeding territoial robins. The effect on ADMR of using territories of different sizes was modelled based on two energy costs; +10% and +33% of $EE_{active}$ for a robin using a territory of median size (4 core-nuclei; Table 3.3.). These represent the mean and maximum values in table I of Walsberg (1983), and were used because accurate measurements of the energy cost and duration of individual evictions are not available (Riechert 1988). P(intruding) is an accellerating function with territory size (Fig.5.4.1.). The robins were assumed to evict all intruders, and the eviction cost was increased or decreased with territory size such that the cost was directly proportional to P(intruding).

| | **Eviction costs negligible** | | | | **Eviction costs additional 10% $EE_{active}$ for robin occupying median territory size** | | | | **Eviction costs additional 33% $EE_{active}$ for robin occupying median territory size** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. core-nuclei | | | | No. core-nuclei | | | | No. core-nuclei | | | |
| | 1 | 2 | 4 | 6 | 1 | 2 | 4 | 6 | 1 | 2 | 4 | 6 |
| $EE_{active}$ (kJ)# | 31.685 | 36.888 | 45.850 | 54.671 | 31.685 | 36.888 | 45.850 | 54.671 | 31.685 | 36.888 | 45.850 | 54.671 |
| $EE_{evictions}$ (kJ) * | 0 | 0 | 0 | 0 | 0 | 2.278 | 4.585 | 12.036 | 0 | 7.096 | 15.131 | 39.719 |
| $EE_{roost}$ (kJ)# | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 | 24.140 |
| DEE (kJ $day^{-1}$) | 55.825 | 61.028 | 69.990 | 78.811 | 55.825 | 63.306 | 74.575 | 90.847 | 55.825 | 68.124 | 85.121 | 111.530 |
| ADMR ($cm^3CO_2g^{-1}hr^{-1}$) | 4.512 | 4.932 | 5.656 | 6.369 | 4.512 | 5.116 | 6.027 | 7.342 | 4.512 | 5.505 | 6.879 | 9.579 |

\# Values from Table 6.12.

* Energy expended evicting intruders during active period. See Table 6.6. & 6.12. for definitions of the other measures of energy expenditure.

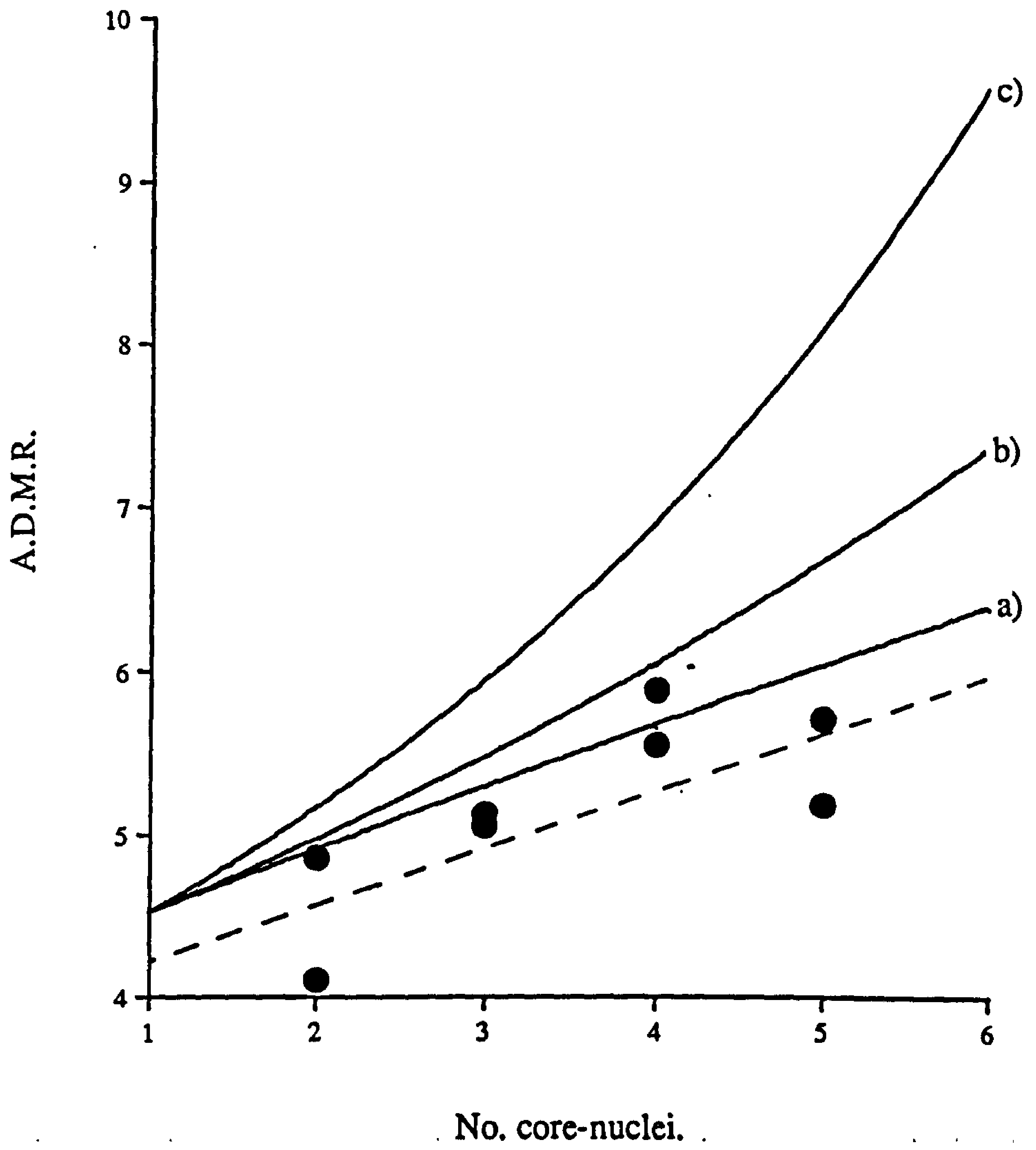


Fig.7.2. Energy cost constraints on territory size in the robin. For line (a) eviction costs were negligible. For line (b) eviction costs were an additional 10% $EE_{active}$, and for line (c) eviction costs were an additional 33% $EE_{active}$ for a robin occupying a territory of median size (see Table 7.2.). The dashed line indicates a linear regression fitted to the observed data.

vocalisations increased with territory size in a linear way (section 5.3.), the cost constraint would still follow a linear form. At present there are no studies in which the cost of fighting and evictions of intruders have been measured (Riechert 1988). Even if these activities were very energetically costly, their short duration (except during attempted territory takeovers; Harper 1984) would result in a very small effect on overall energy expenditure.

Stephens & Dunbar (1993) have used dimensional analysis to propose a cost constraint that decelerates with territory size. Considering the stepwise increase in exploitation costs with the number of foraging patches used and the observed increase in intruder pressure with number of patches, this is not appropriate in the robin.

### 7.3.2. The effects of territory shape.

The slope of the cost constraint in the robin was most sensitive to the cost of perch & drop foraging (Table 6.15.). This activity, although of relatively short duration in time/activity budgets, represents flight at speeds less than $V_{mp}$ and so has a very high energy cost, relative to the cost of the other component activities (Tatner & Bryant 1986).

The only parameter to change between territory networks containing similar numbers of foraging patches is the length of the foraging circuit (Table 6.1). Since the commuting costs, a component of total flight costs, are very small (0.2% $EE_{active}$ for median number of foraging patches) compared to the costs of perch & drop foraging (55.6% $EE_{active}$ for median number of foraging patches), the effects of network configuration and territory shape will be very small. The energy expenditure of robins using territories of ideal-polygonal configuration (low eccentricity $\epsilon$ and linearity L), therefore, will be only slightly less than that of robins using territories of ideal linear configuration (High $\epsilon$ and L).

### 7.3.3. Evidence from direct measurements of energy expenditure.

It was difficult to fully endorse one particular form for the energy cost constraint on territory size from the observed values of energy expenditure, because of the small number of measurements successfully completed. Since the data obtained on changes in patterns of use and intruder pressure with territory size prevent the possibility of a decelerating constraint, however, the observed data suggest the linear constraint predicted by the assumptions of Model III is most likely to be correct (Fig.7.2.). Nevertheless the eviction costs, even if very small as the data suggest, will result in a small degree of acceleration in the cost constraint, which would be difficult to detect even with a much larger sample size.

### 7.3.4. The effects of bird morphology.

The morphology of birds can have consequences for their behavioural ecology (Herrera 1978). Examples of this range from differences in food-niche width, for example variation in the bill length of the robin (Herrera 1978), to differences in foraging strategy, for example via wing-disc loadings and flight costs in hummingbirds (Feinsinger & Chaplin 1975).

In the present study of the robin, energy expenditure predicted from the assumptions of Model III could be shown to vary with the morphology of individuals, suggesting implications for their territorial behaviour. Robins of high body mass size or small wing span had associated higher wing-disc loadings and consequently higher flight costs (section 6.4.2.). The robin population exhibited natural variation in both of these characteristics (Appendix 10.). Therefore an association of morphology with territory size was predicted, generated by differences in the energy costs of using territories of the same size. It was suggested that an additional cause of this predicted association could be the existence of relationships between body size and dominance status. Correlational analysis provided support for the predictions. Consequently, although the slope of the energy cost constraint will vary slightly between individuals (Fig.6.5.), the slope of the population energy cost constraint will be slightly less than that for each individual, since robins occupying territories which are more costly to use are more likely to have adaptations which reduce their energy expenditure (Fig.6.8.).

It would be valuable to compare the morphology of robin populations from habitats of different patch structure, to see if natural selection has acted to adapt birds to the aerodynamic requirements for defending particular configurations of foraging patches. For example robins defending small, closely packed territories in the dense shrub layer of a lowland deciduous woodland may have higher wing-loadings than robins eking out an existence in sparsely populated upland coniferous forest. The possibility of high degrees of gene flow between robins occupying different but adjacent habitats may, however, result in any differences being negligible. Alternatively, inherent variability between robins allows individuals to distribute themselves appropriately between different habitat types.

Data from Cramp (1988) suggest the existence of a cline in wing-loading across the western Palaearctic (Table 7.3.); eastern robins having lower flight costs. Unlike robins from western Europe, these eastern populations are also predominately migratory (Cramp 1988),

**Table 7.3.** The geographical range, breast colour, wing chord, body mass and wingdisc-loading of the three races of the European robin which form an east-west cline in breast colour across the western Palaearctic (after Cramp 1988).

| Race | Range | Wing chord (mm)[#] | Body mass (g)[#] | Wingdisc-loading (g mm$^{-2}$)[$] | Breast colour |
|---|---|---|---|---|---|
| *melophilus* | Britain & Ireland | 73 (69-78) | 19.7 (15.5-25.3) | 0.000486 | Deep rufous orange |
| *rubecula* | Continental Europe & Asia Minor | 72 (68-77) | 17.7 (14.0-22.0) | 0.000441 | Orange, no full red tone |
| *tataricus* | Northwest Asia | 73 (70-78) | 16.3 (14.2-20.2) | 0.000403 | Faded orange |

[#] Mean and range of available data from the geographical range of each race (after Cramp 1988). All sample sizes >10.

[$] Wingdisc-loading equals body mass divided by $\pi(\text{wingspan}/2)^2$ (Feinsinger & Chaplin 1976), where wingspan was calculated from the equation in Table 2.13.

and this may be reflected in lower wing-loadings and reduced flight costs. Alternatively, eastern robins may occupy territories in poorer habitat, which requires more time in flight during exploitation and defense, for example many small and widely spaced foraging patches, lower prey densities or longer recovery times within patches. At present there are no data on territory size for robins living in eastern Europe and north west Asia. Furthermore, the problems inherent in measuring territories using common criteria makes a test of these hypotheses impossible here.

### 7.3.5. Implications for the cost constraint on territory size in the dipper.

The foraging strategies employed by dippers include walking/wading and diving (Bryant *et al* 1985, Bryant & Tatner 1988). The energy costs of these activities, at the same ambient temperature for which the activity costs of the robin were calculated, are shown in Table 7.4. Also shown are the average time budgets for each species during non-breeding territoriality. It is already apparent that, due to its relatively high cost, the time expended in perch & drop foraging in the robin has a profound impact on the slope of the energy cost constraint on territory size (Table 6.15.). The costs of commuting between foraging patches, in contrast, comprises a very small part of the total energy budgets. The energy costs of foraging (walking/wading and diving) in the dipper are considerably less than those of the robin, although this is to some extent offset by a greater time engaged in feeding activities (Table 7.4.). The energy cost of flight in the dipper is nearly 40% greater than that of the next most costly activity (Table 7.4.). Unlike the robin, however, flight is not used during foraging. Therefore, the cost of commuting between foraging patches might be expected to have a greater impact on the energy budget of the dipper.

Nevertheless, since like the robin, the usual-lengths occupied by non-breeding dippers all contained similar core-lengths (Fig 4.7.), the energy cost of territory exploitation would also be likely to increase in a linear manner with territory size, if inter-patch commuting distances were similar for all territories. The low levels of intrusions into dipper territories (section 4.2.4) suggests that eviction costs, like those of the robin, were negligible and unlikely to cause the overall cost constraint on territory size to accelerate.

Finally, male dippers are structurally larger and of greater body mass than females (Newton 1989). This has already been shown to have implications for DEE (Bryant & Tatner 1988), partially due to possible differences in their respective flight costs. Because of this, the

**Table 7.4.** Comparison between activity costs, as multiples of basal metabolic rate, and proportion of the active period engaged in different activities for robins and dippers at the same ambient temperature (6.8°C; Table 6.11.).

| **Robin** [#] | | | **Dipper** [$] | | |
|---|---|---|---|---|---|
| Activity | M* | % active period | Activity | M* | % active period |
| Perched quietly | 2.0 | 56 | Resting | 1.9 | 32 |
| Hopping | 3.3 | 13 | Walking/wading | 2.6 | 26 |
| Perch & drop | 22.5 | 11 | Diving | 6.2 | 38 |
| Flying | 22.5 | <1 | Flying | 8.5 | 4 |

[#] Activity categories from Table 6.2.; time budget for a robin using a territory containing the median number of foraging patches from Table 6.4.; activity costs from Table 6.11.

[$] Activity categories, activity costs and time budget from Bryant *et al* (1985).
The time budget represents a mean for the winter months.

[*] Metabolic intensity M equals activity cost as a multiple of basal metabolic rate.

energy cost constraint on territory size experienced by female dippers will have a slightly lower elevation and slope, enabling them to economically exploit and defend configurations of foraging patches that males, due to their greater energy demands, cannot.

## 7.4. Costs, benefits and the optimal territory.

### 7.4.1. The form of the benefit constraint.

Territoriality should be expected when the benefits of territorial behaviour are greater than the costs (Brown 1964). The constraint on benefits available with variation in size of territory used by the robin may take one of several forms (Table 7.5.). If the robin defends the constant resource territories of Stephens & Dunbar (1993), then the benefit constraint will take the form of a line of slope zero, the elevation representing the benefits in terms of energy gains required for continued existence (Constraint 1; Table 7.5.).

There was some evidence, however, that the total core area increased linearly with the number of foraging patches used (Fig.5.3.3.1.). Since the results from pit-fall trap catches suggested that prey density did not vary within or between patches (section 5.3.3.2.), the observed increase in total core area with number of foraging patches used will result in a corresponding increase in available energy benefits. This benefit constraint will be a linear function with positive slope (Constraint 2; Table 7.5.). The slope should equal that of the proportional change in total core area with number of patches used (Table 6.1.). This is because a territory which increases in core area by 10% will increase the number of prey items available per foraging circuit by 10% also.

For individual feeding territories, the benefit constraint in models of territorial behaviour has usually been described as a decelerating function with territory size. This is because benefits will increase at first and then level off as the prey availability becomes superabundant in relation to the animals needs (Kodric-Brown & Brown 1978, MacLean & Seastedt 1979, Myers *et al* 1981, Davies & Houston 1984)(Constraint 3; Table 7.5.).

In chapter 6. it was suggested that there was a constraint on the maximum daily energy expenditure of robins, which could explaine the occurrence of nomadic non-territorial individuals. Work in excess of this threshold (achieved when territory networks contain in excess of six core-nuclei) is possible, although individuals may incur costs such as loss of condition or increased predation risk (Drent & Dann 1980). Furthermore, this level of energy expenditure in the robin may be approached by any individual for short periods regardless of the size of territory occupied. For example those occupying small number of foraging patches

**Table 7.5.** Three possible forms for the benefit constraint on territory size in the robin and their associated assumptions.

| Form of the benefit constraint | Associated assumptions |
|---|---|
| **1.** Linear, with slope zero. | Territory networks containing different numbers of foraging patches provide the same total energy benefit (constant resource territories; Stephens & Dunbar 1993). |
| **2.** Linear, with slope positive. | Since there was no difference in the prey density within or between foraging patches of different size, energy benefit should be directly proportional to territory size and associated core area. |
| **3.** Decelerating. | Energy benefits will follow a decelerating function with increasing territory size and associated core area, since prey will eventually become super-abundant in relation to the individuals requirements (Kodric-Brown & Brown 1978, MacLean & Seastedt 1979, Myers *et al* 1981, Davies & Houston 1984). |

and responding to short periods of increased intruder pressure. This supposition allowed a further series of hypotheses to be formulated and tested.

It is possible, however, that the occurrence of non-territorial individuals is due to the energy costs of using a range of a size in excess of six core-nuclei being greater than the energy gains provided by its territorial defense. Under this assumption it is possible to illustrate the role of the cost constraint in the determination of optimal territory size.

### 7.4.2. The currency optimised.

The possible benefit constraints are shown diagrammatically in relation to the form of the cost constraint measured using the doubly labelled water technique in Fig.7.3. Also shown is the observed frequency distribution of territory sizes, measured by the number of foraging patches used. Optimal territory sizes under different currencies are indicated in Fig.7.3. and summarised in Table 7.6. to illustrate how the cost and benefit functions may be used to predict territorial behaviour. The maximum territory size observed in the robin was six foraging patches. If it was assumed that this represented the point at which costs exceeded benefits and territorial behaviour was no longer economically sustainable, then only robins that are maximising their net energy benefits under benefit Constraint 3 would occupy territories that resemble the observed median territory size (Fig.7.3.).

Robins were observed to occupy a range of territory sizes around the median, and presumably optimum value. It may be that only a few individuals managed to optimise territory size, or, as the morphological data may suggest, a broad range of optima exist, which most birds manage to achieve. Observed territory size will still be normally distributed since more individuals will be of average rather than unusual morphology. This possibility has been suggested previously (Stamps *et al* 1987, Mares & Lachter 1987, Schoener 1987). Other reasons for the existence of such "optimal surfaces" (Schoener 1987) may include habitat geometry; intruder pressure may depend on the position of the territory in an insular habitat patch (Stamps *et al* 1987), and variation in cost and benefit constraints over time (Mares & Lachter 1987).

### 7.4.3. Non-economic costs and benefits.

Up to this point, the costs of territory exploitation and defense have been considered purely in terms of energy expenditure. The exploitation and defense of territories, however,

**Fig.7.3.** Diagrammatic cost/benefit models of territory size compared to the observed distribution of territory sizes in the robin.

In (a) are shown alternative benefit constraints 1 (thin horizontal line) and 2 (thin line of positive slope)(Table 7.5.). In (b) is shown the remaining possible benefit constraint 3.(Table 7.5.). The cost constraint predicted by Model III is represented by the thick line throughout.

In (a) the slope of benefit constraint 2 is greater than that of the cost constraint since the proportional change in total core area as the number of foraging patches changes (Table 6.1.) is greater then the proportional change in energy expenditure predicted by Model III.(Table 6.12.). Lower case roman numerals correspond with those in Table 7.6.

For comparison in (c) is shown the observed distribution of territory sizes in the robin as measured by the number of foraging patches used.

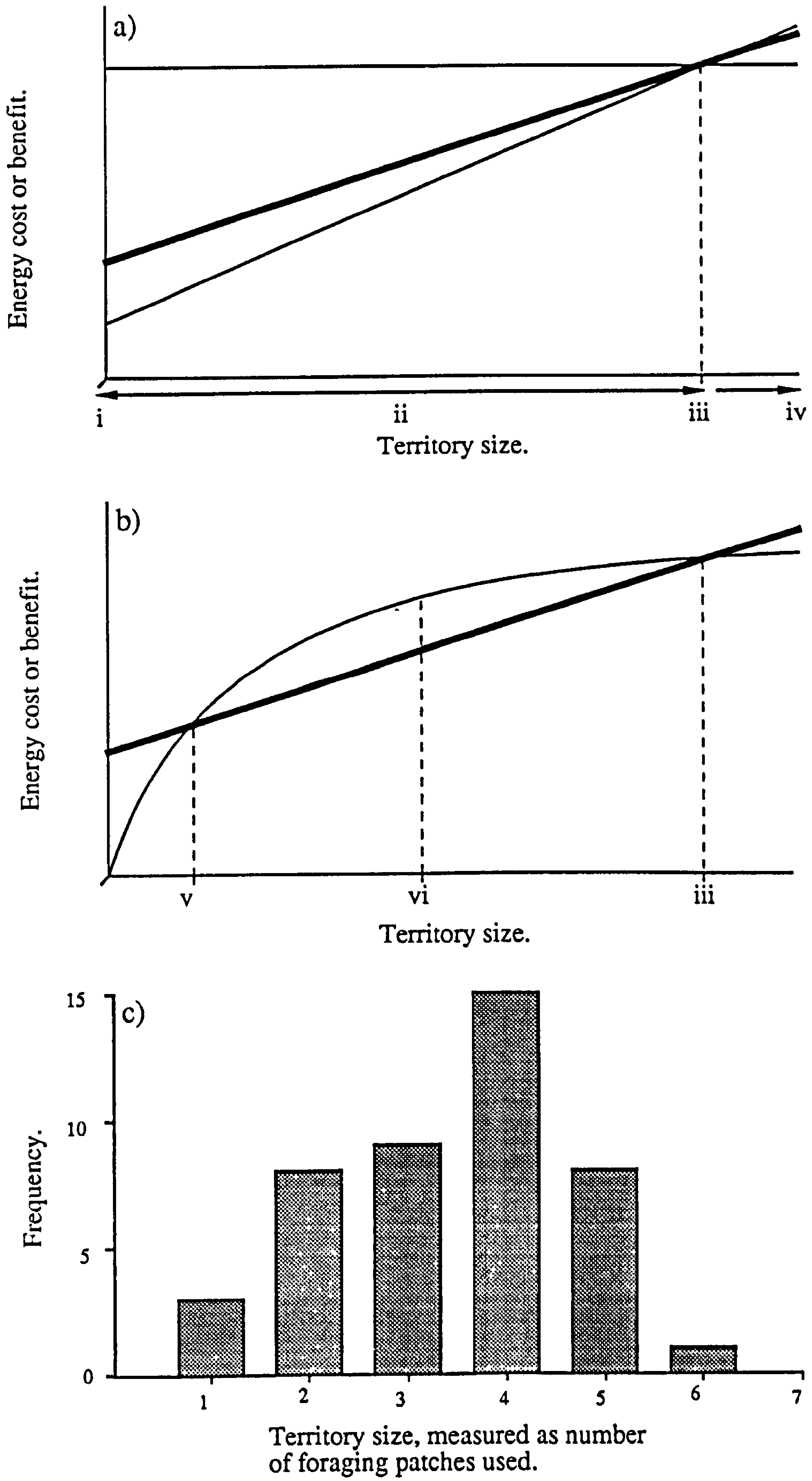

a)
Energy cost or benefit.
i
ii
iii
iv
Territory size.
b)
Energy cost or benefit.
v
vi
iii
Territory size.
c)
Frequency.
15
10
5
0
1
2
3
4
5
6
7
Territory size, measured as number of foraging patches used.

**Table 7.6.** The relative optimal territory size under different currencies from Fig.7.3. The three proposed benefit constraints are described in Table.7.5. The cost constraint was linear, following Model III and direct measurements of free-living energy expenditure. Lower case roman numerals correspond to territory sizes indicated in Fig.7.3.

| **Form of benefit constraint** | **Relative territory size when optimising different currencies** | | |
|---|---|---|---|
| | Cost minimisation | Benefit maximisation | Net benefit maximisation |
| **1.** Linear, slope zero | Zero (i) | Range of sizes (ii) | Zero (i) |
| **2.** Linear, slope positive | Large (iii) | Infinite (iv) | Infinite (iv) |
| **3.** Decelerating | Small (v) | Large (iii) | Intermediate (vi) |

may also involve non-economic costs (Davies 1980). These are costs which cannot be measured in terms of time or energy. Such non-economic costs may affect territorial behaviour in a number of ways.

All individuals, in the course of daily territory exploitation and defense, may experience non-economic costs such as risk of dying during some necessary activity. It is already apparent that the commuting movements between foraging patches represent a very small proportion of $EE_{active}$. Such movements across the open spaces between patches may nevertheless carry a very high cost in the form of predation risk. Sparrowhawks can fly faster than robins (Newton 1986), and given a long enough pursuit would be able to capture them in flight. There is evidence that robins minimise the lengths of individual commuting distances between patches, by using configurations of patches in a highly linear manner even though this increases the total length of foraging circuits (section 5.3). Furthermore, robins are more likely to use "short cuts" between patches if they do not require flights over distances much greater than average (section 5.3.). Furthermore, since robins occupying large territory networks must commute between patches more often, they will experience increased predation risk in addition to increased energy costs. To some extent this may be offset by lower wingloading, since they will reduce flight costs and possibly increase an individuals ability to flee from an attack. Robins may attempt territory defense by resource depression rather than aggressive eviction of intruders. An advantage of this may be the minimisation of another form of risk. This is the possibility of injury during interactions with conspecifics. Any injuries sustained may compromise an individuals fitness (Arcese 1987). Nevertheless, for the goal of territory occupancy, robins may even risk the possibility of the ultimate cost of being killed during territorial interactions (Harper 1984).

The occupation and maintenance of a territory requires experience in the form of resource holding potential (Parker 1974). When robins establish new defended foraging patches, during either initial territory establishment or as a result of territory drift, some of the costs incurred may be non-economic. For example, the assimilation of experience of the local habitat and neighbouring territory occupants may be an important factor in determining success (Smith 1978, Yasukawa 1979 Stamps 1987).

Robins are the host of a wide range of external and internal parasites (Mead 1984). Individuals in the present study were frequently observed to carry mites, fleas and Hippoboscid flies externally. A cost of occupying a large number of foraging patches spread over a large total flight distance may increase the chances of contracting such parasites if they are randomly distributed through the habitat. Since robins are only likely to encounter parasites during foraging (infective stages laying dormant in leaf litter or bird faeces, invertebrate prey items acting as intermediate hosts), the effects of this cost on territory configurations will be minimal.

The breast patch colour of the robin varies between individuals (Cramp 1988). Examples of the range of colour present in the central Scottish population are shown in Plate 7.1. It has been suggested that conspicuous plumage signals of status will evolve when there is interference competition for resources and repeated confrontations between individuals (Rohwer 1982). The ultimate source of differences in status is differences in aggression and fighting ability. A high fighting ability will allow an individual to dominate and displace conspecifics in competitive interactions. A dominant individual therefore benefits from exclusive access to, for example, territories of high quality. It has been suggested that development of extent or colour of the plumage badge is controlled by the same gene or gene group that endows some individuals with superior fighting ability, such that the two are correlated (Rohwer 1982). Consequently, individuals of unequal status competing for limited resources need not risk accidental injury or waste energy assessing the relative fighting ability of opponents (Parker 1974, Rohwer 1982). Support for this hypothesis has since been demonstrated (Jarvi & Bakken 1984, Studd & Robertson 1985, Moller 1987). Alternatively, differences in breast colour may simply be a result of differences in diet quality during growth (Slagsvold & Lifjeld 1985); a redder breast signalling high quality parental provisioning. Furthermore, it has been suggested that plumage brightness may reliably signal parasite load (Hamilton & Zuk 1982). Birds with low parasite loads are fitter and signal this by brighter plumage. Evidence supporting this hypothesis has since been produced (Read 1987).

During encounters between robins, the participants initially adopt postures that present the maximum area of orange breast patch to the opponent, sometimes associated with swaying from side to side, the erection of orange feathers on the throat and song (Lack 1965, Cramp 1988). At this point, if on a territory, one birds normally retreats, failure to do so initiating physical contact. Many interactions, however, occurred in the neutral interstices between territories, and involved display but no aggression. The song of the robin facilitates individual recognition (Brindley 1991). Therefore, the interactions outside territories, usually involving

**Plate 7.1.** Comparison between the breast colour of two robins which formed part of the sample collected for body composition analysis. The individual on the left was adult female F646424, breast colour score 6.0. The individual on the right was juvenile male A27, breast colour score 2.5 (see Appendix 11. for methodology of breast colour scoring).

neighbours, possibly represent dyads of birds learning to identify each other on the basis of plumage differences, so that song subsequently heard from hidden neighbours can be associated with a particular breast colour and competitive ability.

The breast colour of robins could be scored in live birds using a custom made colour chart. Preliminary results with this colour chart suggested adults were significantly redder than juveniles, and females were significantly redder than males (Appendix 11.). Acrese & Smith (1985) found that age and sex had the most profound effect on dominance. It is possible that the variation in the breast colour of robins similarly functions as a signal of dominance, both between and within age and sex classes.

Across the western Palaearctic there is a cline in breast colour in the robin (Cramp 1988). Robins along the western seaboard of Europe being redder then robins in northwest Asia (Table 7.3.). It would be valuable to investigate the function of this difference. Possibly eastern robins must exist on diets which are deficient in particular pigments or minerals. Alternatively, perhaps individuals in the eastern part of their geographic range are less aggressive, as an adaptation to living in poor habitat where a large investment in aggressive interactions would reduce the time available for foraging.

The most dominant robins in the population would be expected, by virtue of their dominant status, to monopolise optimal territories. Subordinate robins, therefore, may be forced to occupy territories that are larger or smaller than their individual optima, as dictated by their morphology. This second kind of non-economic cost will bare differently on different individuals. The role of plumage variability in the life of the robin, and its consequences for patterns of territory occupancy represents a promising and ongoing area of research.

## 7.5. Conclusions.

This work represents one of the first large-scale radio-tracking studies of small birds in winter. Coupled with the doubly-labelled water technique for measuring free-living energy expenditure, radio-tracking proved to be a powerful technique for determining both what features small birds use in their habitat, the temporal scheduling with which they are visited and the energy costs incurred.

Territorial behaviour is one of the most conspicuous activities of many birds. Ownership of a fixed area, usually surrounded by a clearly defined boundary, is proclaimed with vocalisations, displays and escalated fighting (Kaufmann 1983). The techniques used by the present study have allowed this concept to be rigorously tested for the first time. Some of the previous ideas about territory structure and patterns of territory exploitation and defense have been found inadequate to describe observed territorial behaviour in non-breeding robins.

The primary aim of this study was to assess the reality and form of the energy cost constraint on territory size. Data for the robin suggested a cost constraint of linear form, although exceptionally high investment in evicting intruders would cause the constraint to accelerate overall.

There are insufficient data to endorse any particular energy benefit function for non-breeding territorial robins. More studies are required of foraging behaviour in the robin, in addition to studies of patterns of prey availability, depletion and subsequent recovery, in relation to the use of defended networks of foraging patches. This information would allow the form of the benefit constraint on territory size to be verified, whereupon it may then be possible to construct a complete energy model for the territorial behaviour of the robin. This could then be assessed in the field to examine; a) the extent to which real individuals, which also experience non-economic costs and benefits, depart from the predictions; and b) the extent to which the economic and non-economic factors determining territorial behaviour influence overwinter survival both at the level of the individual and the population.

# Chapter 8.

# Bibliography.

Adriaensen F. & Dhondt A.A. (1983). Dynamics of a robin *Erithacus rubecula* population outside the breeding season. **Bird Study** 31 69-75.

Adriaensen F. & Dhondt A.A. (1984). Dynamics of a robin population outside the breeding season. **Bird Study** 31 69-75.

Adriaensen F. & Dhondt A.A. (1990). Territoriality in the continental European robin *Erithacus rubecula*. **Ardea** 78 459-465.

Aldridge H.D.J.N. & Brigham R.M. (1988). Load carrying and manouverability in an insectivorous bat: a test of the 5% rule of radio-telemetry. **J. Mammology** 69 379-382.

Alves M-A.S. & Johnstone I.G. (In press). Radio-tracking small aerial foraging birds: a preliminary study of the sand martin *Riparia*. **Avocetta.**

Anderson D.E. & Rongstad O.J. (1989). Home-range estimates of red-tailed hawks based on random and systematic relocations. **J. Wildl. Manage.** 53 802-807.

Arcese P. & Smith J.N.M. (1985). Phenotypic correlates and ecological consequences of dominance in song sparrows. **J. Anim. Ecol.** 54 817-830.

Arcese P. (1987). Age, intrusion pressure and defense against floaters by territorial male song sparrows. **Anim. Behav.** 35 773-784.

Arnold S.J. (1988). Behaviour, energy and fitness. **Amer. Zool.** 28 815-827.

Aschoff J. & Pohl H. (1970). Der Ruheumsatz von Vogeln als Funktion der Togeszeit und der Korpergrosse. **J. Ornithol.** 111 38-47.

Atum (1868). Der Vogel und sein Leben. Munster, Niemann. Translated by Mayer E.(1935). **Proc. Linn. Soc. New York.** 45-46 1-15.

Bakus G.J. (1959). Territoriality, movement and population density of the dipper in Montana. **Condor** 61 410-425.

Beletsky L.D. & Orians G.H. (1987). Territoriality among male redwinged blackbirds: I. Site fidelity and movement patterns. **Behav. Ecol. Sociobiol.** 20 21-34.

Beletsky L.D. (1992). Social stability and territory acquisition in birds. **Behaviour** 123 290-313.

Biebach H. (1983). Genetic determination of partial migration in the European robin. **Auk** 100 610-606.

Birkhead T.R. & Moller A.P. (1990). *Sperm Competition in Birds.* Academic Press, London.

Boag P.T. (1983). The heritability of external morphology in Darwin's ground finches *Geospiza* on Isla Daphne Major, Galapagos. **Evolution** 37 877-894.

Brander R.B. & Cochran W.W. (1969). In *Wildlife Management Techniques.* Ed. by Giles R.H. Washington D.C. Wildlife Soc.

Brigham R.M. (1989). Effects of radio-transmitters on the foraging behaviour of barn swallows, *Hirundo rustica.* **Wilson Bull.** 101 505-506.

Brindley E.L. (1991). Response of European robins *Erithacus rubecula* to playback of song: neighbour recognition and overlapping. **Anim. Behav.** 41 503-512.

Brody S. (1945). *Bioenergetics and Growth: with Special Reference to the Efficiency Complex in Domestic Animals.* Hafner.

Brown J.K. (1969). Territorial behaviour and population regulation in birds: a review and re-evaluation. **Wilson Bull.** 81 293-329.

Brown J.L. (1964). The evolution of diversity in avian territorial systems. **Wilson Bull.** 76 160-169.

Brown J.L. & Orians G.H. (1970). Spacing patterns in mobile animals. **Ann. Rev. Ecol. System.** 1 239-262.

Bryant D.M. Hails C.J. & Prys-Jones R. (1985). Energy expenditure by free-living dippers in winter. **Condor** 87 177-186.

Bryant D.M. Hails C.J. & Prys-Jones R. (1985). Energy expenditure by free-living dippers *Cinclus* in winter. **Condor** 87 177-186.

Bryant D.M. & Tatner P. (1988). Energetics of the annual cycle of dippers. **Ibis** 130 17-38.

Bryant D.M. & Tatner P. (1988). Energetics of the annual cycle of dippers *Cinclus cinclus.* **Ibis** 130 17-38.

Bryant D.M. (1989). Determination of respiration rates of free-living animals by the doubly-labelling technique. In *Toward a More Exact Ecology.* Ed. by Grubb P.J.& Whittaker J.B. Blackwell, Oxford.

Bryant D.M. & Tatner P. (1991). Intraspecies variation in avian energy expenditure: correlates and constraints. **Ibis** 133 236-245.

Burkitt J.P. (1924). A study of the robin by means of marked birds. **Brit. Birds** 26 294-303.

Burton R. (1990). *Bird Flight: An Illustrated Study of Birds' Aerial Mastery.* Facts on File, Oxford.

Caccamise D.F. & Hedin R.S. (1985). An aerodynamic basis for selecting transmitter loads in birds. **Wilson Bull.** 97 306-318.

Calvo B. & Furness R.W. (1992). A review of the use and effects of marks and devices on birds. **Ring. Migr.** 13 129-151.

Carpenter C.R. (1934). A field study of the behaviour and social relations of the howling monkey *Aloualta palliata.* **Comp. Psychol. Monogr.** 10.

Carpenter C.R. (1958). Territoriality: a review of concepts and problems. In *Behaviour and Evolution*, Ed. by Roe A.& Simpson G.G. Yale Uni. Press.

Carpenter F.L. & MacMillen R.E. (1976). Energetic cost of feeding territories in an Hawaiian honeycreeper. **Oecologica** 26 213-223.

Carpenter F.L. Hixon M.A. Temeles E.J. Russell R.W. & Paton D.C. (1993). Exploiive compensation by subordinate age-classes of migrant rufous hummingbirds. **Behav. Ecol. Sociobiol.** 33 305-312.

Carpenter F.L. Hixon M.A. Russell R.W. Paton D.C. & Temeles E.J. (1993). Interference asymmetries among age-sex classes of rufous hummingbirds during migratory stopovers. **Behav. Ecol. Sociobiol.** 33 297-304.

Cave A.J. & Perdeck A.C. (1990). Size and quality of the coot territory in relation to age of its tennants and neighbours. **Ardea** 77 87-98.

Chantry D.F. & Workman L. (1984). Song and plumage effects on aggressive display in the European robin. **Ibis** 126 366-371.

Charnov E.L. Orians G.H. & Hyatt K. (1976). Ecological implications of resource depression. **Amer. Nat.** 110 247-259.

Cochran W.W. (1980). Wildlife telemetry. In *Wildlife Techniques Manual* (4th Ed.). Wildlife Soc., Washington D.C.

Cousins S.A. (1985). Non-breeding of dippers, *Cinclus cinclus*, and the influence of environmental conditions on their behaviour. Unpublished Honours Thesis, University of Stirling.

Cramp S. (1988). *Birds of the Western Palaearctic Vol.V.* Oxford Uni. Press, Oxford.

Cresswell B.H. & Summers R.W. (1988). A study of breeding purple sandpipers *Calidris maritima* on the Hardanger-vidda using radio-telemetry. **Fauna. Norv. Ser. C. Cinclus.** 11 1-6.

Cuthill I.C. & Macdonald W.A. (1990). Experimental manipulation of the dawn and dusk chorus in the Blackbird, *Turdus merula.* **Behav. Ecol. Sociobiol.** 26 209-216.

Davenport C. (1983). Non-breeding territoriality and the influence of environmental conditions on the distribution and behaviour of the dipper, *Cinclus cinclus.* Unpublished Honours Thesis, University of Stirling.

Davies N.B. (1976). Food, flocking and territorial behaviour of the pied wagtail *Motacilla alba yarrellii* in winter. **J. Anim. Ecol.** 45 235-253.

Davies N.B. (1978). Ecological questions about territorial behaviour. Ch.11 In *Behavioral ecology an Evolutionary Approach.* Ed. Krebs J.R. & Davies N.B. Blackwell Scientific Publications.

Davies N.B. (1980). The economics of territorial behaviour in birds. **Ardea** 68 63-74.

Davies N.B. & Houston A.I. (1981). Owners and satellites: the economics of territory defense in the pied wagtail. **Ecology** 50 157-180.

Davies N.B. & Houston A.I. (1984). Territory economics. In *Behavioral Ecology: an evolutionary approach,* Ed. by Krebs J.R.& Davies N.B. Blackwell, Oxford.

Davies N.B. & Lundberg A. (1984). Food distribution and a variable mating system in the dunnock *Prunella modularis.* **J. Anim. Ecol.** 53 895-912.

Dhondt A.A. (1966). A method to establish the boundaries of bird territories. **Le Gerfault** 56 404-408.

Dill L.M. (1978). An energy based model of optimal feeding territory size. **Theor. Pop. Biol.** 14 396-429.

Dixon R.K. & Chapman J.A. (1980). Harmonic mean measure of animal activity areas. **Ecology** 61 1040-1044.

Doncaster C.P. (1990). Non-parametric estimates of interaction from radio-tracking data. **J. Theor. Biol.** 143 431-443.

Doncaster C.P. & MacDonald D.W. (1992). Drifting territoriality in the red fox *Vulpes.* **J. Anim. Ecol.** 60

Drent R.H. & Daan S. (1980). The prudent parent: energetic adjustments in avian breeding. **Ardea** 68 225-252.

Eason P. (1992). Optimization of territory shape in heterogeneous habitats: a field study of the red-capped cardinal *Paroaria gularis.* **J. Anim. Ecol.** 61 411-424.

East M. (1980). Sex differences and the effect of temperature on the foraging behaviour of robins. **Ibis** 122 517-520.

East M. (1982). Time budgeting by European robins: inter and intrasexual comparisons during Autumn, Winter and early Spring. **Ornis. Scand.** 13 85-93.

East M.L. & Hoffer H. (1986). The use of radio-tracking for monitoring great tit behaviour: a pilot study. **Ibis** 128 103-114.

Emlen J.T. (1957). Defended area: a critique of the territory concept and of conventional thinking. **Ibis** 99 352.

Erington P.L. (1946). Predation and vertebrate populations. **Q. Rev. Biol.** 21 144-177.

Ettinger A.O. & King J.R. (1980). Time and energy budgets of the willow flycatcher (*Empidonax trailii*) during the breeding season. **Auk** 97 533-546.

Ewald P.W. & Carpenter F.L. (1978). Territorial responses to energy manipulations in the anna hummingbird. **Oecologica** 31 277-292.

Exo K.-M. Eggers U. Laschefski-Sievers R. & Scheiffarthl G. (1992). Monitoring activity patterns using a microcomputer-controlled radio-telemetry system, tested for waders as an example. In *Wildlife Telemetry: Remote Monitoring and Tracking of Animals* Ed by Priede I.G. & Swift S. Ellis Horwood, Chichester.

Freeman S. & Jackson W. (1990). Univariate metrics are not adequate to measure avian body size. **Auk** 107 69-74.

Feinsinger P. & Chaplin S.B. (1975). On the relationship between wingdisc loading and foraging strategy in hummingbirds. **Am. Nat.** 109 217-224.

Ford R.G. & Krumme D.W. (1979). The analysis of space use patterns. **J. Theor. Biol.** 76 125-155.

Furmann M. & Seitz A. (1992). Nocturnal activity of the brown long-eared bat *Plecotus auritus*: data from radio-tracking in the Lenneberg Forest near Mainz, Germany. In *Wildlife Telemetry: Remote Monitoring and Tracking of Animals*. Ed. by Priede T.G.& Swift S.M. Ellis Horwood, Chichester.

Garson P.J.& Hunter M.L. (1979). Effects of temperature and time of year on the singing behaviour of wrens and great tits. **Ibis** 121 481-487.

Gettinger R.D. (1983). The use of doubly labelled water ($^3HH^{18}O$) for determination of $H_2O$ flix and $CO_2$ production by a mammal in a humid environment. **Oecologica** 59 54-57.

Gibb J. (1956). Food, feeding habits and territory of the rock pipit. **Ibis** 98 509-530.

Gill F.B. & Wolf L.L. (1975). Economics of feeding territoriality in the goldenwinged sunbird. **Ecology** 56 333-345.

Goldberg T.L. & Ewald P.W. (1991). Territorial song in the anna's hummingbird *Calyptie anna*: costs of attraction and benefits of deterrence. **Anim. Behav.** 42 221-226.

Grajetsky (1993). Feeding ecology of adult robins *Erithacus rubecula* in a hedgerow habitat. **J. Fur. Ornith.** 134 13-22.

Grant P.R. (1969). Polyhedral territories of animals. **Am. Nat.** 102 75-80.

Grieg-Smith P.W. (1985). Winter survival, home-ranges and feeding of first year and adult bullfinches. In *Behavioral Ecology: ecological consequences of adaptive behaviour.* Ed. by Sibly R.M.& Smith R.H. Blackwell, Oxford.

Hamilton W.D. (1970). Selfish and spiteful behaviour in an evolutionary model. **Nature** 228 1218-1220.

Hamilton W.D. & Zuk M. (1982). Heritable true fitness and bright birds: a role for parasites? **Science** 218 384-387.

Hanski I.K. & Haila Y. (1988). Singing territories and home ranges of breeding chaffinches: visual observations vs. radio-tracking. **Ornis. Fennica** 65 97-103.

Hanski I.K. & Laurila A. (1993). Male chaffinches do not enlarge their territories to prevent cuckoldry. **Anim. Behav.** 46 1036-1038.

Harper D.G. (1984). The energetics of territoriality in the European robin *Erithacus rubecula.* Unpublished Ph.D. Thesis, University of Cambridge.

Harper D.G. (1985). Pairing strategy and mate choice in female robins. **Anim. Behav.** 33 862-875.

Harper D.G. (1986). The robin. In *The Atlas of Wintering Birds of Britain and Ireland.* Comp. by Lack P. T.& A.D.Poyser.

Harris S. Cresswell W.J. Forde P.G. Trewhella W.J. Wollard T. & Wray S. (1990). Home-range analysis using radio-tracking data: a review of problems and techniques particularly as applied to the study of mammals. **Mammal Rev.** 20 97-123.

Herrera C.M. (1978). Individual dietary differences associated with morphological variation in robins, *Erithacus rubecula.* **Ibis** 120 542-545.

Hewson R. (1969). Roosts and roosting habits of the dipper. **Bird Study** 16 89-100.

Hinde R.A. (1956). The biological significance of the territories of birds. **Ibis** 98 340-369.

Hixon M.A. Carpenter F.L. & Paton D.C. (1983). Territory area, flower density and time budgeting in hummingbirds: an experimental and theoretical analysis. **Am. Nat.** 122 366-391.

Hoelzel A.R. (1986). Song characteristics and response to playback of male and female robins *Erithacus rubecula.* **Ibis** 128 115-127.

Hoelzel A.R. (1989). Territorial behaviour of the robin: the importance of vegetation density. **Ibis** 131 432-436.

Hogstad O. (1988). Rank related resource access in winterflocks of willow tits *Parus montanus*. **Ornis. Scand.** 19 169-174.

Holley A.J.F. (1993). Do brown hares signal to foxes? **Ethology** 94 21-30.

Houston A.I. & McNamara J.M. (1993). A theoretical investigation of the fat reserves and mortality levels of small birds in winter. **Ornis. Scand.** 24 205-219.

Howard R.D. (1983). Sexual selection and variation in reproductive success in a long-lived organism. **Am. Nat.** 122 301-325.

Jackson R.D. (1958). A study of a population of robins *Erithacus rubecula.* **Irish Naturalists Journal** 12 1-8.

Jarvi T. & Bakken M. (1984). The function of the variation in the breast stripe of the great tit *Parus major.* **Anim. Behav.** 32 590-596.

Jennrich R.I. & Turner F.B. (1969). Measurement of non-circular home-range. **J. Theor. Biol.** 22 227-237.

Johnson G.D. Pebworth J.L. & Krueger H.O. (1991). Retention of transmitters attached to passerines using a glue-on technique. **J. Field Ornithol.** 62 486-491.

Kacelnik A. Houston A.I. & Krebs J.R. (1981). Optimal foraging and territorial defense in the Great Tit. **Behav. Ecol. Sociobiol.** 8 35-40.

Kacelnik A. & Krebs J.R. (1982). Optimal foraging and teritorial defense in the great tit *Parus major.* **Behav. Ecol. Sociobiol.** 8 35-40.

Karlsson L. Persson K. & Waninder G. (1986). Age criterions in robins *Erithacus rubecula.* **Anser** 25 15-28.

Kaufmann J.H. (1983). On the definitions and functions of dominance and territoriality. **Biol. Rev.** 58 1-20.

Kenward R. (1987). *Wildlife Radio-tagging: Equipment, Field Techniques and Data Analysis.* Academic Press, London.

Kenward R. (1990). *Ranges IV: Software for Analysing Animal Location Data.* Institute of Terrestrial Ecology, Wareham.

Kenward R.E. (1982a). Techniques for monitoring the behaviour of grey squirrels by radio. In *Telemetric Studies of Vertebrates.* Ed. by Cheeseman C.L.& Mitson R.B. Academic Press, London.

Kenward R.E. (1982b). Goshawk *Accipiter gentilis* hunting behaviour and range size as a function of food and habitat availability. **J. Anim. Ecol.** 51 69-80.

Kenward R.E. (1992). Quantity versus quality: programmed collection and analysis of radio-tracking data. In *Wildlife Telemetry: Remote Monitoring and Tracking of Animals.* Ed. by Priede T.G.& Swift S.M. Ellis Horwood, Chichester.

Kirkwood J.K. (1983). A limit to metabolisable energy intake in mammals and birds. **Comp. Biochem. Physiol.** 75A 1-3.

Klaassen M. Becker P.H. & Wagner M. (1992). Transmitter loads do not effect the daily energy expenditure of nesting common terns. **J. Field Ornith.** 63 181-185.

Knapton R.W. & Krebs J.R. (1974). Settlement patterns, territory size and breeding density in the song sparrow. **Can. J. Zool.** 52 1413-1420.

Kodric-Brown A. & Brown H.J. (1978). Influence of economics, interspecific competition and sexual dimorphism on territoriality of mogrant rufous hummingbirds. **Ecology** 59 285-296.

Korn G.A. & Korn T.M. (1968). *Mathematical Handbook for Scientists and Engineers: Definitions, Theorems and Formulas for Reference and Review,* 2nd Ed. McGraw-Hill.

Krebs J.R. (1971). Territory and breeding density in the great tit. **Ecology** 52 2-22.

Krebs J.R. (1977). Song and territory in the great tit *Parus major.* In *Evolutionary Ecology.* Ed. by Stonehouse B.& Perrins C. MacMillan.

Krebs J.R. (1982). Territorial defense in the great tit: do residents always win? **Behav. Ecol. Sociobiol.** 11 185-194.

Krebs J.R. & Cowie R.J. (1976). Foraging strategies in birds. **Ardea** 64 98-116.

Krebs J.R. & Davies N.B. (1987). *An Introduction to Behavioral Ecology* 2 Blackwell, Oxford.

Lack D. (1940). The behaviour of the robin: population changes over four years. **Ibis** 82 299-234.

Lack D. (1948). Notes on the ecology of the robin. **Ibis** 90 252-279.

Lack D. (1965). *The Life of the Robin*. Witherby.

Lifson N. Gordon G.B. Visscher M.B. & Nier A.O. (1949). The fate of utilised molecular oxygen of respiratory carbon dioxide, studies with the aid of heavy oxygen. **J. Biol. Chem.** 180 803-811.

Lifson N. & McLintock R. (1966). Theory of use of the turnover rates of body water for measuring energy and material balance. **J. Theor. Biol.** 12 46-74.

Logie J. (in press). Effects of stream acidity on non-breeding dippers, *Cinclus cinclus*, in the south-cental highlands of Scotland. **Aquatic Conservation.**

MacLean S.F. & Seastedt T.R. (1979). Avian territoriality: sufficient resources or interference competition. **Am. Nat.** 114 308-312.

Mares M.A. & Lacher T.E. (1987). Social spacing in small mammals: patterns of individual variation. **Amer. Zool.** 27 293-306.

Marcström V. & Kenward R. (1981). Sexual and seasonal variation in condition and survival in Swedish goshawks *Accipiter gentilis*. **Ibis** 123 311-327.

McLaren I.A. (1972). Polygyny as the adaptive function of breeding territory in birds. **Trans. Connecticut Acad. Arts Sci.** 44 191-210.

Mead C. (1984). *Robins*. Whittet Books.

Moller A.P. (1987). Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signallinng. **Anim. Behav.** 35 1637-1644.

Moller A.P. (1991). Parasite load reduces song output in a passerine bird. **Anim. Behav.** 41 723-730.

Myers J.P. Connors P.G.& Pitelka F.A. (1981). Optimal territory size and the sanderling: compromises in a variable environment. In *Foraging Behaviour: ecological, ethological and psychological approaches*, Ed. by Kamil A.C. & Sargent T.D. Garland.

Nagy K.A. (1980). $CO_2$ production in animals: analysis of potential errors in the doubly labelled water method. **Am. J. Physiol.** 238 R466-473.

Newton I. (1986) *The Sparrow Hawk.* T & A.D. Poyser, Carlton.

Newton S.F. (1989). Recruitment dynamics of a resident passerine: dippers *Cinclus* in Scotland. Unpublished PhD. Thesis, University of Stirling.

Nobel G.K. (1939). Dominance in the life of birds. **Auk** 56 263-273.

Nutall P.A.G. (1988). A study of non-breeding territoriality in dippers, *Cinclus cinclus,* using radio-telemetry. Unpublished Honours thesis, University of Stirling.

Nygard T. & Einavik K. (1992). Radio-tracking of a British storm petrel *Hydrobates pelagicus* proves a probable new breeding site in Norway. **Seabird** 13 59-62.

O'Connor P.J. Pyke G.H. & Spencer H. (1987). Radio-tracking honeyeater movements. **Emu** 87 249-252.

Obrecht H.H. Pennycuick C.J. & Fuller R.J. (1988). Wind tunnel experiments to assess the effect of back mounted radio-transmitters on bird body drag. **J. Exp. Biol.** 135 265-273.

Odum E.P. & Kuenzler E.J. (1955). Measurement of territory and home-range size in birds. **Auk** 72 128-137.

Ormerod S.J. & Tyler S.J. (1990). Population characteristics of dipper roosts in mid and south Wales. **Bird Study** 37 165-170.

Ormerod S.J. Tyler S.J.& Lewis J.M.S. (1986). Is the breeding distribution of dippers influenced by stream acidity. **Bird Study** 32-39.

Ormerod S.J. & Tyler S.J. (1986). The diet of dippers *Cinclus* wintering in the catchment of the River Wye, Wales. **Bird Study** 33 36-45.

Parker G.A. (1974). Assessment strategy and the evolution of fighting behaviour. **J. Theor. Biol.** 47 223-243.

Parker G.A. & Knowlton N. (1980). The evolution of territory size: some ESS models. **J. Theor. Biol.** 84 445-476.

Paton D.C. & Carpenter F.L. (1984). Peripheral foraging by territorial rufous hummingbirds: defense by exploitation. **Ecology** 65 1808-1819.

Pennycuick C.J. (1989). *Bird Flight Performance: A Practical Calculation Manual.* Oxford University Press. Oxford.

Pennycuick C.J. Schaffner F.C. Fuller M.R. Obrecht H.H. & Sternberg L. (1990). Foraging flights of the white tailed tropic bird *Phaethon lepturus*: radio-tracking and doubly-labelled water. **Colonial Waterbirds** 13 96-102.

Peterson K.L. & Best L.B. (1987). Territory dynamics in a sage sparrow population: are shifts in site use adaptive? **Bahav. Ecol. Sociobiol.** 21 351-358.

Petrie M. (1984). Territory size in the moorhen *Gallinula chloropus*: an outcome of RHP asymmetry between neighbours. **Anim. Behav.** 32 861-870.

Pitelka F.A. (1959). Numbers, breeding schedule and territoriality in pectoral sandpipers in northern Alaska. **Condor** 61 233-264.

Price F.E. & Bock C.E. (1983). Population ecology of the dipper in the Front Range of Colorado. In *Studies in Avian Biology 7*. Ed. by Raitt R.J. & Thompson J.P.

Pyke G.H. Pulliam H.R. & Charnov E.L. (1977). Optimal foraging: a selective review of theory and tests. **Q. Rev. Biol.** 52 137-154.

Pyke G.H. (1979). The economics of territory size and time budget in the goldenwinged sunbird. **Am. Nat.** 114 131-144.

Rae C.A.M. (1979). Ecological significance of Autumn song in the European robin *Erithacus rubecula*. Unpublished Honours. Thesis, University of Stirling.

Rand A.S. (1967). The adaptive significance of territoriality in iguanid lizards. In *Lizard Ecology: a Symposium*, Ed. by Milstead W.W. Missouri Uni. Press, Columbia.

Read A.F. (1987). Comparative evidence supports the Hamilton and Zuk hypothesis on parasites and sexual selection. **Nature** 328 68-70.

Robson R.W. (1956). The breeding success of the dipper in north Westmorland. **Bird Study** 3 170-180.

Rohwer S. (1982). The evolution of reliable and unreliable badges of fighting ability. **Amer. Zool.** 22 531-546.

Saltz D. & Alkon P.U. (1985). A simple computer aided method for estimating radio-location error. **J. Wildl. Managm.** 49 664-668.

Schoeller D.A. Minagawa M. Slater R. & Kaplan I.R. (1986a). Stable isotopes of carbon nitrogen and hydrogen in the contemporary North American food web. **Ecol. Food Nutrition.** 18 159-170.

Schoeller D.A. Ravussin E. Schutz Y. Acheson K.J. Baertschi P. & Jequier E. (1986b). **Am. J. Physiol.** 250 R823-830.

Schoener T.W. (1969). Optimal size and specialization in constant and fluctuating environments: an energy time approach. **Brookhaven Symp. Biol.** 22 103-114.

Schoener T.W. (1971). Theory of feeding strategies. **Ann. Rev. Ecol. System.** 2 369-404.

Schoener T.W. (1981). An empirically based estimate of home range. **Theor Pop. Biol.** 20 281-325.

Schoener T.W. (1983). Simple models of optimal feeding territory size: a reconciliation. **Am. Nat.** 121 608-629.

Schoener T.W. (1987). Time budgets and territory size: some simultaneous optimization models for energy maximizers. **Amer. Zool.** 27 259-291.

Schoener T.W. (1987). Time budgets and territory size: some simultaneous optimization models for energy maximizers. **Amer. Zool.** 27 259-291.

Shaw G. (1979). Functions of dipper roosts. **Bird Study** 26 171-178.

Shooter P. (1970). Dipper populations of Derbyshire 1958-1968. **British Birds** 63 158-168.

Slagsvold T. & Lifjeld J.T. (1985). Variation in plumage colour of the great tit, *Parus major*, in relation to habitat, season and food. **J. Zool. Lond. (A)** 206 321-328.

Smith A.T. & Invins B.L. (1986). Territorial intrusions by pikas as a function of occupant activity. **Anim. Behav.** 34 392-397.

Smith S.M. (1976). Ecological aspects of dominance hierarchies in black-capped chickadees. **Auk** 93 95-107.

Smith S.M. (1978). The underworld in a territorial sparrow: adaptive strategy for floaters. **Am. Nat.** 112 571-582.

Smith T.M. Shugart H.H. (1987). Territory size variation in the ovenbird: the role of habitat structure. **Ecology** 68 695-704.

Snow D.W. (1956). Territory in the blackbird. **Ibis** 98 438-447.

Speakman J.R. & Racey P.A. (1988). The doubly-labelled water technique for measurements of energy expenditure in free-living animals. **Sci. Progr.** 72 227-237.

Speakman J.R. (1990). Principles, problems and a paradox with the measurement of energy expenditure in free-living subjects using doubly-labelled water. **Statistics in Medicine** 9 1365-1380.

Springer J.T. (1979). Some sources of bias and sampling error in radio triangulation. **J. Wildl. Managm.** 43 926-935.

Stamps J.A. & Buechner M. (1985). The territorial defense hypothesis and the ecology of insular vertebrates. **Q. Rev. Biol.** 60 155-181.

Stamps J.A. Buechner M. & Krishnan V.V. (1987). The effect of habitat geometry on territorial defense costs: intruder pressure in bounded habitats. **Am. Nat.** 27 307-325.

Stebbings R.E. (1982). Radio-tracking greater horseshoe bats with preliminary observations on flight patterns. In *Telemetric Studies of Vertebrates*. Ed. by Cheeseman C.L.& Mitson R.B. Academic Press, London.

Stenger J. (1958). Food habits and available food of ovenbirds in relation to territory size. **Auk.** 75 335-346.

Stephens D.W. & Dunbar S.R. (1993). Dimensional analysis in behavioral ecology. **Behav. Ecol.** 4 172-183.

Strain J.G. & Mumme R.L. (1988). Effects of food supplementation, song playback and temperature, on vocal territorial behaviour of Carolina wrens. **The Auk** 105 11-16.

Studd M.V. & Robertson R.J. (1985). Evidence for reliable badges in territorial yellow warblers (*Dendroica petechia*). **Anim. Behav.** 33 1102-1113.

Swann R.L. (1975). Communal roosting of robins in Aberdeenshire. **Bird Study** 22 93-98.

Swinhart R.K. & Slade N.A. (1985). Influence of sampling interval on estimates of home-range size. **J. Wildl. Managm.** 49 1019-1025.

Sykes P.W. Carpenter J.W. Holzman S. & Geissler P.H. (1990). Evaluation of three minature radio-transmitter attachment methods for small passerines. **Wildl. Soc. Bull.** 18 41-48.

Tatner P. & Bryant D.M. (1986). Flight cost of a small passerine measured using doubly-labelled water: implications for energetics studies. **Auk** 103 169-180.

Tatner P. (1988). A model of the natural abundance of oxygen-18 and deuterium in the body water of animals. **J. Theor. Biol.** 133 267-280.

Tatner P. & Bryant D.M. (1989). Doubly-labelled water technique for measuring energy expenditure. In *Techniques in Comparative Respiratory Physiology: an Experimental Approach.* Ed. by Bridges C.R.& Butler P.J. Cambridge Uni. Press, Cambridge.

Tinbergen N. (1957). The functions of territory. **Bird Study** 4 14-27.

Verner J. (1977). On the adaptive significance of territoriality. **Am. Nat.** 111 769-775.

Vickery J. (1992). Breeding density of dippers, grey wagtails and common sandpipers in relation to the acidity of streams in south west Scotland. **Ibis** 133 178-185

Walsberg G.E. (1983). Avian ecological energetics. Ch.3. In *Avian Biology vol VII.* Ed. by Farner D.S. King J.R. & Parkes K.C. Academic Press.

Walsberg G.E. (1986). Thermal consequences of roost-site selection: the relative importance of three modes of hest conservation. **Auk** 103 1-7.

Ward S. (1992). Energetics of laying and incubation in birds: studies of swallows *Hirundo rustica*, dippers *Cinclus* and Japanese quail *Cotrunix coturnix*. Unpublished PhD. Thesis, University of Stirling.

Warnock N. & Warnock S. (1993). Attachment of radio-transmitters to sandpipers: review and methods. **Wader Study Group Bull.** 70 28-30.

Weary D.M. & Krebs J.R. (1992). Great tits classify songs by individual voice characteristics. **Anim. Behav.** 43 283-287.

Weathers W.W. & Nagy K.A. (1980). Simultaneous doubly-labelled water ($^3HH^{18}O$) and time budget estimates of energy expenditure in *Phainopepla nitens*. **Auk** 97 861-867.

Webb D.R. & Rodgers C.M. (1988). Nocturnal energy expenditture of dark-eyed juncos, roosting in Indiana during winter. **Condor** 90 107-112.

White G.C. & Garrot R.A. (1990). *Analysis of Wildlife Radio-tracking Data.* Academic Press, London.

Williams P.L. (1990). Use of radio-tracking to study foraging in small terrestrial birds. **Studies in Avian Biology** No.13 181-186.

Wilson E.O. (1975). *Sociobiology: the New Synthesis.* Harvard Uni. Press, Cambridge.

Wilson R.P. & Culik B.M. (1992). Packages on penguins and device induced data. In *Wildlife Telemetry: Remote Monitoring and Tracking of Animals.* Ed. by Priede T.G.& Swift S.M. Ellis Horwood, Chichester.

Wong W.W. & Klein P.D. (1986). A review of techniques for the preparation of biological samples for mass spectrometric measurements of hydrogen-2/hydrogen-1 and oxygen-18/oxygen-16 isotope ratios. **Mass Spectrometry Review** 5 313-342.

Worton B.J. (1987). A review of models of home-range for animal movement. **Ecol. Model.** 38 277-298.

Worton B.J. (1989). Kernal methods for estimating the utilization distribution in home-range studies. **Ecology** 70 164-168.

Wray S. Cresswell W.J. White P.C.L. & Harris S. (1992a). What, if anything, is a core area? An analysis of the problems of describing internal range configurations. In *Wildlife Telemetry: Remote Monitoring and Tracking of Animals.* Ed. by Priede T.G.& Swift S.M. Ellis Horwood, Chichester.

Wray S. Cresswell W.J. & Rogers D. (1992b). Dirichlet tesselations: a new non-parametric approach to home range analysis. In *Wildlife Telemetry: Remote Monitoring and Tracking of Animals* Ed by Priede I.G. & Swift S. Ellis Horwood, Chichester.

Ydenberg R.C. (1984). The conflict between feeding and territorial defense in the great tit. **Behav. Ecol. Sociobiol.** 15 103-108.

Ydenberg R.C. & Krebs J.R. (1987). The tradeoff between territorial defense and foraging in the great tit. **Amer. Zool.** 27 337-346

Zar N. (1984). *Biostatistical Analysis.* Prentice Hall, New Jersey.

# Chapter 9.

**Appendix 1.** Cause of death and body composition for a sample of robin carcasses (n=27). Missing values indicate carcasses which became severely dehydrated while frozen.

| Code No. | Age * | Sex # | Cause of death ψ | Day of year of death ∞ | Mass at death (g) | Predicted mass (g) $ | Condition (g) † | Total fat score ‡ | Gut component | | Fat component | | Water component | | Lean component | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | Mass (g) | % § | Mass (g) | % § | Mass (g) | % § | Mass (g) | % § |
| F646516 | A | M | Found dead | 131 | 16.8 | 19.4 | -2.6 | 0 | 3.63 | 22 | 0.13 | 1 | 8.29 | 49 | 4.75 | 28 |
| F646517 | J | M | Taken under licence | 183 | 18.1 | 18.3 | -0.2 | 0 | 3.21 | 18 | 1.19 | 7 | 8.19 | 45 | 5.51 | 30 |
| F646519 | A | M | Found dead | 131 | 18.8 | 19.7 | -0.9 | 0 | 4.73 | 25 | 0.15 | 1 | 8.75 | 47 | 5.17 | 27 |
| F646524 | A | F | Found dead | 182 | 16.1 | 18.8 | -2.7 | 0 | 2.43 | 15 | 0.15 | 1 | 8.23 | 51 | 5.29 | 33 |
| F646554 | J | F | Found dead | 126 | 13.2 | 18.2 | -5.0 | 0 | 2.22 | 17 | 0.05 | 0 | 6.48 | 49 | 4.45 | 34 |
| F646585 | J | M | Found dead | 177 | 15.4 | 17.9 | -2.5 | 0 | 2.98 | 19 | 0.12 | 1 | 7.18 | 47 | 5.12 | 33 |
| H227558 | A | F | Accident | 132 | 18.6 | 18.6 | 0.0 | 0 | 3.91 | 21 | 0.47 | 3 | 8.84 | 48 | 5.38 | 29 |
| 1 | A | F | Domestic cat | 198 | 20.5 | 18.9 | 1.6 | 7 | 3.52 | 17 | 2.75 | 13 | 8.33 | 41 | 5.90 | 29 |
| 2 | J | F | Domestic cat | 198 | 19.9 | 19.1 | 0.8 | 5 | 3.20 | 16 | 2.04 | 10 | 8.97 | 45 | 5.69 | 29 |
| 3 | J | F | Accident | 185 | 19.0 | 18.2 | 0.8 | 4 | 3.39 | 18 | 2.06 | 11 | 8.34 | 44 | 5.21 | 27 |
| 4 | J | F | Domestic cat | 198 | 21.0 | 19.8 | 1.2 | 3 | 5.78 | 28 | 2.42 | 12 | 7.51 | 36 | 5.29 | 25 |
| 5 | A | M | Unknown | 195 | 14.0 | 17.6 | -3.6 | 0 | 2.15 | 15 | 0.44 | 3 | 6.82 | 49 | 4.59 | 33 |
| 6 | J | M | Accident | 159 | 20.9 | 19.9 | 1.0 | 1 | 5.25 | 25 | 1.06 | 5 | 8.65 | 41 | 5.94 | 28 |
| 7 | J | M | Domestic cat | 215 | 16.0 | 19.9 | -3.9 | 0 | - | - | 1.17 | 7 | - | - | 5.28 | 33 |
| 8 | A | F | Accident | 38 | 18.7 | 18.4 | 0.3 | 0 | 3.62 | 19 | 0.38 | 2 | 9.30 | 50 | 5.40 | 29 |
| 9 | A | F | Found dead | 41 | 13.9 | 18.9 | -5.0 | 0 | 1.80 | 13 | 0.11 | 1 | 6.92 | 50 | 5.07 | 36 |
| 10 | J | F | Accident | 51 | 17.2 | 17.3 | -0.1 | 0 | 2.12 | 12 | 0.80 | 5 | 8.84 | 51 | 5.44 | 32 |
| 20 | J | F | Unknown | 183 | 21.3 | 18.4 | 2.9 | 5 | - | - | 2.63 | 12 | - | - | 5.56 | 26 |
| 21 | J | M | Domestic cat | 190 | 23.8 | 20.2 | 3.6 | 2 | - | - | 2.71 | 11 | - | - | 6.33 | 27 |
| 22 | J | M | Taken under licence | 239 | 16.0 | 19.2 | -3.2 | 0 | - | - | 0.64 | 4 | - | - | 5.72 | 36 |
| 24 | J | F | Accident | 32 | 18.3 | 20.2 | -1.9 | 0 | - | - | 0.37 | 2 | - | - | 5.51 | 30 |
| 26 | J | M | Taken under licence | - | 18.1 | 19.5 | -1.4 | 0 | - | - | 0.64 | 4 | - | - | 5.29 | 29 |
| 27 | J | M | Domestic cat | 104 | 21.0 | 19.1 | 2.0 | 2 | - | - | 1.14 | 5 | - | - | 5.86 | 28 |
| 28 | A | F | Domestic cat | 36 | 21.7 | 19.7 | 2.0 | 0 | - | - | 0.52 | 2 | - | - | 5.93 | 27 |
| 29 | A | M | Taken under licence | - | 20.4 | 20.3 | 0.1 | 1 | - | - | 0.75 | 4 | - | - | 6.08 | 30 |
| 30 | A | M | Unknown | 257 | 18.0 | 21.5 | -3.5 | 0 | - | - | 0.20 | 1 | - | - | 5.32 | 30 |
| 31 | A | M | Accident | 60 | 20.0 | 19.7 | 0.3 | 0 | - | - | 0.84 | 4 | - | - | 6.05 | 30 |

| | |
|---|---|
| * | A=adult, J=juvenile. |
| # | M=male, F=female. |
| ∞ | Day 1 set to 1st August. |
| $ | Body mass predicted from keel length and bill depth. |
| † | Body mass at death minus predicted mass. |
| ‡ | Tracheal pit score plus anterior abdominal score. |
| § | Component mass as % total mass at death. |

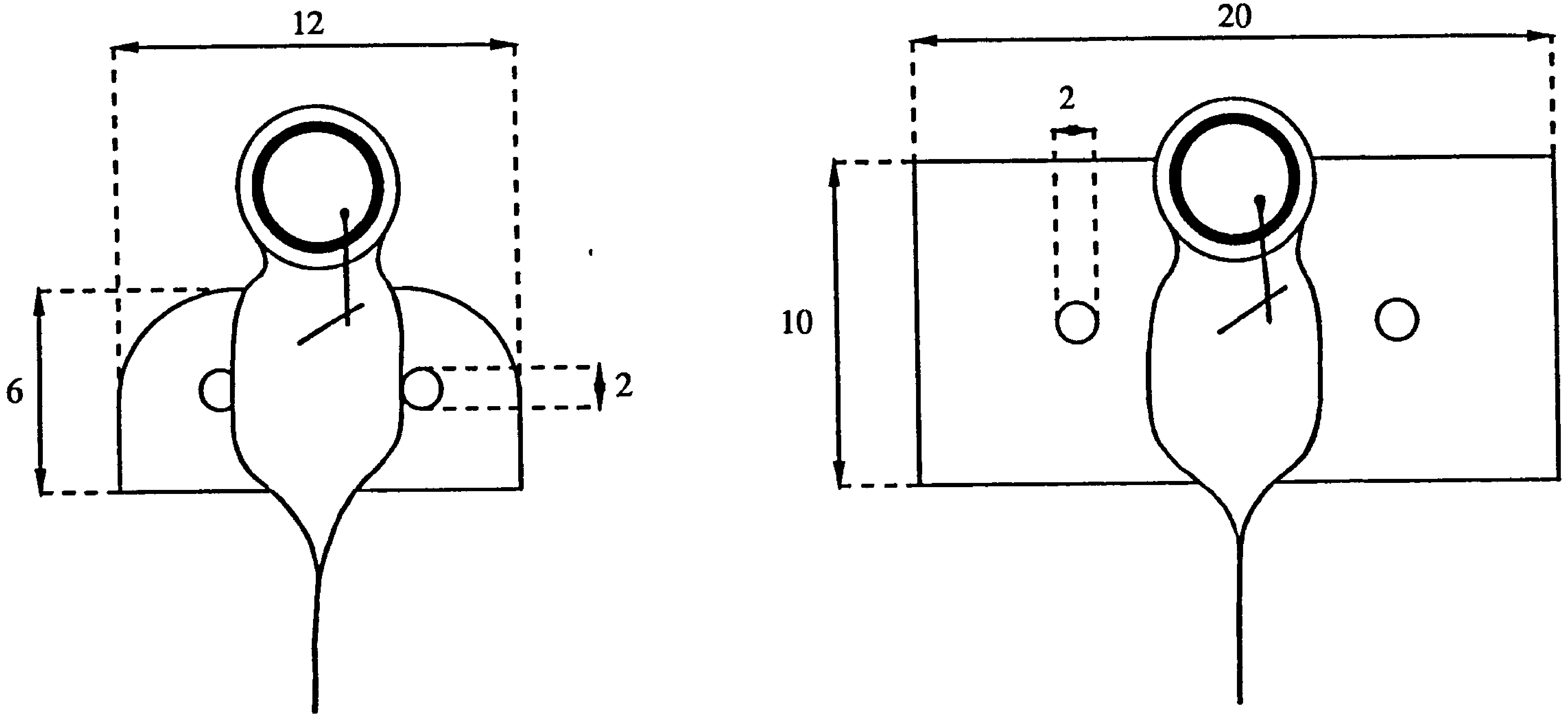
| | | |
|---|---|---|
| ψ | Taken under licence | ; killed for scientific purposes under licence from the N.C.C. |
| | Found dead | ; Found dead with no external injuries and no apparent cause of death. |
| | Accident | ; Road and window casualties. |
| | Domestic cat | ; Predated by domestic cat and found by owner. |

```
robin   no radio-tag

Assumed values:

Empty body mass = .0193 kg
Payload mass    = 0 kg
All-up mass     = .0193 kg
Span            = .228 m
g     = 9.810001 m s-2                          (Gravity)
rho   = 1.23 kg m-3                             (Air density)
e     = 3.9E+07 J/kg                            (Energy density of fat)
eta   = .23                                     (Conversion efficiency)
k     = 1.2                                     (Induced power factor)
r     = 1.1                                     (Circulation/respiration factor)
X1    = 1.2                                     (Profile power ratio)
X2    = .811                                    (Metabolic power ratio)
Disk area                 = .0408 sq m
Body frontal area         = .000587 sq m
Body drag coefficient     = .4
Flat-plate area           = .000235 sq m
Pmet                      = 8.250001E-02 W (mechanical)
BMR                       = .359 W (chemical)
Fat consumption for zero wind

Airspeed       Power            Eff. L/D         Power          Fat consumption
m/s            W mechanical                      W chemical     g/km (ground)

 4             .353             2.15             1.53           9.840001E-03
 5             .339             2.79             1.47           .00756
 6             .338             3.36             1.47 *         .00628
 7             .347             3.82             1.51           .00552
 8             .365             4.15             1.59           .00509
 9             .393             4.33             1.71           .00487
 10            .431             4.39             1.87           .00481

Computed values:

Vmp                       = 5.7 m/s
Vmr                       = 10.1 m/s
Pmin                      = .337 W (mechanical)
Pmr                       = .435 W (mechanical)
L/D max                   = 4.39
Fat consumption at Vmr    = .00481 g/km (air distance)

Power estimates include basal metabolism, and
requirements for respiration and circulation
```

```
robin   with 1.8 g radio-tag

Assumed values:

Empty body mass = .0193 kg
Payload mass    = 0 kg
All-up mass     = .0211 kg
Span            = .228 m
g     = 9.810001 m s-2                          (Gravity)
rho   = 1.23 kg m-3                             (Air density)
e     = 3.9E+07 J/kg                            (Energy density of fat)
eta   = .23                                     (Conversion efficiency)
k     = 1.2                                     (Induced power factor)
r     = 1.1                                     (Circulation/respiration factor)
X1    = 1.2                                     (Profile power ratio)
X2    = .709                                    (Metabolic power ratio)
Disk area                 = .0408 sq m
Body frontal area         = .000587 sq m
Body drag coefficient     = .4
Radio mass                = .0018 kg
Radio flat-plate area     = 0 sq m
Flat-plate area           = .000235 sq m
Pmet                      = 8.250001E-02 W (mechanical)
BMR                       = .359 W (chemical)
Fat consumption for zero wind

Airspeed       Power            Eff. L/D         Power          Fat consumptio
m/s            W mechanical                      W chemical     g/km (ground)

 4             .395             2.09             1.72           .011
 5             .377             2.75             1.64           .0084
 6             .372             3.33             1.62 *         .00692
 7             .379             3.82             1.65           .00604
 8             .396             4.18             1.72           .00552
 9             .423             4.41             1.84           .00524
 10            .46              4.5              2              .00512
 11            .5070001         4.49             2.2            .00514

Computed values:

Vmp                       = 6 m/s
Vmr                       = 10.5 m/s
Pmin                      = .372 W (mechanical)
Pmr                       = .482 W (mechanical)
L/D max                   = 4.51
Fat consumption at Vmr    = .00512 g/km (air distance)

Power estimates include basal metabolism, and
requirements for respiration and circulation
```

**Appendix 2.** Examples of output from Program 1 of Pennycuick (1989) for a robin with, and without, a 1.8 g radio-tag of zero drag.

* Chemical power required for level flight at $V_{mp}$ (to convert W to $kJhr^{-1}$ multiply by (60x60)/1000).



Appendix 3. Dimensions (mm) of radio-tag tail-clip plates for robins and dippers.

**Appendix 4.** The space-use statistics for the independent sample of standardised ranges used by non-breeding robins and recorded by radio-tracking (n=51).

| Ring No. | Age [*] | Sex [#] | Day of year [$] | Core area ($m^2$) | Usual-area ($m^2$) | Maximum-area ($m^2$) | No. core nuclei | Defended area ($m^2$) | % locations with advert & defense behav. | % locations contributing to core regions | % locations that were excursive | Core area including 2m boundary strip ($m^2$) | Revised No. core-nuclei | Linear length (m) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| F073988 | A | M | 123 | 43 | 796 | 2289 | 4 | 1225 | 23 | 75 | 20 | 180 | 4 | 74 |
| F139219 | A | F | 133 | 36 | 112 | 11690 | 3 | - | 0 | 75 | 25 | 156 | 2 | 17 |
| H227544 | J | ? | 85 | 143 | 632 | 9658 | 5 | 338 | 3 | 65 | 35 | 377 | 5 | 52 |
| H227546 | J | ? | 111 | 319 | 2837 | 19210 | 4 | - | 7 | 65 | 35 | 739 | 4 | 96 |
| H227547 | J | ? | 111 | 181 | 567 | 8361 | 2 | 690 | 25 | 75 | 17 | 336 | 2 | 42 |
| H227553 | J | ? | 194 | 101 | 4084 | 9764 | 4 | - | 6 | 70 | 20 | 363 | 4 | 213 |
| H227556 | A | ? | 107 | 54 | 276 | 1566 | 4 | - | 3 | 85 | 15 | 235 | 3 | 39 |
| H227557 | A | F | 125 | 86 | 468 | 2605 | 5 | 1395 | 3 | 90 | 7 | 306 | 5 | 57 |
| H227558 | A | F | 131 | 139 | 7528 | 26710 | 7 | - | 0 | 70 | 30 | 619 | 7 | 378 |
| H227559 | J | ? | 125 | 63 | 989 | 23980 | 4 | - | 0 | 65 | 35 | 293 | 4 | 83 |
| F646516 | A | M | 13 | 84 | 760 | 2239 | 4 | 504 | 0 | 80 | 20 | 341 | 4 | 41 |
| F646519 | A | M | 126 | 37 | 224 | 1651 | 3 | - | 0 | 70 | 30 | 153 | 3 | 26 |
| F646521 | J | M | 121 | 83 | 1228 | 2222 | 4 | - | 5 | 80 | 15 | 357 | 4 | 77 |
| F646521 | A | M | 181 | 55 | 1935 | 3840 | 6 | - | 0 | 75 | 20 | 291 | 6 | 117 |
| F646536 | A | F | 42 | 146 | 2776 | 20730 | 2 | - | 0 | 90 | 10 | 313 | 2 | 189 |
| F646540 | A | F | 26 | 58 | 2495 | 8561 | 4 | - | 0 | 80 | 20 | 218 | 4 | 119 |
| F646540 | A | F | 26 | 85 | 194 | 748 | 4 | - | 0 | 85 | 15 | 256 | 4 | 46 |
| F646541 | A | ? | 38 | 35 | 107 | 287 | 3 | 162 | 28 | 80 | 20 | 126 | 1 | 0 |
| F646546 | J | F | 127 | 26 | 448 | 1299 | 7 | - | 3 | 90 | 10 | 198 | 3 | 36 |
| F646546 | A | F | 77 | 46 | 625 | 3265 | 6 | 820 | 3 | 90 | 10 | 240 | 4 | 58 |
| F646550 | J | F | 76 | 60 | 60 | 1208 | 1 | - | 0 | 80 | 20 | 142 | 1 | 0 |
| F646551 | J | M | 76 | 44 | 484 | 1361 | 4 | 496 | 0 | 70 | 27 | 238 | 4 | 45 |
| F646551 | A | M | 57 | 73 | 134 | 5987 | 2 | 105 | 5 | 85 | 15 | 218 | 2 | 13 |
| F646554 | A | F | 119 | 126 | 11830 | 28520 | 5 | - | 0 | 65 | 35 | 321 | 5 | 394 |
| F646561 | A | ? | 43 | 30 | 109 | 230 | 3 | - | 0 | 85 | 15 | 160 | 3 | 16 |
| F646562 | J | ? | 119 | 43 | 330 | 510 | 4 | - | 5 | 90 | 10 | 211 | 4 | 33 |

[*] A=adult, J=juvenile.

[#] M=male, F=female, ?=unknown.

[$] Day 1 set to 1st August.

## Appendix 4. continued.

| Ring No. | Age [*] | Sex [#] | Day of year [$] | Core area ($m^2$) | Usual-area ($m^2$) | Maximum-area ($m^2$) | No. core nuclei | Defended area ($m^2$) | % locations with advert & defense behav. | % locations contributing to core regions | % locations that were excursive | Core area including 2m boundary strip ($m^2$) | Revised No. core-nuclei | Linear length (m) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| F646564 | A | M | 78 | 32 | 419 | 10310 | 3 | 655 | 3 | 80 | 20 | 142 | 3 | 40 |
| F646565 | A | ? | 78 | 64 | 108 | 2930 | 2 | - | 0 | 90 | 10 | 130 | 2 | 10 |
| F646567 | A | ? | 78 | 33 | 803 | 9159 | 5 | 1300 | 3 | 80 | 17 | 207 | 5 | 80 |
| F646568 | A | ? | 121 | 63 | 348 | 2399 | 3 | - | 0 | 80 | 20 | 244 | 3 | 31 |
| F646569 | A | M | 57 | 142 | 812 | 1315 | 5 | 924 | 3 | 85 | 15 | 415 | 5 | 68 |
| F646578 | J | ? | 18 | 58 | 255 | 1112 | 4 | 214 | 10 | 85 | 10 | 240 | 4 | 28 |
| F646579 | J | ? | 19 | 50 | 410 | 2056 | 5 | 301 | 13 | 75 | 25 | 196 | 5 | 43 |
| F646581 | J | M | 57 | 45 | 543 | 1090 | 4 | 303 | 6 | 80 | 15 | 239 | 4 | 49 |
| F646582 | J | F | 184 | 171 | 6765 | 12080 | 5 | - | 0 | 80 | 17 | 469 | 5 | 231 |
| F646583 | J | ? | 107 | 108 | 277 | 11550 | 2 | 179 | 0 | 80 | 20 | 241 | 2 | 14 |
| F646585 | J | M | 165 | 169 | 2041 | 10310 | 4 | - | 0 | 75 | 22 | 313 | 4 | 127 |
| F646586 | J | ? | 27 | 197 | 937 | 11430 | 3 | 478 | 0 | 75 | 22 | 451 | 3 | 62 |
| F646587 | J | ? | 37 | 15 | 381 | 8333 | 5 | - | 0 | 55 | 45 | 147 | 4 | 63 |
| F646589 | A | ? | 27 | 28 | 751 | 3340 | 6 | 709 | 6 | 80 | 20 | 231 | 4 | 61 |
| F646590 | A | ? | 107 | 44 | 165 | 1414 | 3 | 228 | 5 | 60 | 40 | 164 | 2 | 15 |
| F646591 | A | ? | 107 | 48 | 532 | 966 | 7 | 507 | 8 | 80 | 20 | 275 | 5 | 55 |
| F646592 | J | ? | 77 | 51 | 459 | 1851 | 4 | 465 | 13 | 80 | 17 | 202 | 3 | 35 |
| F646593 | J | ? | 57 | 39 | 117 | 723 | 4 | 151 | 11 | 85 | 15 | 179 | 2 | 12 |
| F646594 | J | M | 194 | 53 | 295 | 6824 | 4 | - | 0 | 70 | 30 | 237 | 4 | 35 |
| F646595 | J | M | 181 | 121 | 516 | 1723 | 2 | 808 | 48 | 70 | 30 | 289 | 2 | 28 |
| F646596 | J | ? | 77 | 150 | 2476 | 8159 | 3 | 2136 | 6 | 90 | 10 | 406 | 3 | 104 |
| F646597 | J | ? | 85 | 28 | 1118 | 34550 | 5 | - | 3 | 55 | 40 | 213 | 5 | 331 |
| F646598 | J | ? | 83 | 83 | 1112 | 5133 | 5 | 929 | 15 | 60 | 32 | 311 | 5 | 86 |
| F646599 | J | ? | 85 | 147 | 13200 | 24430 | 6 | - | 0 | 75 | 22 | 527 | 6 | 300 |
| F646727 | A | M | 176 | 227 | 3037 | 7834 | 5 | - | 0 | 75 | 17 | 569 | 5 | 136 |

[*] A=adult, J=juvenile.

[#] M=male, F=female, ?=unknown.

[$] Day 1 set to 1st August.

**Appendix 5.** The statistics for the independent sample of standardised ranges used by non-breeding dippers and recorded by radio-tracking (n=16).

| Ring No. | Age [†] | Sex [#] | Day of year [§] | Core length | Usual-length | Maximum-length | % locations contributing to core regions | % locations that were excursive | Range type [$] | Water course occupied |
|---|---|---|---|---|---|---|---|---|---|---|
| XS44879 | A | M | 159 | 300 | 450 | 650 | 85 | 15 | I | River Devon |
| XP05152* | J | F | 80 | 400 | 1500 | 1500 | 70 | 0 | I | River Devon |
| XP05010* | J | M | 80 | 450 | 2250 | 2450 | 70 | 10 | I | River Devon |
| XS44829 | A | M | 120 | 150 | 650 | 650 | 80 | 0 | I | River Devon |
| XS44849* | A | M | 120 | 300 | 2000 | 3400 | 65 | 30 | Y | River Devon |
| RA84852 | A | F | 26 | 200 | 450 | 650 | 90 | 5 | I | River Devon |
| RA84900 | A | M | 49 | 350 | 400 | 900 | 75 | 25 | I | River Devon |
| RA84809 | A | F | 61 | 250 | 350 | 700 | 80 | 20 | I | River Devon |
| RA84901 | A | M | 75 | 350 | 400 | 600 | 80 | 20 | I | River Devon |
| RB93652* | J | M | 111 | 500 | 2450 | 2650 | 85 | 5 | I | River Devon |
| RS93655 | A | M | 55 | 600 | 1400 | 2300 | 85 | 15 | Y | Ardoch Burn |
| RS51307 | A | M | 56 | 300 | 1200 | 1350 | 55 | 45 | I | Ardoch Burn |
| XP05229 | A | F | 55 | 250 | 250 | 600 | 70 | 30 | I | Ardoch Burn |
| XR68870 | J | F | 102 | 500 | 900 | 1150 | 80 | 10 | I | Ardoch Burn |
| RS03258 | J | M | 102 | 200 | 800 | 800 | 60 | 0 | I | Ardoch Burn |
| XR68570 | A | M | 93 | 300 | 1300 | 1650 | 80 | 10 | L | Wharry Burn |

[†] A=adult, J=juvenile.
[#] M=male, F=female.
[§] Day one set to 1st August.
[$] I=simple linear, L=use of tributary at end of range, Y=use of tributary in middle of range.
[*] Non-territorial following definition based on overlap between neighbours.

**Appendix 6.** The stomach contents of dead robins quantified by presence and absence recording (n=28).
Symbols indicate the presence of different categories in each individual.

| **Phylum** | Class | *Order* | Code number of each robin | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | F646516 | F646517 | F646519 | F646524 | F646554 | F646585 | H227558 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 20 | 21 | 22 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 |
| **Mollusca** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Gastropoda | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | *Pulmonata* | | | | | | ● | | | | | | | | | | | | | | | | | | | | | | |
| **Annelida** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Oligochaeta | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | *Lumbricidae* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| **Arthropoda** | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Arachnida | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | *Acarina* | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | ● |
| | | *Pseudoscorpiones* | | | | | | | | | | | | | | | | | | | | | ● | | | | | | | |
| | | *Araneae* | | | | | | | | ● | | | | | ● | | | | | | | | ● | | | | | | | |
| | Crustacea | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | *Isopoda* | | | | | | | | ● | | | | | | | | | | | | | | | | | | | | |
| | Myriapoda | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | *Diplopoda* | ● | | | | | | | | | | | | | | | | | | | | ● | | ● | | | | | |
| | | *Chilopoda* | | | | | | | | | | | | | | | | | | | | | ● | | | ● | ● | | | |
| | Insecta | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | *Thysanoptera* | | | | | | | | | | | | | | | | | | | | | | ● | | | | | | |
| | | *Hemiptera* | | | | | | | | | ● | | | | | | | | | | | | | | | | | | | ● |
| | | *Coeloptera* | ● | ● | | | | ● | ● | ● | ● | | | | ● | ● | ● | | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| | | *Lepidoptera* | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | *Diptera* | ● | ● | | | | | ● | ● | ● | | | | ● | ● | ● | | | ● | | ● | ● | ● | ● | ● | ● | | | ● |
| | | *Hymenoptera* | ● | ● | | | | | | | | | | | ● | | | | | | | | | | | | | | | |
| | | *Dermaptera* | | | | | | | | | | | | | | | | | | | ● | ● | ● | ● | ● | | | | | |
| Vegatable matter | | | ● | ● | | | | | | ● | | | | | | | | | | | ● | | | | ● | ● | | | | |
| Seeds | | | | | | | | | | | | | | | | | ● | | | | ● | | | | | ● | | | | |
| Grit | | | | ● | | | | ● | ● | ● | ● | | | | ● | ● | | | | ● | | | | ● | ● | | ● | ● | ● | ● |

## **Appendix 7.** Summary of continuous tracking data for non-breeding territorial robins that were monitored at different times of day.

| Ring No. | Proportion of time on usual-area | | | | Commuting rate (movements $hr^{-1}$) | | | | Time singing (sec) | | | | Proportion of locations at which birds vocalised | | | | % departure from ideal linear use | | | | Proportion of movements that were backtracks | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dawn | Midday | Dusk | Mean* | Dawn | Midday | Dusk | Mean | Dawn | Midday | Dusk | Mean | Dawn | Midday | Dusk | Mean | Dawn | Midday | Dusk | Mean | Dawn | Midday | Dusk | Mean |
| F646581 | 1.00 | 1.00 | 1.00 | 1.00 | 17.0 | 7.0 | 5.0 | 9.7 | 142 | 0 | 0 | 47 | 0.36 | 0.03 | 0.00 | 0.13 | 10.4 | 16.9 | 12.9 | 13.1 | 0.44 | 0.33 | 0.25 | 0.34 |
| F646569 | 0.83 | 0.47 | 0.60 | 0.63 | 13.0 | 0.0 | 10.0 | 7.7 | 11 | 0 | 0 | 4 | 0.16 | 0.13 | 0.03 | 0.11 | 59.7 | - | 20.7 | 30.4 | 0.33 | - | 0.20 | 0.27 |
| F646546 | 0.79 | 1.00 | 0.90 | 0.90 | 19.5 | 18.0 | 21.0 | 19.5 | 148 | 7 | 139 | 98 | 0.43 | 0.17 | 0.10 | 0.32 | 6.8 | 16.3 | 1.9 | 8.3 | 0.08 | 0.24 | 0.24 | 0.19 |
| F646551 | 0.70 | 0.87 | 0.60 | 0.72 | 4.3 | 5.8 | 6.7 | 5.6 | 0 | 0 | 0 | 0 | 0.00 | 0.00 | 0.07 | 0.02 | 17.2 | 0.0 | 0.0 | 5.7 | 1.00 | 1.00 | 1.00 | 1.00 |
| H227566 | 1.00 | 0.73 | 0.53 | 0.75 | 9.0 | 6.8 | 7.5 | 7.8 | 0 | 0 | 0 | 0 | 0.00 | 0.17 | 0.07 | 0.08 | 27.9 | 15.9 | 20.0 | 21.3 | 0.56 | 0.50 | 0.60 | 0.55 |
| F646547 | 1.93 | 0.93 | 0.75 | 0.89 | 6.0 | 6.4 | 1.7 | 4.7 | 30 | 0 | 0 | 10 | 0.13 | 0.03 | 0.00 | 0.05 | 0.0 | 0.0 | 0.0 | 0.0 | 0.40 | 0.40 | 0.40 | 0.40 |
| F646590 | 1.00 | 1.00 | 0.42 | 0.81 | 5.0 | 3.0 | 0.0 | 2.7 | 4 | 12 | 0 | 5 | 0.06 | 0.10 | 0.07 | 0.08 | - | - | - | - | - | - | - | - |
| Median | 0.10 | 0.93 | 0.06 | | 6.0 | 6.8 | 6.7 | | 11 | 0 | 0 | | 0.13 | 0.11 | 0.07 | | 13.8 | 15.9 | 1.9 | | 0.42 | 0.36 | 0.25 | |

* Mean prefered over median for combined measure of network use over whole day, see text.

\- Individual did not commute between nuclei during observation period or number of nuclei less than three.

**Appendix 8.** List of recordings of robin song used during experimental playback manipulations. All recordings were obtained from the British Library of Wildlife Sounds, 29 Exhibition Road, London SW7.

| Ref. No. | Date of recording | Time of recording | Duration (sec) | Location | Habitat | Recorded by |
|---|---|---|---|---|---|---|
| 586 | 18 September 1963 | 06.30 | 172 | Worcestershire | Rural | Field A.G. |
| 7171 | 26 September 1978 | 19.00 | 200 | Surrey | Suburban | Sellar P. |
| 17657 | 12 October 1976 | 17.30 | 185 | Blackheath, London | Urban | Stjernstedt R. |
| 9841 | 14 October 1973 | 10.30 | 35 | Gloucestershire | Parkland | Pedley W. |
| 9842 | 14 October 1973 | 11.15 | 110 | Gloucestershire | Parkland | Pedley W. |
| 22619 | 16 October 1965 | - | 48 | Surrey | Suburban | Lewis V.C. |
| 22620 | 20 October 1965 | - | 48 | Herefordshire | Rural | Lewis V.C. |
| 23979 | 22 October 1985 | - | 70 | Blackheath, London | Urban | Stjernstedt R. |
| 9845 | 30 October 1977 | 07.30 | 140 | Buckinghamshire | Rural | Pedley W. |
| 1203 | Late November 1964 | 15.45 | 141 | Worcestershire | Rural | Field A.G. |

**Appendix 9.** Summary of continuous tracking data for robins that were monitored at different times of day while subjected to experimental playback of song.

| Ring No. | Proportion of time on usual-area | | | | Commuting rate (movements hr$^{-1}$) | | | | Time singing (sec hr$^{-1}$) | | | | Proportion of locations at which birds vocalised | | | | % departure from ideal linear use | | | | Proportion of movements that were backtracks | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dawn | Midday | Dusk | Mean | Dawn | Midday | Dusk | Mean | Dawn | Midday | Dusk | Mean | Dawn | Midday | Dusk | Mean | Dawn | Midday | Dusk | Mean | Dawn | Midday | Dusk | Mean |
| F646581 | 1.00 | 1.00 | 1.00 | 1.00 | 11.0 | 5.0 | 13.0 | 9.7 | 3 | 0 | 0 | 1 | 0.07 | 0.00 | 0.00 | 0.02 | 11.4 | 5.3 | 7.7 | 8.1 | 0.33 | 0.50 | 0.63 | 0.49 |
| F646569 | 0.90 | 1.00 | 0.70 | 0.87 | 10.0 | 1.0 | 8.6 | 6.5 | 113 | 17 | 10 | 47 | 0.23 | 0.10 | 0.03 | 0.20 | 17.9 | 45.2 | 32.7 | 30.9 | 0.57 | 0.45 | 0.33 | 0.45 |
| F646546 | 1.00 | 0.90 | 1.00 | 0.97 | 25.0 | 15.5 | 22.0 | 20.8 | 265 | 62 | 74 | 134 | 0.86 | 0.10 | 0.30 | 0.42 | 9.8 | 2.4 | 1.3 | 4.5 | 0.59 | 0.42 | 0.22 | 0.41 |
| F646551 | 0.63 | 0.30 | 0.80 | 0.58 | 6.3 | 9.0 | 10.0 | 8.4 | 0 | 0 | 0 | 0 | 0.17 | 0.00 | 0.03 | 0.07 | 0.0 | 0.0 | 0.0 | 0.0 | 1.00 | 1.00 | 1.00 | 1.00 |
| H227566 | 0.90 | 0.67 | 0.10 | 0.56 | 3.3 | 6.0 | 0.0 | 3.1 | 0 | 0 | 0 | 0 | 0.00 | 0.10 | 0.13 | 0.08 | 31.8 | 28.9 | - | 30.4 | 0.50 | 0.00 | - | 0.25 |
| F646547 | 0.90 | 1.00 | 0.50 | 0.80 | 4.4 | 7.0 | 11.3 | 7.6 | 18 | 20 | 9 | 16 | 0.10 | 0.17 | 0.07 | 0.11 | 0.0 | 0.0 | 0.0 | 0.0 | 1.00 | 0.17 | 0.00 | 0.39 |
| F646590 | 1.00 | 1.00 | 0.73 | 0.91 | 8.0 | 6.0 | 2.7 | 5.6 | 111 | 12 | 0 | 41 | 0.37 | 0.10 | 0.03 | 0.17 | - | - | - | - | - | - | - | - |
| Median | 0.90 | 1.00 | 0.73 | | 8.0 | 6.0 | 10.0 | | 18 | 12 | 0 | | 0.17 | 0.10 | 0.07 | | 10.6 | 3.9 | 1.3 | | 0.57 | 0.47 | 0.48 | |

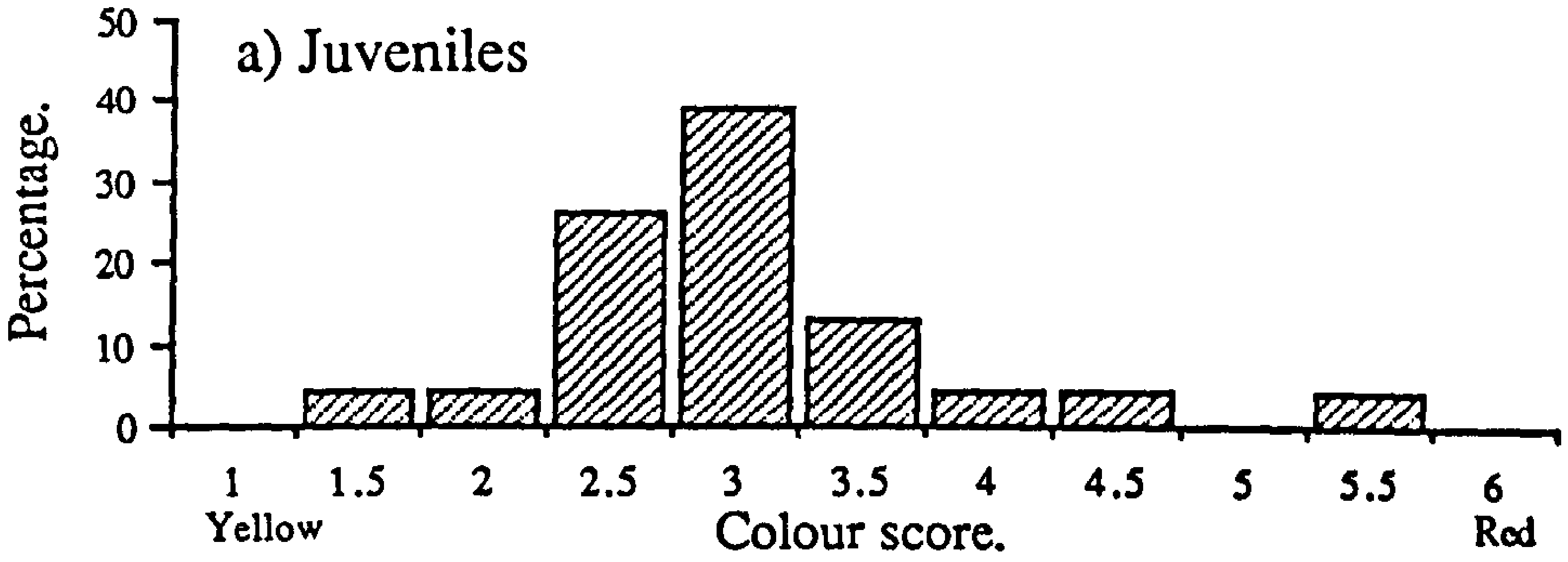
- Individual did not commute between nuclei during observation period or number of nuclei less than three.

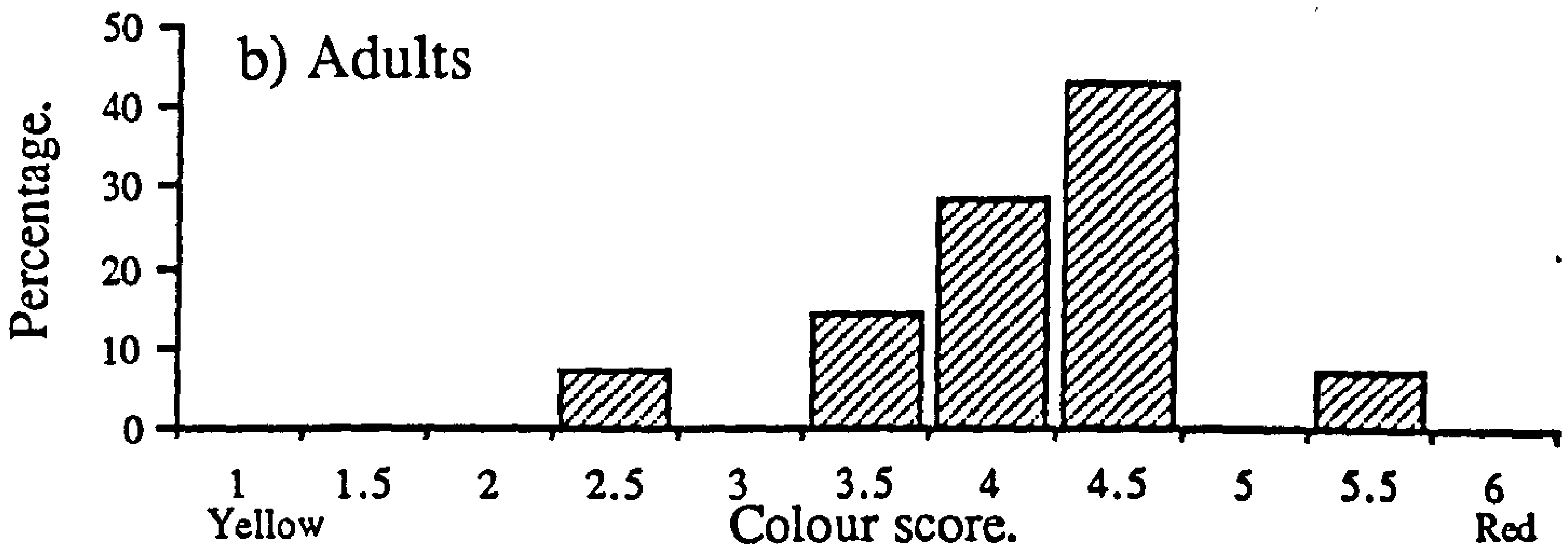
## **Appendix 10.** Structural size, body mass, condition and aerodynamic statistics for the independent sample of robins for which space use was measured using radio-tracking (n=51).

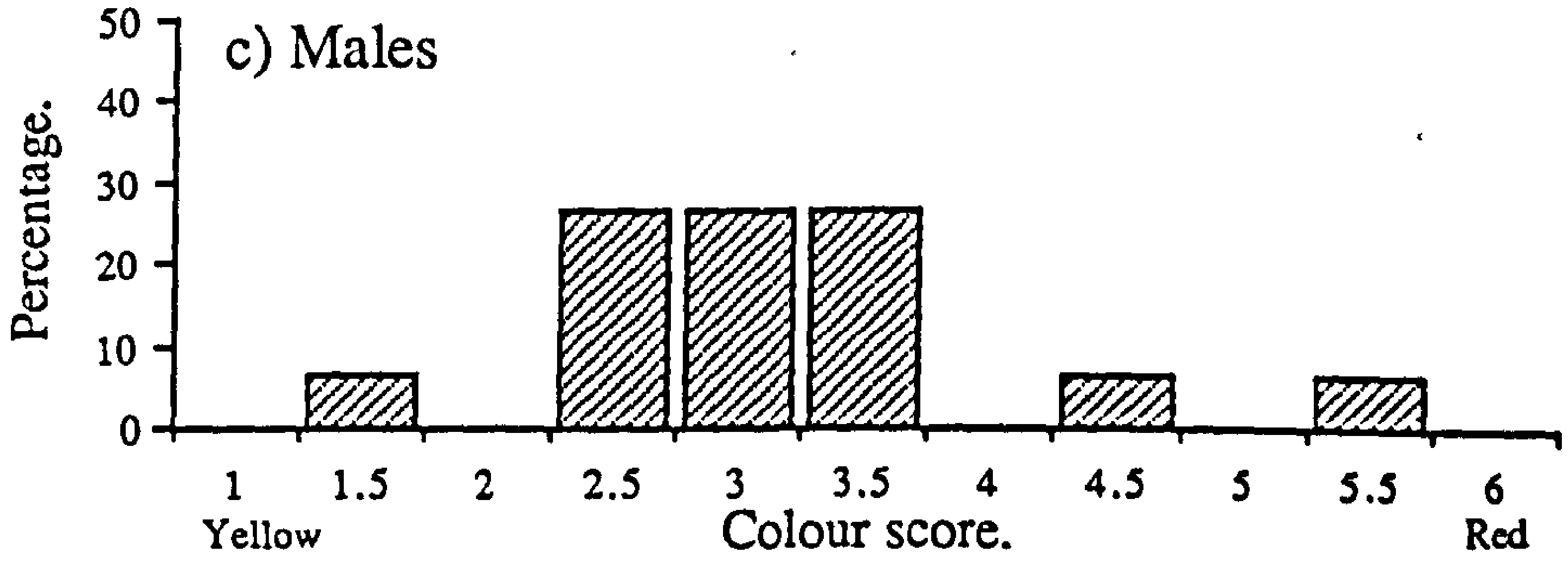
| Ring No. | Predicted mass (g) § | Wing span (mm) * | Wingdisc area (mm$^2$) # | Structure dependent wingdisc-loading (g mm$^{-2}$) $ | Observed body mass (g) | Condition dependent wingdisc-loading (g mm$^{-2}$) † | Condition (g) ‡ | Total fat score |
|---|---|---|---|---|---|---|---|---|
| F073988 | 18.84 | 232 | 42244 | 0.000446 | 21.30 | 0.000504 | 2.46 | 1 |
| F139219 | 19.52 | 225 | 39768 | 0.000491 | 19.50 | 0.000490 | -0.02 | 1 |
| H227544 | 19.93 | 227 | 40585 | 0.000491 | 18.30 | 0.000451 | -1.63 | - |
| H227546 | 18.02 | 225 | 39768 | 0.000453 | 19.00 | 0.000478 | 0.98 | 0 |
| H227547 | 20.27 | 228 | 40997 | 0.000494 | 18.30 | 0.000446 | -1.97 | 0 |
| H227533 | 19.52 | 227 | 40585 | 0.000481 | 21.20 | 0.000522 | 1.68 | 0 |
| H227556 | - | 227 | 40585 | - | 21.10 | 0.000495 | - | 0 |
| H227557 | 20.20 | 231 | 41826 | 0.000483 | 18.50 | 0.000442 | -1.70 | 2 |
| H227558 | 18.64 | 228 | 40997 | 0.000455 | 19.90 | 0.000461 | 0.26 | 1 |
| H227559 | 18.43 | 230 | 41410 | 0.000445 | 17.10 | 0.000413 | -1.33 | 0 |
| F646516 | 19.42 | 228 | 40997 | 0.000474 | - | - | - | - |
| F646519 | 19.73 | 226 | 40175 | 0.000491 | 20.60 | 0.000513 | 0.87 | 0 |
| F646521 | 18.43 | 224 | 39362 | 0.000468 | 18.20 | 0.000462 | -0.23 | 2 |
| F646521 | 18.43 | 224 | 39362 | 0.000468 | 21.90 | 0.000556 | 3.47 | - |
| F646536 | 18.98 | 231 | 41826 | 0.000454 | 19.90 | 0.000476 | 0.92 | 0 |
| F646540 | - | 225 | 39768 | - | 17.70 | 0.000445 | - | - |
| F646540 | - | 225 | 39768 | - | 20.20 | 0.000503 | - | - |
| F646541 | 19.55 | 227 | 40585 | 0.000482 | 17.60 | 0.000434 | -1.95 | 0 |
| F646546 | 19.25 | 228 | 40997 | 0.000470 | 22.10 | 0.000539 | 2.85 | 0 |
| F646546 | 19.25 | 228 | 40997 | 0.000470 | - | - | - | - |
| F646550 | 18.98 | 226 | 40175 | 0.000472 | 19.50 | 0.000485 | 0.52 | 0 |
| F646551 | - | 232 | 42244 | - | 20.10 | 0.000476 | - | 0 |
| F646551 | - | 232 | 42244 | - | 19.70 | 0.000466 | - | 0 |
| F646544 | - | 225 | 39768 | - | 19.20 | 0.000483 | - | 0 |
| F646561 | 19.07 | 228 | 40997 | 0.000465 | 18.40 | 0.000449 | -0.67 | 0 |
| F646562 | 19.41 | 230 | 41410 | 0.000469 | 21.00 | 0.000507 | 1.59 | 4 |
| F646564 | 19.01 | 230 | 41410 | 0.000459 | 19.60 | 0.000473 | 0.59 | 0 |
| F646565 | 19.25 | 228 | 40997 | 0.000470 | 18.80 | 0.000459 | -0.45 | 0 |
| F646567 | 19.79 | 232 | 42244 | 0.000468 | 19.70 | 0.000466 | -0.09 | 0 |
| F646568 | 19.99 | 231 | 41826 | 0.000478 | 18.30 | 0.000438 | -1.69 | 0 |
| F646569 | 19.49 | 228 | 40997 | 0.000475 | 17.80 | 0.000434 | -1.69 | 0 |
| F646578 | - | 224 | 39362 | - | 19.40 | 0.000493 | - | - |
| F646579 | - | 227 | 40585 | - | 20.20 | 0.000498 | - | - |
| F646581 | 19.62 | 231 | 41826 | 0.000469 | 18.50 | 0.000442 | -1.12 | - |
| F646582 | - | 225 | 39768 | - | 18.70 | 0.000470 | - | 1 |
| F646583 | - | 226 | 40175 | - | 18.40 | 0.000458 | - | 0 |
| F646585 | 19.11 | 230 | 41410 | 0.000461 | 18.20 | 0.000440 | -0.91 | 3 |
| F646586 | - | 227 | 40585 | - | 17.70 | 0.000436 | - | - |
| F646587 | - | 227 | 40585 | - | 20.40 | 0.000503 | - | - |
| F646589 | - | - | - | - | 19.10 | - | - | - |
| F646590 | 19.25 | 228 | 40997 | 0.000470 | - | - | - | - |
| F646591 | 18.67 | 226 | 40175 | 0.000465 | 20.20 | 0.000503 | 1.53 | 0 |
| F646592 | - | 231 | 41826 | - | - | - | - | - |
| F646593 | 19.50 | 226 | 40175 | 0.000485 | 19.90 | 0.000495 | 0.40 | 0 |
| F646594 | 20.20 | 232 | 42244 | 0.000478 | 20.50 | 0.000485 | 0.30 | 1 |
| F646595 | 19.99 | 230 | 41410 | 0.000483 | 21.50 | 0.000519 | 1.51 | 0 |
| F646596 | 18.74 | 231 | 41826 | 0.000448 | 17.50 | 0.000418 | -1.24 | 0 |
| F646597 | 18.88 | 226 | 40175 | 0.000470 | 17.60 | 0.000438 | -1.28 | 1 |
| F646598 | - | 228 | 40997 | - | 18.20 | 0.000444 | - | - |
| F646599 | - | 227 | 40585 | - | 16.70 | 0.000411 | - | 0 |
| F646727 | 19.15 | 230 | 41410 | 0.000462 | 21.20 | 0.000512 | 2.05 | 5 |

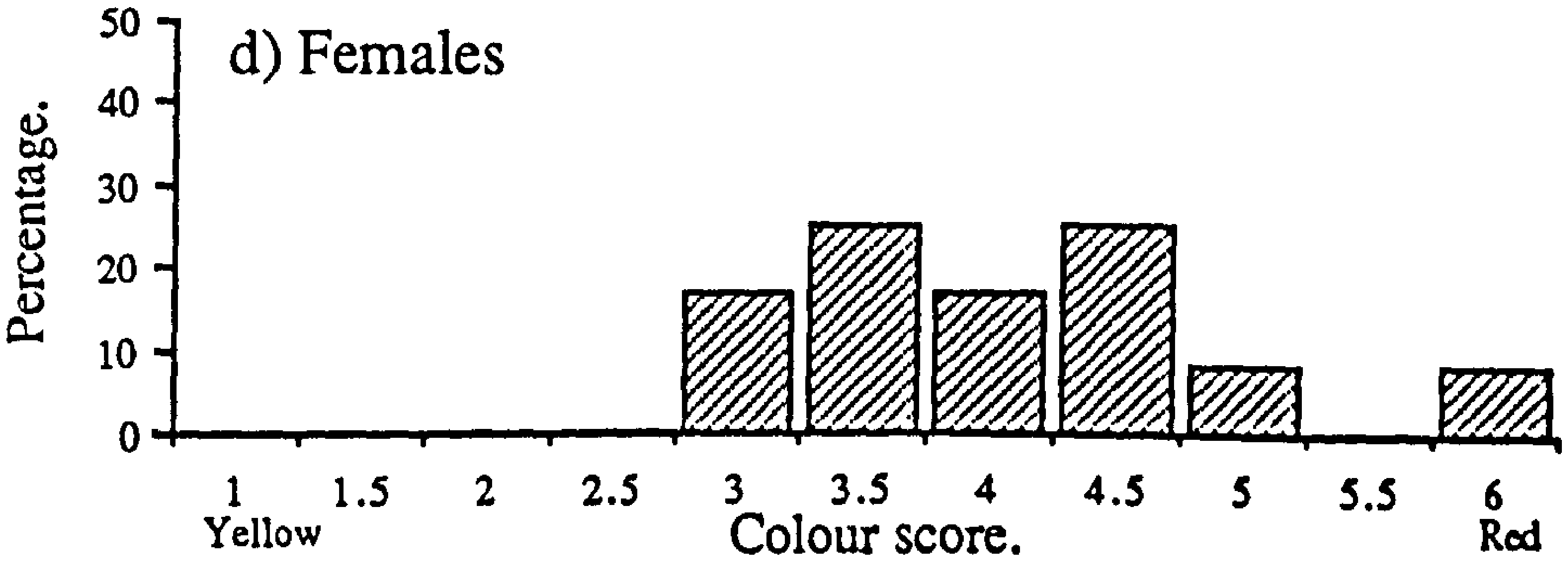
§ From equation in chapter 2, Table 2.11.
* From equation in chapter 2, Table 2.13.
# $\pi(\text{wingspan}/2)^2$ (Feinsinger & Chaplin 1975).
$ Predicted body mass divided by wingdisc area (Feinsinger & Chaplin 1975).
† Observed body mass divided by wingdisc area (Feinsinger & Chaplin 1975).
‡ Observed *minus* predicted body mass.

**Appendix 11.** The colours of robins were scored in shaded daylight by comparing their breast directly with the colours on a custom made standard chart, which ranged from faded orange (score 1) to deep rufous orange (score 8). This reflected the cline in breast colour across the wester Palaearctic (Table 7.3; after Cramp 1988). Individuals were matched to a particular shade, or scored as intermediate between two consecutive shades. The eight colour shades therefore allowed a range of 15 possible scores. Histograms (a) and (b) show data for live juveniles and adults scored while in the hand (Mann-Whitney U-test W=417 $p<0.0005$, juvenile median=3.0 n=23, adult median=4.5 n=15). Histograms (c) and (d) shown data for males and females scored from the dead birds in Appendix 1, than had been sexed by dissection (Mann-Whitney U-test W=221 $p<0.01$, male median=3.0 n=14, female median=4.0 n=12). No attempt was made to assess repeatability of scores, or changes in scores over the season.


a) Juveniles
Percentage.
0
10
20
30
40
50
1
Yellow
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
Red
Colour score.


b) Adults
Percentage.
0
10
20
30
40
50
1
Yellow
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
Red
Colour score.


c) Males
Percentage.
0
10
20
30
40
50
1
Yellow
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
Red
Colour score.


d) Females
Percentage.
0
10
20
30
40
50
1
Yellow
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
Red
Colour score.

**Appendix 12.** Common and scientific names of all plants and animals mentioned in the text, listed in systematic order.

### Plants

| | |
|---|---|
| Bramble | *Rubus fruticosus* |
| Hawthorn | *Crataegus monogyna* |

### Invertebrates

| | |
|---|---|
| Mites | Order Acrina |
| Bird fleas | Family Ceratophyllidae |
| Flatflies | *Ornithomyia avicularia* |

### Birds

| | |
|---|---|
| White-tailed tropicbird | *Phaethon lepturus* |
| Henharrier | *Cirus cyaneus* |
| Sparrowhawk | *Accipiter nisus* |
| Red-tailed hawk | *Buteo jamaicensis* |
| Pectoral sandpiper | *Calidris melanotos* |
| Sanderling | *Calidris alba* |
| Common tern | *Sterna hirundo* |
| Rufous hummingbird | *Selasphorus rufus* |
| Swallow | *Hirundo rustica* |
| Piedwagtail | *Motacilla alba* |
| Dipper | *Cinclus cinclus* |
| American dipper | *Cinclus mexicanus* |
| Robin | *Erithacus rubecula* |
| Spotted flycatcher | *Muscicapa striata* |
| Golden-winged sunbird | *Nectarinia reichenowi* |
| Nothern cardinal | *Cardinalis cardinalis* |
| Common yellowthroat | *Geothlypis trichas* |

### Mammals

| | |
|---|---|
| Rabbit | *Oryctolagus cuniculus* |
| Hare | *Lepus capensis* |
| Pika | *Ochotona princeps* |
| Fox | *Vulpes vuples* |
| Stoat | *Mustela erminea* |

# Chapter 10.

Johnstone I.G. (1992). Home range utilization and roost selection by non-breeding territorial European robins *Erithacus rubecula.*

A paper presented at the 4th European International Conference on Wildlife Telemetry held in Aberdeen, September 1991, where it was awarded the Mariner Radar Prize for the best contribution by a student. It was subsequently published in *Wildlife Telemetry: Remote Monitoring and Tracking of Animals* Ed by Priede I.G. & Swift S. Ellis Horwood, Chichester.

# 56

# Home range utilization and roost selection by non-breeding territorial European robins (*Erithacus rubecula*)

**I. G. Johnstone**
Avian Ecology Group, University of Stirling, Stirling FK9 4 LA, UK

The European robin *Erithacus rubecula* is one of the few small western Palaearctic passerines to defend individual territories during the autumn and winter (Cramp & Simmons 1988). Such defended areas are believed to be maintained by singing and the aggressive repulsion of intruders (Lack 1965).

A number of studies on the territorial behaviour of the robin have been published (e.g. Lack 1939, 1965, Harper 1984, Adriaensen & Dhondt 199). However, very few have considered what elements of the habitat are used by individuals within territories, and the degree to which they exploit regions outside their defended areas. This kind of information has been impossible to collect from small woodland birds, which are difficult to locate on a regular basis or to follow for extended periods (East & Hoffer 1986).

The use of radio-tracking has greatly facilitated the study of how animals use the habitat over which they range, and how utilization distributions (UD) overlap with those of neighbouring conspecifics. However, this technique has rarely been applied to small birds (Grieg-Smith 1985, East & Hoffer 1986, O'Connor *et al.* 1987, Hanski & Haila 1988).

The aim of this study was to measure the maximum home range size and UD of the robin during non-breeding territoriality in relation to defended areas, habitat structure and the range use of neighbouring conspecifics.

Territories cease to have any value for foraging after dusk. Individuals must select sites in which they can roost safely until dawn. Radio-tracking provides a unique method for the position of roost sites to be determined.

A second aim was therefore to measure roost quality and location in relation to the UD.

## METHODS AND MATERIALS

### The study area

Fieldwork was carried out between August and December 1990 on the campus of the University of Stirling, in central Scotland. Individuals which were radio-tracked were part of a population of European robins, *Erithacus rubecula*, inhabiting a 4-ha area of woodland and an adjacent 4-ha of parkland.

The woodland habitat was characterized by a closed canopy of mature trees, with a shrub layer covering 10% of the woodland floor. The parkland area consisted of a more open canopy, the shrub layer accounting for 5% of the area.

### Radio-tracking protocol

In their pilot study of monitoring the behaviour of great tits, *Parus major*, using radio-tracking, East & Hoffer (1986) attached radio tags using tail-clips. This method of attachment has several advantages over harnesses and glue-on techniques. The tail-clips will not disrupt the insulating qualities of the plumage, and if the bird is not recaptured tags are safely shed during the annual moult. This method of attachment was adopted for the robin.

Tail-clips weighing 0.4 g consisted of two perspex plates clamped together using a pair of nylon bolts. The single-stage radio tags used weighed 1.8 g (Biotrack, Dorset, UK). Antennas were 15-cm long external whips. Cell life frequently exceeded four weeks. the complete packages weighed 2.2 g, representing 11% of the mean body mass of the robin (19.5 g). Although this was over twice the widely recommended 5% limit (Cochran 1980), it was considered acceptable since the power surplus available to small birds is such that an additional 50% of body mass may be carried in flight by a 20-g passerine with only a 15% loss in power (Caccamise & Hedin 1985). The radio tag could be positioned closer to the bird's centre of gravity by being placed with the bulk of the package beneath the tail. This also maintained the aerodynamic profile of the bird.

All radio-tracking was done using a hand-held three-element Yagi antenna and RX-81 receiver. The 0.95 error arc (Springer 1979) of the antenna was measured as ±1.5°. Due to the confiding nature of the robin, bearings could be taken from between 10 and 20 m away and triangulated 'by eye' to determine the location of the bird. Using this method, tagged birds could confidently be pinpointed to the nearest metre.Radio-locations were allocated a grid reference on an accurate map of the study area.

Independence between successive radio-locations is an implicit assumption in statistical measurements of animal movement (Swihart & Slade 1985, Worton 1987). Samples of continuous tracking data were analyzed to determine the $t^2/r^2$ ratio and the time to independence (Swihart & Slade 1985). Results indicated that independence was achieved after 2–4 min. However, the sample interval adopted for this study was 60 min, since this enabled up to six radio-tagged individuals to be monitored simultaneously.

The number of statistically independent location estimates required accurately to represent a UD was determined by calculating observation-area asymptotes (Odum & Kuenzler 1955, Harris *et al.* 1990) using minimum convex polygons as the measure of range area, since they are sensitive to edge locations. The results from ten individuals indicated that a sample of 40 locations represented the true range size. Since it is conceivable that an individual which is actively defending a territory may spend more time near the edges of its range than near the centre, an asymptote based on the number of 5-m grid cells visited was derived for five individuals to ensure saturated sampling of the interior. When sample size exceeded 40, the rate at which new cells were visited dropped from one in three to one in 12. Consequently a standardized sample size (Harris *et al.* 1990) of 40 statistically independent location estimates was adopted for this study.

Radio-locations were collected throughout the daylight hours, the required sample size being obtained after four to five days.

The locations of roost sites were recorded in the same way as daytime radio-locations. The nature of the roost sites was recorded on the following day. Sites were assigned to the categories shown in Table 1.

### Measuring defended area

The definition of a territory as a defended area has been widely accepted (Kaufmann 1983), and is easily applied to measuring territories in the field.

Defended areas were determined by recording the locations at which robins chased intruders and exhibited behaviour involved with advertising territorial status (singing, 'tic' calling (Cramp & Simmons 1988)). Independent observations were made at all times of the day.

The number of observations required to represent the defended area of individuals accurately was determined by constructing observation-area asymptotes, an asymptotic sample being achieved at ten observations.

Observations concerning the defended area associated with a particular utilization distribution were always made during or close to the time of tracking data.

## RESULTS

### Effects of radio-tagging

On release, tagged birds immediately flew strongly and behaved apparently normally.

There was no difference in the change in body mass of six radio-tagged birds compared to six controls over the five-day period during which radio-locations were collected. Data from four individuals which carried radio tags for a mean duration of 31 days showed a 0.12% increase in body mass per day. This was considered to represent normal winter fattening. Quantitative comparison of time-budgets was not possible. However, qualitative observations led to the conclusion that the radio tags had no obvious effect on foraging or territorial behaviour.

### Defended areas and range use

Eighteen individuals were tracked between August and December 1990. Asymptotic sample sizes for defended areas were available for only nine of these, although all individuals showed some defensive behaviour.

The data from two females tracked during August and September showed considerable changes in their space use over time, and both subsequently migrated. These individuals were excluded from this analysis.

To allow comparisons with other studies of territoriality, the sizes of maximum ranges and defended areas were calculated using the minimum convex polygon (MCP) range estimator. All analysis was carried out using the Ranges IV computer package (Biotrack).

The MCP areas of maximum ranges recorded in this study were divided into three categories according to the type of habitat in which the individuals were tracked. These were woodland, parkland or mixed, when ranges overlapped the boundary between the two. Fig. 1 illustrates the strong trend towards increasing maximum range size from woodland to parkland habitat. Because of the small sample sizes statistical comparisons were not possible; however, all trends described were quite distinct. The subsample of individuals for which defended areas were available showed exactly the same trend in increasing maximum range area, although the sizes of defended areas remained relatively constant between the different habitats (Fig. 2).

Table 1. Categories used to quantify the nature of roost sites used by robins

(1) On ground in open
(2) On ground in hole
(3) Above ground in sparse vegetation (deciduous trees and shrubs, e.g. young birch and sycamore)
(4) Above ground in medium vegetation (evergreen shrubs, e.g. rhododendron and broom (*Cytisus*)
(5) Above ground in dense vegetation (thorny shrubs, gorse (*Ulex*), brambles (*Rubus*)
(6) Above ground in hole

The percentage of the defended areas which lay within maximum ranges was consistently high (Table 2), although the percentage of maximum range areas which were covered by the defended areas declined between the woodland and parkland residents (Table 2).

Of three pairs of concurrently tracked neighbours for which defended areas were known, only one pair showed any overlap between their defended areas (<1%). However the maximum ranges showed more substantial overlap, varying from 2.5% in parkland birds (two pairs of neighbours) to 13.2% in woodland birds (six pairs of neighbours).

The most appropriate technique for the estimation of core nuclei was two-dimensional cluster analysis (Kenward 1987), since UDs were predominantly non-uniform and multinuclear (the smoothing inherent in contouring methods was considered unrealistic for the robin).

Cluster analysis was carried out on each range, and plots of percentage maximum area against percentage maximum number of locations produced. The inflexion point, at which additional locations no longer contribute towards the core regions, was taken as the percentage of locations making up the cores (Kenward 1987, Harris *et al.* 1990). In the majority of ranges this was easy to define.

The core area and number of nuclei in each range remained constant relative to maximum range area. Both measures of core structure remained constant between the different habitats (Fig. 1). The subset of individuals for which defended areas were available showed the same trend (Fig. 2). The plot of maximum range area against the core area (as a percentage of the maximum range) shows the expected distribution if all ranges contained the same core area (Fig. 3). The observed distribution closely approached this.

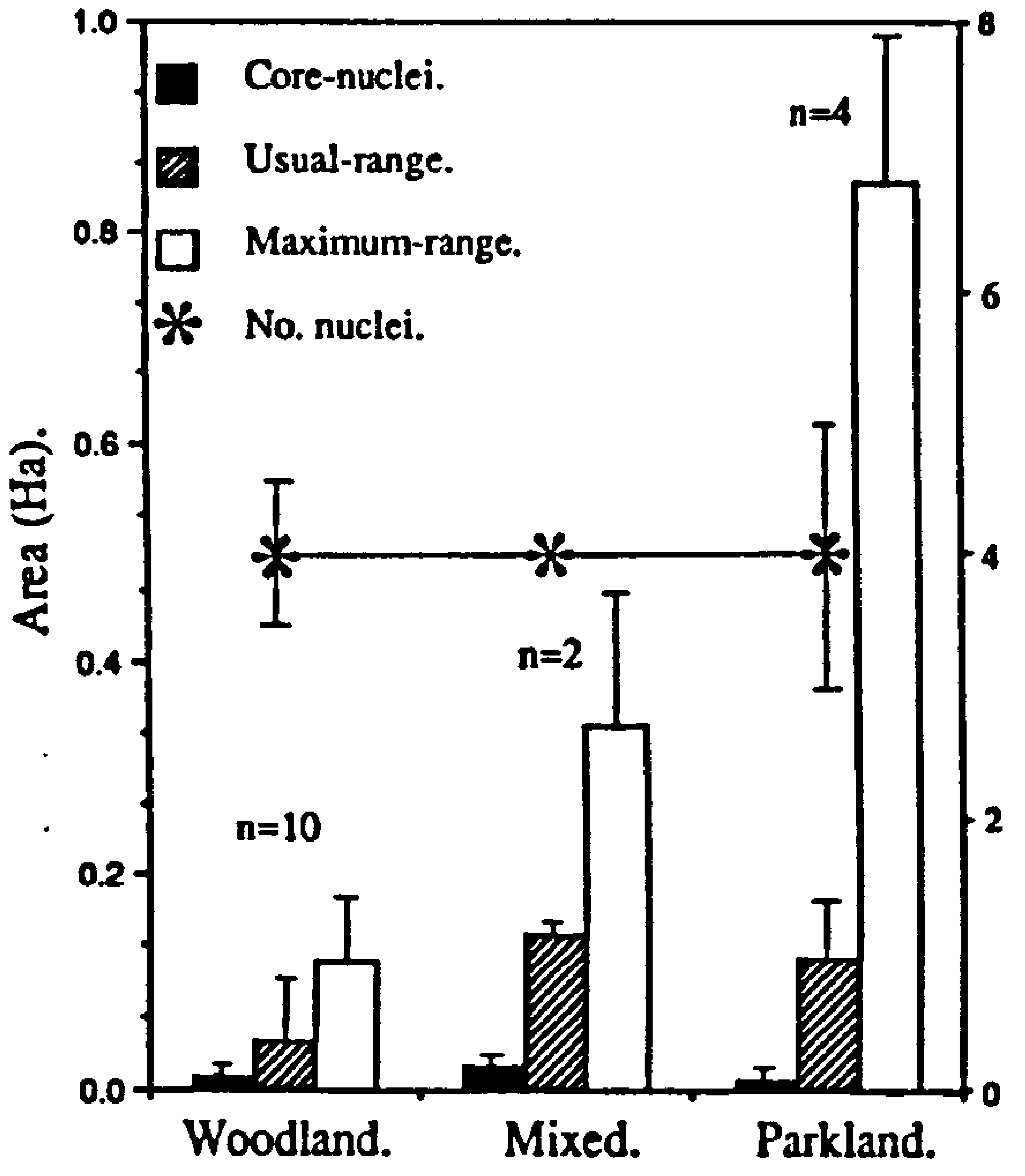


Fig. 1. Comparison of median measures of utilization distribution between different classes of habitat. Error bars show interquartile range.

Data from continuous tracking indicated that birds moved between their core nuclei using the most direct routes, usually by flying. A measure of the area within which individuals normally moved (usual range) was consequently defined as an MCP containing all of the individuals' core nuclei. This has the advantage over other measures of UD in that its definition is based on the actual pattern of movement rather than a generalized mathematical algorithm. Fig. 1 shows usual ranges compared to maximum rages for the different habitats. Usual ranges remained relatively constant in comparison to maximum ranges, while maximum rages increased from woodland to parkland. Fig. 2 illustrates the same trend for the subset of ranges for which defended areas were known. The sizes of usual ranges and defended areas showed a strong similarity. If the usual range and defended area of each individual were the same size, the expected geometric mean regression of one upon the other would have a slope of one. The observed data produced a regression of slope 1.14 (Pearson's product moment correlation coefficient = 0.702 ($n = 9$, $p<0.05$).

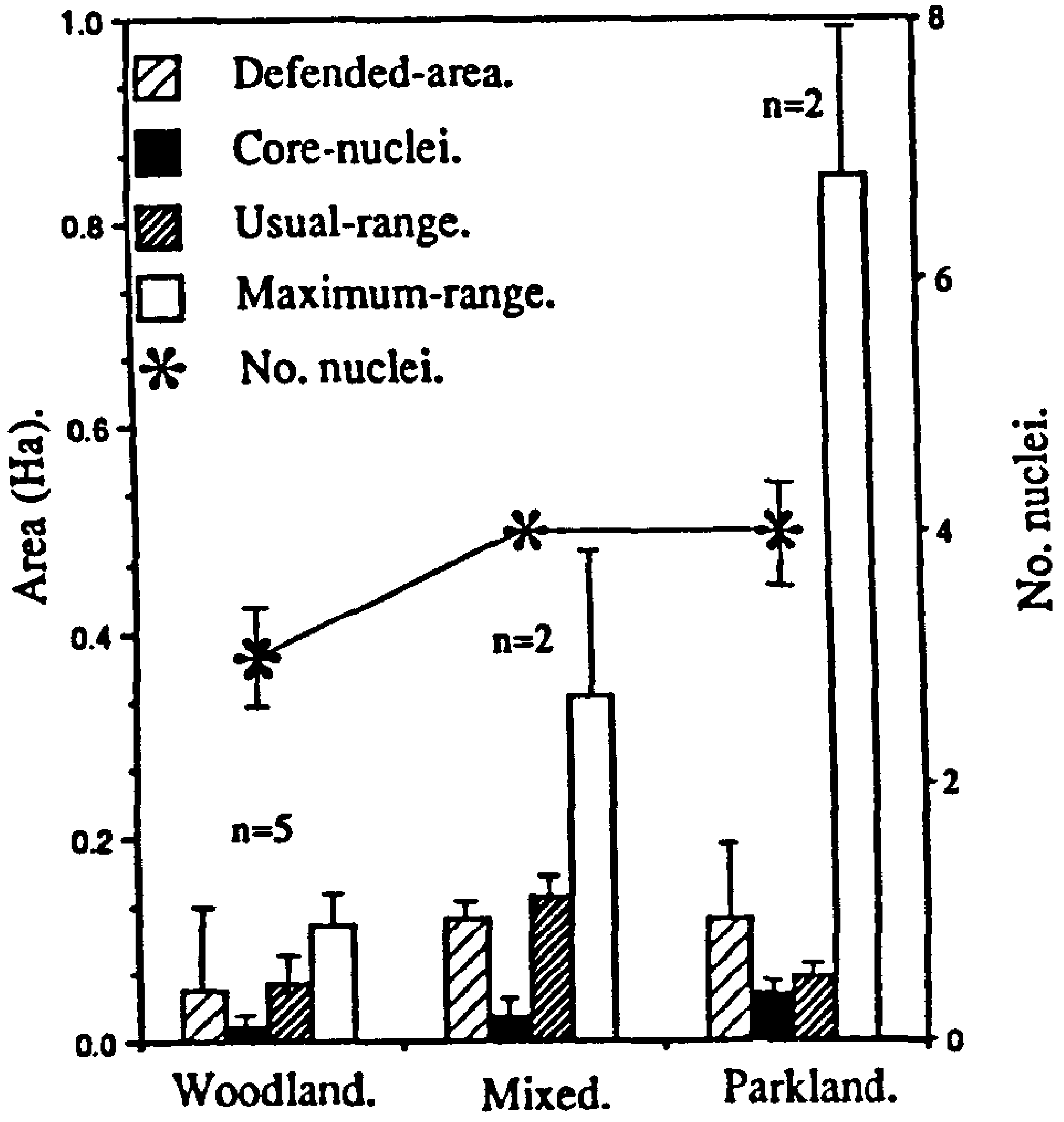


Fig. 2. Comparison of median measures of utilization distribution and defended area between different habitats. Error bars indicate interquartile range.

The results of an analysis of overlap between the different measures of UD and defended area within individuals are shown in Table 2. By definition usual ranges lay entirely within maximum ranges (Table 2). The percentage of the maximum ranges that were covered by usual ranges show the same trend as found in Table 2. for maximum ranges and defended areas. The percentage of usual range area, and numbers of nuclei that lay within defended areas, were consistently high (Table 2), as was the percentage of defended area that lay within usual ranges (Table 2) (one individual inhabiting the mixed habitat was excluded from this analysis since it had a very atypical range).

Of the eight pairs of concurrently tracked neighbours, only one pair showed any degree of overlap in their core areas (9%). Consequently, by definition, the same pair were the only individuals in which usual ranges overlapped (39%).

All locations outside the usual range were considered to be excursive activity. The excursive area was the difference between the usual range and the maximum range. This increased consistently between woodland and parkland habitats (Fig. 4). However, the proportion of fixes making up the area of excursive activity remained constant between the different habitats.

**Table 2.** Comparison of median percentage overlap between measures of utilization distribution and defended area within individuals inhabiting the different habitat classes. Values in parentheses below entry indicate interquar tile range where revelant

| | Woodland<br>($n = 5$) | Mixed<br>($n = 2$) | Parkland<br>($n = 2$) |
|---|---|---|---|
| % area of defended area lying within maximum range | 92<br>(90–98) | 91<br>(87–96) | 96<br>(95–98) |
| % area of maximum range lying within defended area | 51<br>(43–62) | 38<br>(31–35) | 15<br>(11–19) |
| % area of usual range lying within maximum range | 100 | 100 | 100 |
| % area of maximum range lying within usual range | 50<br>(34–61) | 41<br>(35–47) | 8<br>(7–10) |
| % area of usual range lying within defended area | 68<br>(44–73) | 84<br>($n = 1$) | 39<br>(38–40) |
| % no. of core nuclei lying within defended area | 71<br>(67–75) | 75<br>($n = 1$) | 67<br>(50–83) |
| % area of defended area lying within usual range | 73<br>(70–75) | 65<br>($n = 1$) | 66<br>(57–75) |

### Range use and habitat preferences

The locations of almost all core nuclei corresponded to the locations of habitat features. These were vegetation patches making up the shrub layer, in particular Rhododendron bushes.

Many of the excursive locations occurred within vegetation patches containing the core nuclei of neighbouring individuals.

Fig. 5. illustrates the UD of a robin defending a typical individual territory.

### Roost selection

Birds which roosted on the ground selected sites inside rabbit (*Oryctolagus cuniculus*) burrows. All other sites were between 1 and 3 m above ground level.

Roost sites were not considered to be part of the daytime UD. Each bird used a mean of two sites, with a minimum of one and a maximum of four. Table 3 shows the proportions of occasions on which sites were used in different locations relative to the measures of UD. These were relatively constant between the different habitat categories, with birds using sites within their own usual ranges on slightly more than half of the occasions.

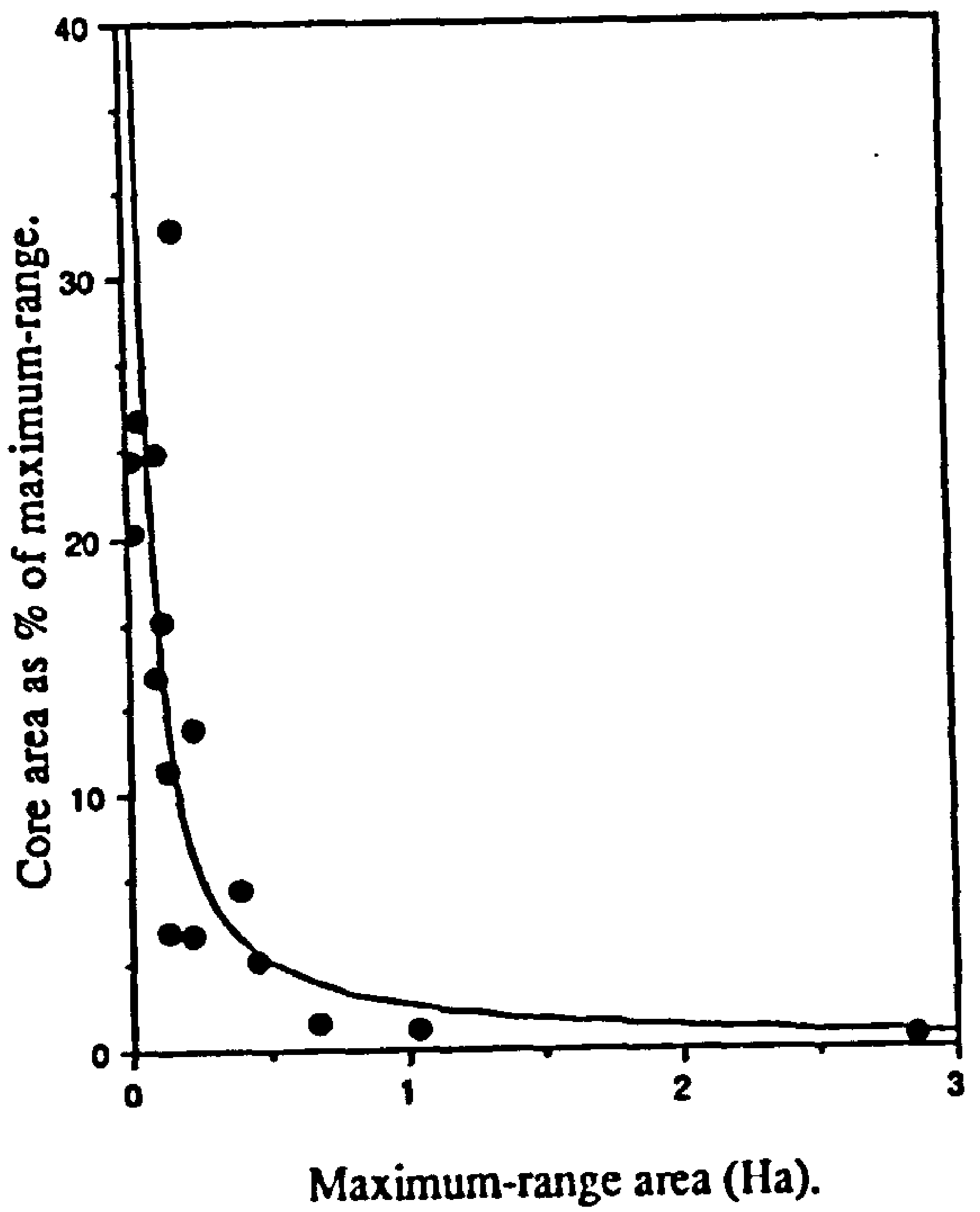


Fig. 3. Plot of maximum range area against core area (as a percentage of the maximum range) (n = 16). The curve shows the expected distribution if all ranges contained the same core area (the mean core area of all birds tracked).

Sites classed as excursive were usually less than 50 m from the usual range of each individual. Individuals which chose to roost in excursive locations were more likely to occupy sites in medium-density vegetation than those which used sites within their usual ranges (Fig. 6). Of the 28 occasions that sites were in excursive locations, 22% were in sites known to be in the core nuclei of neighbouring birds, while 66% were in bushes which were known not to contain core nuclei of other birds (48% of these were in a communal site used by three neighbouring birds). The remaining 12% of sites could not be allocated to these categories.

## DISCUSSION

### Previous studies of territory size

The defended areas recorded in this study are comparable to the values produced by Lack (1965) and Harper (1984) since the definitions used to determine territories are similar, but compared to which they were smaller. This is due to the strict use of the MCP to calculate areas in this study rather than drawing in territory boundaries 'by eye', which overestimates size by assuming territory boundaries are close-packed (e.g. Lack 1965). In support of this, there were often areas of apparently undefended space between the defended areas recorded in this study. This is considered to be neutral ground.

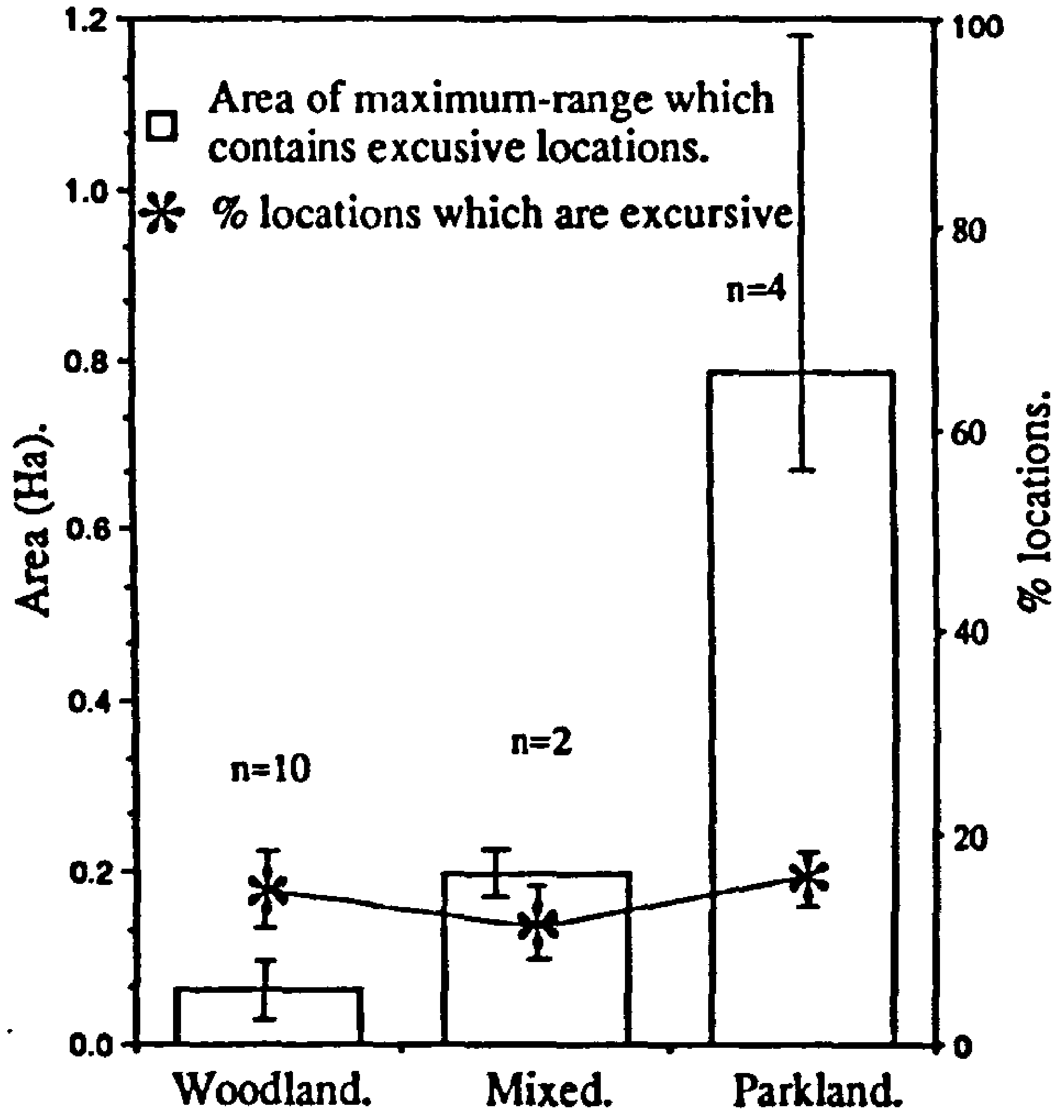


Fig. 4. Comparison of median range areas and proportions of locations which contain excursive activity. Error bars indicate interquartile range.

The data from the study by Adriaensen & Dhondt (1990) are the most comparable to maximum range sizes obtained by radio-tracking, since their definition of territory included observations of individuals not showing territorial defence behaviour. The larger values obtained by Adriaensen & Dhondt (1990) are explained by the fact that radio-tracking records the locations of individuals during excursive activity into neighbouring territories, where their furtive behaviour would prevent them being located visually.

Examination of the descriptions of habitat used to define plots in the study by Adriaensen & Dhondt (1990) shows that their parkland plot is similar to the woodland area in this study, and their wood and garden plots similar to parkland. Seen in this light, there are strong similarities between the data from the two studies, maximum range/territory being markedly bigger in habitat which contains a lower percentage area of dense vegetation.

### Range use and habitat preferences in relation to defended areas

The marked preference for individuals to concentrate their activity within clearly defined core nuclei suggests such locations contain resources of high quality. These resources are considered to be the patches of vegetation within which the nuclei occurred.

Such a preference of the robin for dense, often evergreen vegetation has been recorded previously (Hoelzel 1989, Adriaensen & Dhondt 1990). Advantages for occupying such sites could include a higher availability of food and protection from predators and severe weather.

What has not been revealed by previous studies of non-breeding territoriality in the robin is that the core area used by individuals remained constant regardless of maximum range size. Since core nuclei were concentrated on patches of high-quality habitat, these results suggest that the robin required a particular area of such habitat to survive, larger or smaller areas not being economically defendable. This has also been reported in the dunnock, *Prunella modularis*, a bird of similar habits. The range sizes of the female dunnock were found to vary so that each contained the same average feeding area of thick cover and dense bushes (Davies & Lundberg 1984).

The similar size and high degree of overlap between defended area and usual ranges suggested robins expended time and energy in defending only the core nuclei and the area between them. There was no evidence for the close-packed boundaries assumed by other studies (e.g. Lack 1939). This assumption appears to have remained unchallenged since the pioneering studies of territoriality in the robin 50 years ago (Lack 1939). Such undefended space between territories may represent poor habitat. However, the neutral interstices contained patches of dense vegetation that were indistinguishable from those that contained core nuclei. Such unused vegetation patches could result from the habitat being settled in such a way that those shrubs and bushes of the required optimal area that are in the most economical configuration to defend and exploit are occupied first. This produces numbers of vegetation patches that are suboptimal in terms of available core area and consequently cannot support robin territories.

Results indicated that individuals in each habitat category showed the same amount of excursive activity, during which they often visited the core nuclei of neighbours. However, the larger excursive area in parkland birds relative to those in woodland indicates that such individuals must travel further to achieve intrusions. This reflects the greater distance between vegetation patches, and explains the increase in maximum range between habitats.

It is probable that intruders were obtaining information concerning feeding rates and the identity of neighbours. This could be useful to any individual if food becomes scarce during severe weather, and to males in the spring when non-breeding territories are expanded in preparation for breeding.

### Range use and roost quality

Roost sites were generally similar to those recorded in previous studies (Cramp & Simmons 1988).

Of the categories of roost sites used, sites in sparse and medium-density vegetation were considered to be the highest quality since they were used most often. This is supported by the fact that birds with territories containing predominantly dense vegetation usually moved off territory to roost in areas where sparse and medium-density sites were available. The advantage conferred by such sites is probably the protection they offer from ground predators and ease of escape if disturbed. The advantageous thermal qualities of holes and very dense vegetation (Kendeigh 1961) did not seem to be important considerations for roost selection in this study.

On occasions when territorial birds roosted outside their usual range, they were more likely to acquire high-quality sites than those individuals that roosted in their core nuclei. This was a benefit of selecting excursive roost sites. Furthermore, such individuals

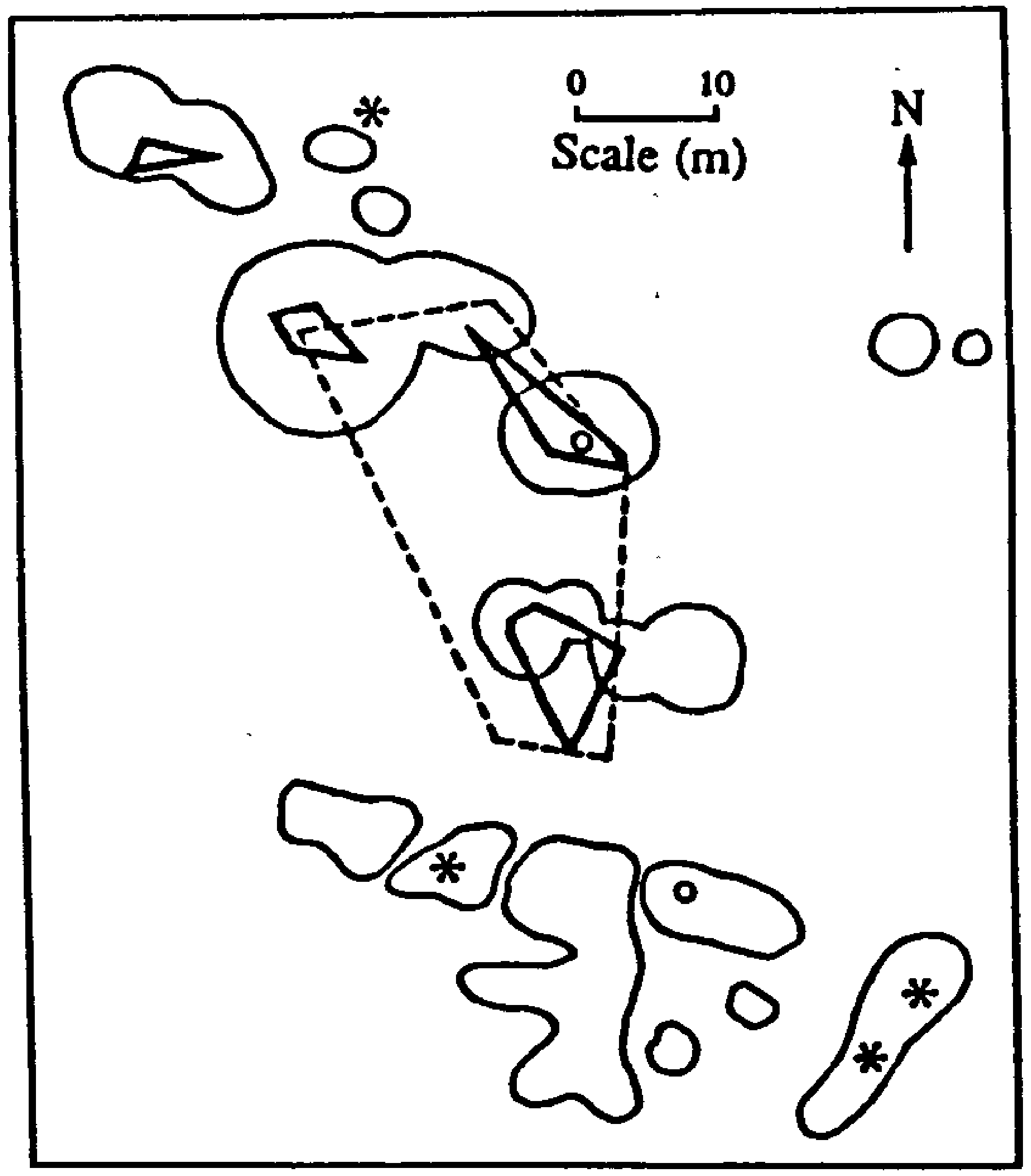


Fig. 5. Example of the UD and defended area of a first-year male robin. Thick lines enclose core nuclei and dashed lines defended areas. Thin lines outline bushes and shrubs. Asterisks represent excursive locations and open circles denote roost sites used during the five days during which it was tracked. The excursive locations to the south of the range are all located in core nuclei of neighbours. However, the excursive roost site is in a neutral interstice.

selected sites in bushes that were located in the neutral interstices between defended areas considerably more often than sites in the core nuclei of neighbours. This enabled birds roosting excursively to avoid potentially costly encounters with neighbours that were on their home ground. Another goal of excursive activity may be finding such sites. A by-product of such choice is the formation of communal roosts, as recorded in this study, where several neighbouring individuals chose the same high-quality site in a neutral interstice between their defended areas.

Such a mechanism could result in the formation of the large communal roosts previously documented (Cramp & Simmons 1988) if the catchment area in which birds lived contained poor-quality roost sites within territories, and a high population resulted in few sites being available in neutral interstices. Such a situation could arise when large numbers of migrant robins were defending feeding sites in suburban gardens.

Table 3. Proportions of occasions on which sites in different parts of the utilization distribution were used by robins in each habitat class

| | % occasions in core nuclei | % occasions in other sites in usual range | % occasions in excursive locations |
|---|---|---|---|
| Woodland | 62<br>($n = 50$) | 0 | 38 |
| Mixed | 50<br>($n = 10$) | 0 | 50 |
| Parkland | 60<br>($n = 20$) | 0 | 40 |

### Implications for the study of territoriality in small birds

Many studies of territorial passerines are purely ethological. In such studies it is often only necessary to determine the identity of resident territorial birds, the identity of their neighbours and the approximate positions of territorial boundaries for the purposes of playback experiments (e.g. Brindley 1991).

When ecological aspects of territoriality are being considered, such as territory quality, researchers must consider carefully how territorial boundaries are to be determined, and be aware that some areas apparently within a defended are may be rarely or never used due to patchiness in the quality of the habitat. The close-packed polygonal territories of Grant (1968), although realistic in uniform habitats such as tundra, are apparently an inadequate model of territory structure in an irregular patchy environment such as that inhabited by the robin.

## ACKNOWLEDGEMENTS

I would like to thank Professor D. M. Bryant and two anonymous referees for helpful comments on the manuscript. This work was funded by a NERC studentship.

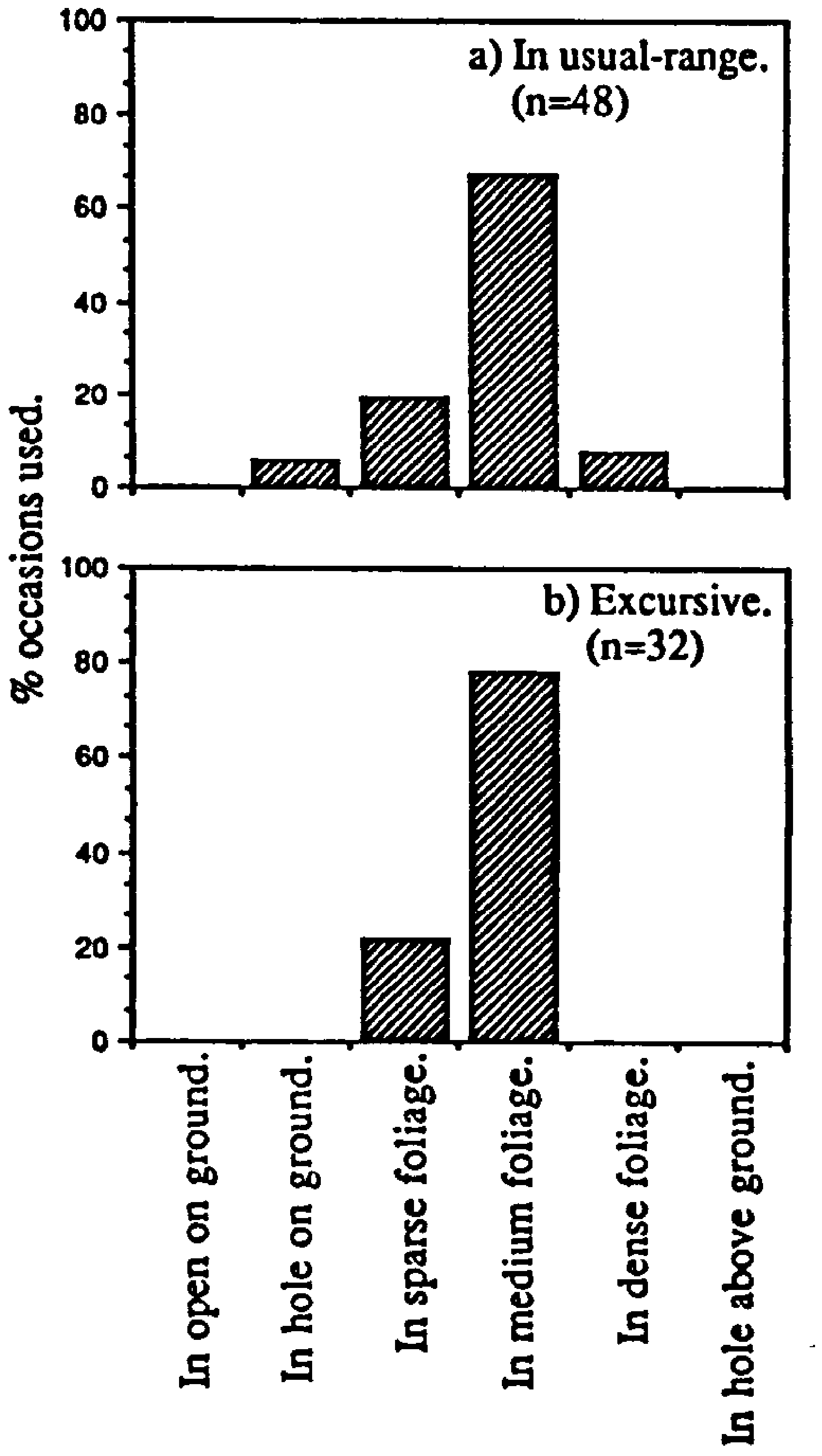


Fig. 6. Proportion of occasions on which robins selected roost sites of a different nature (a) when sites were within usual ranges and (b) when sites were in excursive locations.

## REFERENCES

Adriaensen, F. & Dhondt, A. A. (1990) Territoriality in the continental European robin *Erithacus rubecula*. *Ardea* **78** 459–465.

Brindley, E. L. (1991) Response of European robins *Erithacus rubecula* to playback of song: neighbour recognition and overlapping. *Anim. Behav.* **41** 503–512.

Caccamise, D. F. & Hedin, R. S. (1985) An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bull.* **97** 306–318.

Cochran, W. W. (1980) Wildlife telemetry. In Schemnitz, S. D. (ed.), *Wildlife Management Techniques Manual.* Wildlife society, Washington, DC, pp. 507–520.

Cramp, S. & Simmons, K. E. L. (eds) (1988) *The Birds of the Western Palaearctic*, Vol V. Oxford University Press, Oxford.

Davies, N. B. & Lundberg, A. (1984) Food distribution and a variable mating system in the dunnock. *J. Anim. Ecol.* **53** 895–912.

East, M. L. & Hoffer, H. (1986) The use of radio-tracking for monitoring great tit *Parus major* behaviour: a pilot study. *Ibis* **128** 103–114.

Grant, P. R. (1968) Polyhedral territories of animals. *Am. Nat.* **102** 75–80.

Greig-Smith, P. W. (1985) Winter survival, home ranges and feeding of first year and adult bullfinches *Pyrrhula pyrrhula*. In Sibly, R. M. & Smith, R. H. (eds), *Behavioural Ecology: Ecological consequences of Adaptive Behaviour.* Blackwell Scientific, Oxford, pp. 387–392.

Hanski, I. K. & Haila, Y. (1988) Singing territories and home-ranges of breeding chaffinches, visual observations vs. radio-tracking. *Ornis Fennica* **65** 97–103.

Harper, D. G. C. (1984) The energetics of territoriality in the European robin *Erithacus rubecula*. Unpublished PhD thesis, University of Cambridge.

Harris, S. Cresswell, W. J., Forde, P. G., Trewhella, W. J. Woollard, T. & Wray, S. (1990) Home-range analysis using radio-tracking data: a review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* **20** 97–123.

Hoezel, A. R. (1989) Territorial behaviour of the robin *Erithacus rubecula*: the importance of vegetation density. *Ibis* **131** 432–436.

Kaufmann, J. H. (1983) On the definitions and functions of dominance and territoriality. *Biol. Rev.* **58** 1–20.

Kendeigh, S. (1961) Energy of birds conserved by roosting in cavities. *Wilson Bull.* **73** 140–146.

Kenward, R. (1987) *Wildlife Radio-tagging: Equipment, Field Techniques and Data analysis.* Academic Press, London.

Lack, D. (1939) The behaviour of the robin part I. The life history with special reference to aggressive behaviour, sexual behaviour and territory. *Proc. Zool. Soc. Lond. (A)* **109** 169–178.

Lack, D. (1965) *The Life of the Robin.* Witherby, London.

O'Connor, P. J., Pyke, G. H. & Spencer, H. (1987) Radio-tracking honeyeater movements. *Emu* **87** 249–252.

Odum, E. P. & Kuenzler, E. J. (1955) Measurement of territory and home range size in birds. *Auk* **72** 128–137.

Springer, J. T. (1979) Some sources of bias and sampling error in radio triangulation. *J. Wildl. Manage.* **43** 926–935.

Swihart, R. K. & Slade, N. A. (1985) Testing for independence of observations in animal movement. *Ecology* **66** 1176–1184.

Worton, B. J. (1987) A review of models of home range for animal movement. *Ecol. Model.* **38** 277–298.