SOCIAL ORGANISATION AND FEEDING BEHAVIOUR OF WINTERING TURNSTONE (ARENARIA INTERPRES).

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To Pat and YRM, a couple of lovely ladies.

DECLARATION

I hereby declare that this thesis has been composed by myself and that the work described within it is my own except where duly acknowledged.

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ABSTRACT

The behavioural ecology of wintering turnstone Arenaria interpres was studied over a period of three years at a rocky shore in S.E.Scotland and for one year in captivity. About 75% of the turnstone at the study site were individually colour-ringed.

Individuals tended to be site faithful to the same intertidal area within and between winters, although some indivduals were more itinerant than others. Itinerancy appeared to be related to unstable food supplies, although social status may also have played a role. The basic social unit of turnstone was a flock of about twenty to eighty individuals which had a relatively stable membership.

For each group of birds which shared occupancy of a common intertidal area a linear and stable dominance hierarchy could be constructed. Males were usually dominant over females, and adults were invariably dominant over juveniles. Within a sex, older birds were probably higher ranking. Between birds from the same ´home´ intertidal area dominance was site-independent but between birds from different intertidal areas dominance was site-dependent: an individual´s status appeared to wane with increasing distance from its home area. Levels of aggression were highest in autumn: this appeared to be due to birds asserting and re-establishing their dominance over other individuals on return fom the breeding grounds. In feeding birds the distribution and density of the prey appeared to be the prime determinant of aggression rates.

Wintering turnstone have individually variable plumage. Plumage differences did not reflect social rank differences, so plumage does not signal status as suggested by status signalling theory. Rather turnstone used plumage differences in identifying other individuals.

The main prey of turnstone were amphipods, littorinids and barnacles. Different feeding techniques were used to obtain these different prey: routing seaweed, turning stones, probing and hammer-probing. Each individual bird usually had a predilection to use a particular technique; different individuals often used different techniques even when feeding in the same flock. There were several factors which appeared to influence individuals´ feeding behaviour: phenotypic differences, habitat heterogeneity, status, sex, and to a lesser extent, tide and season. In autumn, juveniles were less efficient foragers than were adults but these differences attenuated over the winter as juveniles´ efficiency increased.

CHAPTER 1

GENERAL INTRODUCTION

Waders or shorebirds (Charadrii) are ideal subjects for testing several problems in behaviour, ecology and evolution. The suitability of waders as research subjects lies in their enormous behavioural and ecological flexibility, the comparative ease with which they can be observed due to the openess of the habitats they live in, and the amenability of their prey to sampling. For instance, waders exhibit a range of mating systems and breeding strategies unrivalled by other birds (e.g. Pitelka _et_ _al_, 1974). Recent studies of wintering and migratory waders are beginning to reveal similar levels of inter- and intra-specific behavioural and ecological variability (e.g. Burger & Olla, 1984).

In the last two decades there has been a substantial increase in the number of studies on waders. Growing realisation in America of the diversity of breeding waders´ mating systems prompted many of the earliest of these studies (summarised by Pitelka _et_ _al_, 1974), but in Britain the initial impetus behind much research was the increasing risk of loss of wintering waders´ intertidal areas through reclamation and, therefore, the possible reduction of wader populations (e.g. Smith & Evans, 1975; Evans _et_ _al_, 1979). Not surprisingly, much work on wintering waders in Britain and, for similar reasons, in the rest of Europe, has been concerned with estuarine populations or sub-populations (e.g. Goss-Custard, 1969; Pienkowski, 1980). These studies have tended to obtain information on population ecology and behaviour rather than focussing on individual birds.

As a result of the challenge to conventional evolutionary theory from the idea of group selection (Wynne-Edwards, 1962), there was a reformulation of ideas about natural selection, emphasising the individual or the gene as the level at which selection acts (Williams, 1966; Dawkins, 1976). In addition, ideas from game theory explicitly recognise that individuals behave differently (Maynard Smith, 1982). Moreover, theoretical treatments of feeding behaviour, social status and movement patterns show that individual differences are expected to have profound effects on the dynamics of populations (Partridge & Green, 1985; Gauthreaux, 1978; Swingland, 1984), yet there have been few empirical studies of the origins of individual behavioural differences, how they are maintained or their ecological consequences. These theoretical developments together with the increasing number of studies of individually marked waders have indicated that many key issues in the biology of wintering waders can only be addressed by studying individuals (Myers, 1984; Goss-Custard, 1985).

The need for work on individually marked waders is also essential both to predict the full impact of habitat disturbance on wintering populations and in the formulation of realistic management plans for the conservation of waders. Information on, for example, site tenacity, populations´ use of food resources, and differential vulnerability to starvation or predation must be considered in any management proposals, and such information will be most accurate if gathered from individually marked populations (e.g. Myers et al, 1979).

Perhaps because of the less immediate destructive threat to the rocky shore habitat and the comparative inconspicuousness of birds in this habitat, the study of rocky shore waders has lagged well behind the study of estuarine birds (Feare & Summers, 1985). Yet recent counts of waders wintering on the rocky coastline of Britain have revealed that large numbers use the rocky shore in winter, the numbers rivalling or exceeding those of estuarine individuals for some species (M. Moser, pers. comm.). The question of whether rocky shores could support extra numbers of waders displaced by estuarine reclamation schemes, the increased likelihood of oil spills, and the importance of the habitat for many species such as the turnstone *Arenaria interpres* and purple sandpiper *Calidris maritima*, all point to the desirability of more rocky shore studies.

Thus, there is an increasing need for research both on the behavioural ecology of individual waders and on rocky shore birds. Marshall's (1981) work on an unmarked wild population and a captive flock of wintering turnstone suggested that major behavioural and ecological differences probably existed among individuals of this species, making it a potentially ideal study species. In this thesis I present results from a study of a rocky shore population of individually marked turnstone in winter. I examine several aspects of this species' wintering behavioural ecology, including home range, dominance and aggression, and feeding behaviour.

The turnstone is a small (around 120g), stockily built wader and is common on most of the coastline in Britain and Ireland during its non-breeding season. The winter population on British estuaries has been estimated at between 10-11,000 birds (Prater, 1981), and on rocky shores the numbers are around 36,000 (M. Moser, pers. comm.). Turnstone usually forage in small flocks of less than one hundred individuals, and with their short, very slightly upturned bill they feed on a variety of foodstuffs using several feeding techniques such as probing, digging and turning over seaweed or stones (Marshall, 1981). Their food items vary with habitat, but include mainly amphipod crustaceans, gastropod molluscs and barnacles (Harris, 1979).

The breeding range includes most of the high arctic but extends southward into Scandinavia. The vast majority of British wintering birds probably breed in Greenland and Ellesmere Island, N.E. Canada (Branson _et al_, 1978). Autumn migration in Britain begins in mid-July and consists of both Greenland/Canadian birds, which moult and remain for the rest of the winter, and Scandinavian birds, which put on fat before continuing their migration to their West African wintering ground (Branson _et al_, 1978, 1979).

Wintering birds seem to be faithful to the same area both within and between winters (Summers _et al_, 1976; Branson _et al_, 1979; Symonds _et al_, 1984), and show a mid-winter peak of fat reserves, presumably to offset the risk of food shortage (Feare & Summers, 1985; Johnson, 1985). Fat is accumulated again in April and May prior to spring migration and return to the breeding grounds but most first-year birds remain for the summer. Few Scandinavian breeding birds pass through Britain in spring (Branson _et al_, 1978).

Annual survival in adult turnstone is high, around 90% (Evans & Pienkowski, 1984; Metcalfe, pers. comm.) but is lower in juveniles (first-year birds) (Boyd, 1962): in southeastern Scotland wintering juveniles were more likely to be killed by sparrowhawks _Accipiter nisus_ than were adults (Whitfield, 1985).

More details of turnstone biology are given by Marshall (1981), and Cramp & Simmons (1983).

1.1 THE STUDY SITE

The study site was about 48km east-north-east of Edinburgh on the East Lothian coast, Scotland, extending from Tantallon Castle in the north to the north side of the Tyne estuary near Tyninghame (hereafter referred to as Tyninghame) in the south (Fig. 1.1). The main study area was between Oxroad Bay, near Tantallon Castle, and Peffer Sands (Fig. 1.2). The rocky shore between Gullane Bay and Tyninghame, on the south side of the outer Forth, holds an internationally important population (.1% of west European population) of wintering turnstone (Campbell, 1978). Most of the littoral zone at the study site was relatively flat, making it a particularly suitable area to observe the social and feeding behaviour of turnstone. In addition, Marshall (1981) had previously carried out a study of turnstone at Scoughall, thereby providing some valuable information on a section of the study population: a detailed description of the study site around Scoughall can be found in Marshall (1981) and Baker (1981).

In the north of the study area between Tantallon Castle and The Gegan the littoral zone is comparatively narrow and lies at the base of cliffs. This section is the most exposed area in the study site and coverage of Fucoid seaweeds is low, being mainly restricted to small short fronds, and barnacles are the commonest invertebrate present. The Gegan is separated from the Great Car by a sandy beach. For over half the tidal cycle the Great Car is cut off from the land and is consequently an important roost site for many birds, particularly around high tide when most of the local waders use it at

Fig. 1.1The study site: the inset shows its location on the Scottish coast

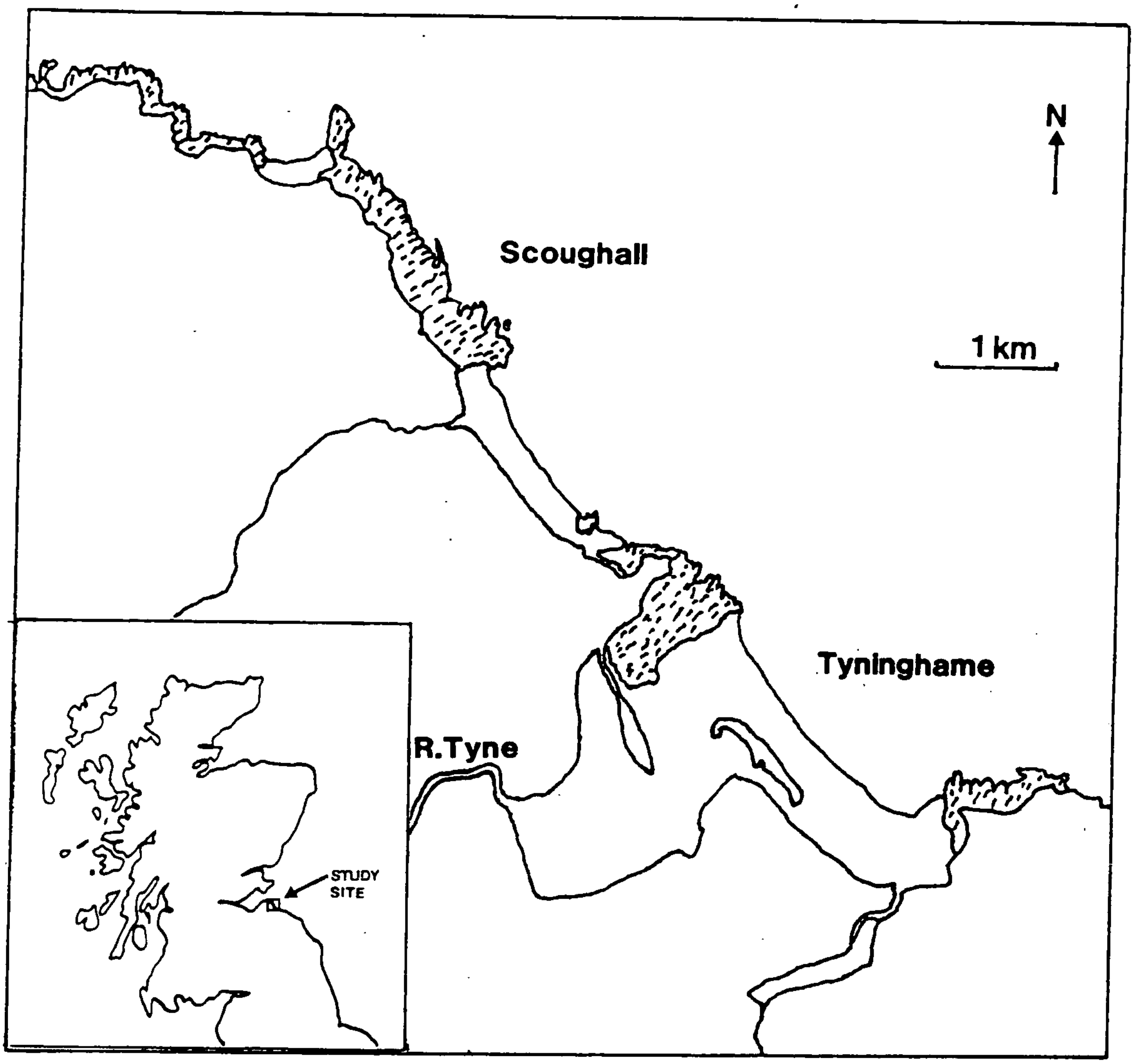
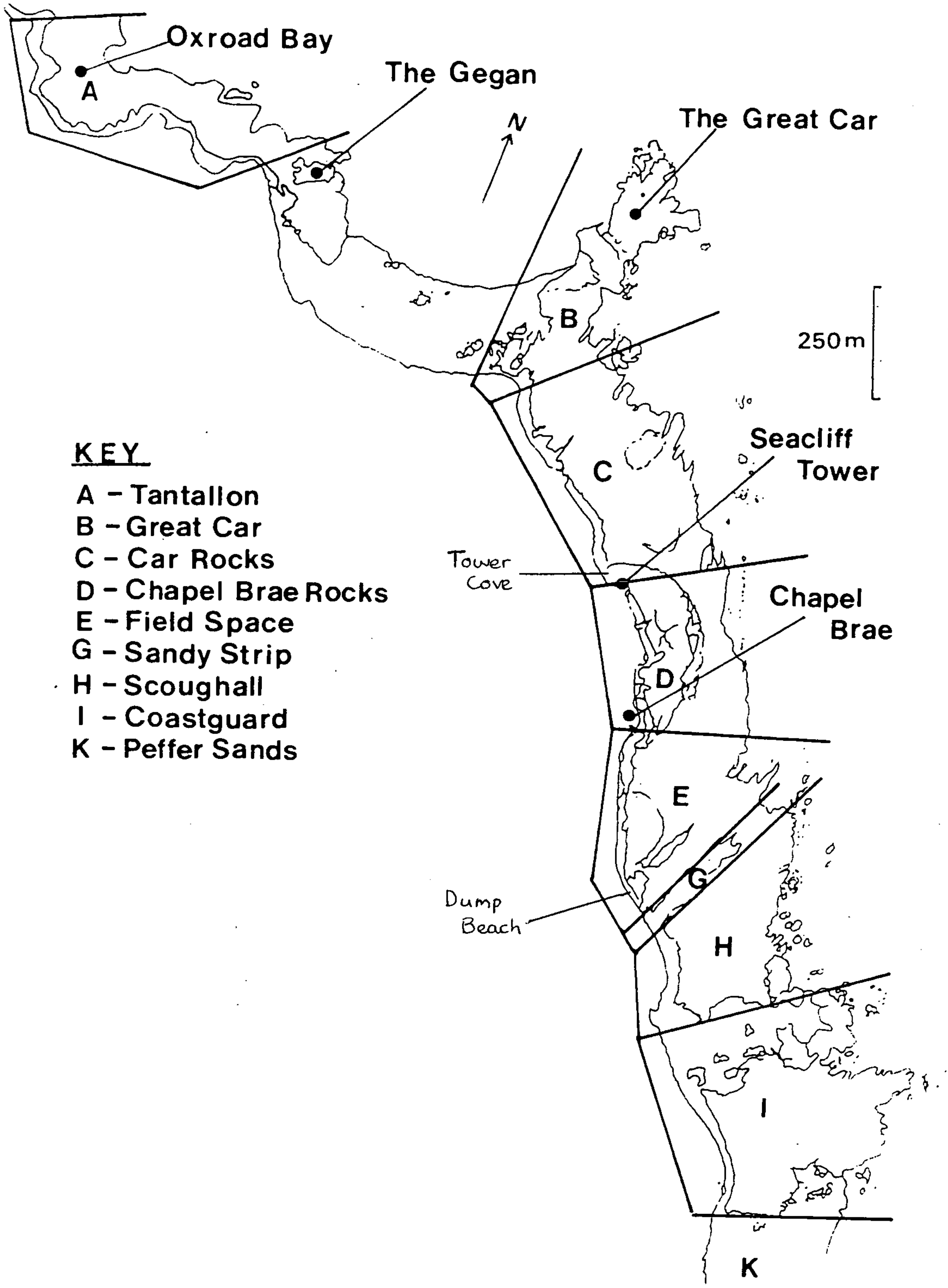

N
Scoughall
1 km
Tyninghame
R.Tyne
STUDY SITE

Fig. 1.2 The main study area showing delineation of main intertidal areas.


Oxroad Bay
The Gegan
The Great Car
N
250m
Seacliff Tower
Tower Cove
Chapel Brae
Dump Beach
A
B
C
D
E
G
H
I
K
KEY
A – Tantallon
B – Great Car
C – Car Rocks
D – Chapel Brae Rocks
E – Field Space
G – Sandy Strip
H – Scoughall
I – Coastguard
K – Peffer Sands

least occasionally. Between the Great Car and the shoreline is an area capable of supporting high densities of large barnacles Balanus balanoides and medium sized mussels Mytilus edulis.

South-east of the Great Car the littoral zone is comparatively wide and flat and riddled with what are frequently large pools. This area, the Car Rocks, has a moderate coverage of Fucoid seaweeds, primarily Fucus serratus, and its southern boundary is delimited by Seacliff Tower. The rocks between Seacliff Tower and Chapel Brae, the Chapel Brae Rocks, are frequently used by waders as a pre-roost site or, on some neap high tides, as a proper roost site. The Field Space lies south-east of Chapel Brae and is basically an extremely flat area holding several very shallow pools separated from the sea at low tide by several ridges of craggy rocks. At Scoughall the littoral zone is still relatively flat but is more undulating than at Field Space and consequently pools are fewer in number but slightly deeper and larger. The most southerly area of the main study site is the Coastguard where the topography of the littoral zone becomes even more undulating and contoured. Between Field Space and Coastguard seaweed (mainly Fucus vesiculosis and F. serratus) coverage is frquently extensive and dense for the most part.

The upper littoral zone was composed mainly of sandy beaches but pebble beaches were found at Dump Beach and Tower Cove (Fig. 1.2). The coastline of the main study area is bordered mainly by open farmalnd interspersed with small deciduous woods and occasional narrow strips of conifers. Sea-buckthorn Hippophae rhamnoides borders much of the shoreline. At Tyninghame the rocky shore and mussel beds used by turnstone are abutted onto a mixed woodland.

1.2 GENERAL METHODS

The study took place in the ´winters´ (August to April) of 1981-82, 1982-83, 1983-84. Some data were also collected in the 1984-85 winter. Observations were made from between, within or just seaward of sea-buckthorn bushes. In areas lacking cover turnstone were watched from a hide, although provided I was reasonably still the birds appeared to be unaffected by my presence in the open: if I was in an open position well before the tide forced birds onto beaches I could often watch them feeding on the strandline some 10 to 15m away. Turnstone were watched through a 15-60x telescope mounted on a tripod, or more rarely, through binoculars. Turnstone (and other waders) less than one year old were termed juveniles and older birds termed adults.

I differentiated between two broad types of littoral habitat: intertidal areas and the strandline. Intertidal areas were the rocky areas seaward of sandy or pebble beaches, the strandline was the sandy or pebble beaches (zone A of Marshall, 1981, p.12).

Unless stated otherwise, all statistical tests were two-tailed. Data analysis was usually performed with the aid of a computer linked to the Edinburgh Regional Computing Centre (ERCC) and I used the SPSS, SPSSX (Nie et al, 1975, 1983) and MINITAB (Ryan et al, 1976) statistical packages. Full descriptions of the statistical tests used can be found in Siegel (1956) and Sokal & Rohlf (1969).

1.3 CANNON-NETTING AND COLOUR-RINGING METHODS

Catching operations were carried out in the four winters from November 1981 to January 1985. Catching attempts were made at several positions on the study site from Peffer Sands in the south to Dump Beach in the north (Fig. 1.2), and every attempt was made at or near high tide on birds feeding or roosting on the beaches. Birds were always caught using cannon-nets belonging to the Zoology Department of Edinburgh University: a full description of these nets and other equipment used in cannon-netting operations are given by Clark (1983). Each captured bird was ringed with a BTO numbered ring on the tibio-tarsus of one leg, and two colour-rings were placed around the tarso-metatarsus of each leg. Each Darvic plastic colour-ring was approximately 7.2mm tall and had an internal diameter of 5.5mm with an overlap of 40%. Eight colours were used; white (W), yellow (Y), orange (O), red (R), lime (L), green (G), blue (B), and black (N), and each bird was given a unique combination. Reading combinations was accomplished by starting on the upper left leg and finishing on the lower right, birds were known by a four letter combination e.g. YONW, BWWR. In each winter separate sets of combinations were used for adults and juveniles, so, for example, in the 1981-82 winter all combinations beginning YG denoted a juvenile i.e. an individual born in the summer of 1981, and in the 1982-83 winter all combinations beginning BG denoted a juvenile, born in the summer of 1982. A total of 275 adults and 38 juveniles were colour-ringed.

As well as being aged (see Prater <u>et al</u>, 1977) each bird was also weighed using a Pesola spring balance, its wing length and tarsus plus toe were measured using a stopped rule and its bill length and total head length was measured using a pair of CAMLAB calipers. More details about how these measurements were taken are given in the relevant sections of the next chapter and by Clark (1983).

1.4 THE CAPTIVE FLOCK OF TURNSTONE

On 25 and 26 October 1984, 14 adult and 1 juvenile turnstone were caught under an NCC licence using cannon-nets at Westhaven, 4km north of Carnoustie on the east coast of Scotland (Fig. 3.1). They were transported to the Zoology Department roof aviary where they were kept until their release at Westhaven on 8 July 1984. In the intervening period two birds died, one on 30 April 1984 from unknown causes and a second on 3 June 1984 as a result of an accident during a gale. Otherwise the turnstone appeared to adapt well to captivity.

The aviary has been described in detail by Marshall (1981). It consisted of two parts, a northerly section with an area of 5.6x4.85m and a southerly section of 4.85x4.95m, which could be connected by opening doors. The aviary was of a lean-to design and built against the east wall of the Department's ventilation and water tank room. A door in this wall led directly into the southerly section of the aviary, and a one way mirror inset into this door allowed observations of the birds to be made from within the ventilation room. The west wall was a 1.1m high concrete parapet, as was the first 1.1m of the north wall The rest of the north wall, the dividing wall, the south wall and the roof was half inch chicken wire netting

The turnstone were fed daily between 9 and 10am. on a standard food mix (Table 1.1) supplemented by mealworms, maggots and natural prey from the seaweed which was regularly placed in the aviary. A

TABLE 1.1

Food mix fed to captive turnstone.

1 litre	dry mixture*
6	hard boiled eggs
2 tablespoons	Cod-liver oil
10 drops	Abidec multi vitamins

Add water until moist.

*

6 parts	puppy mash (dog biscuit)
2 parts	chick layer mash (poultry feed)
1 part	wheatgerm

hosepipe ran from the ventilation room into aluminium trays and provided a constant flow of fresh water for drinking and bathing. Excess water drained through a hole in the floor of the aviary.

Shelter was provided, but the birds rarely used it, even in strong winds when they sheltered on the bottom part of the parapet.

Before the birds were first released into the aviary each bird was ringed with a unique combination of PVC Darvic colour-rings and in the first week of captivity were disturbed as little as possible.

CHAPTER 2

THE STUDY POPULATION AND GENERAL METHODS

2.1 INTRODUCTION

Like all of the turnstone wintering in Europe, the turnstone at Scoughall are of the nominate subspecies Arenaria interpres interpres (Cramp & Simmons, 1983). The vast majority of turnstone which winter in Britain breed in Greenland and Ellesmere Island, N.E. Canada (Branson et al, 1978), and two recoveries of turnstone wintering in southeast Scotland confirm that this is true of the study population: one bird ringed at Scoughall was recovered at Hochstetterforeland, N.E.Greenland, whilst another ringed in Fife was recovered at Alert, Ellesmere Island (Morrison, 1975). In this chapter I document the return of turnstone to Scoughall from the high arctic in late summer, and describe attempts to assess annual variations in their breeding success by monitoring annual variations in the numbers of juveniles in the population. I also describe the techniques I used to sex turnstone, and estimate the sex ratio of the population. Several aspects of weight changes of the study population are also outlined. In addition, I present winter mortality estimates and data on the causes of death.

2.2 COUNTS AND POPULATION ESTIMATES

2.2.1 METHODS

Throughout the study period I counted the turnstone at or near high tide by walking the length of the study site, every two weeks if possible, and noting the numbers of turnstone which I saw. Because of the possibility of birds moving around the study site I attempted to count birds as quickly as possible so I usually went to favoured beaches first. Chapel Brae cliff (see Chapter 1) was a particularly good vantage point from which much of the study site could be seen and it also faced directly onto rocks which were a favoured pre-roost and roost site, so I often began my counts from there.

Whenever possible I also counted the ratio of colour ringed:unringed turnstone in flocks at all stages of the tidal cycle but particularly in high tide flocks.

2.2.2 RESULTS AND DISCUSSION

The numbers of turnstone wintering on the study site during non-migration periods was around 200-250 (Fig.2.1). Numbers also appeared to vary slightly year-to-year, possibly as a result of annual variations in breeding success or movements of adults (see later and also Chapter 3). Numbers were larger in autumn than in spring, perhaps indicating that more migrants used the study site in autumn than in spring. By the 1982-83 winter the proportion of the population which was colour-ringed remained the same at around 70-80%, although the proportion increased after catches had been made (Fig.2.2). This is probably an indication that the population was largely resident (see Chapter 3).

2.3 SEXING AND BIOMETRICS

2.3.1 METHODS

2.3.1.1 SEXING BY BREEDING PLUMAGE

Fig. 2.1. Peak counts of turnstone in the 1982-83 and 1983-84 winters.

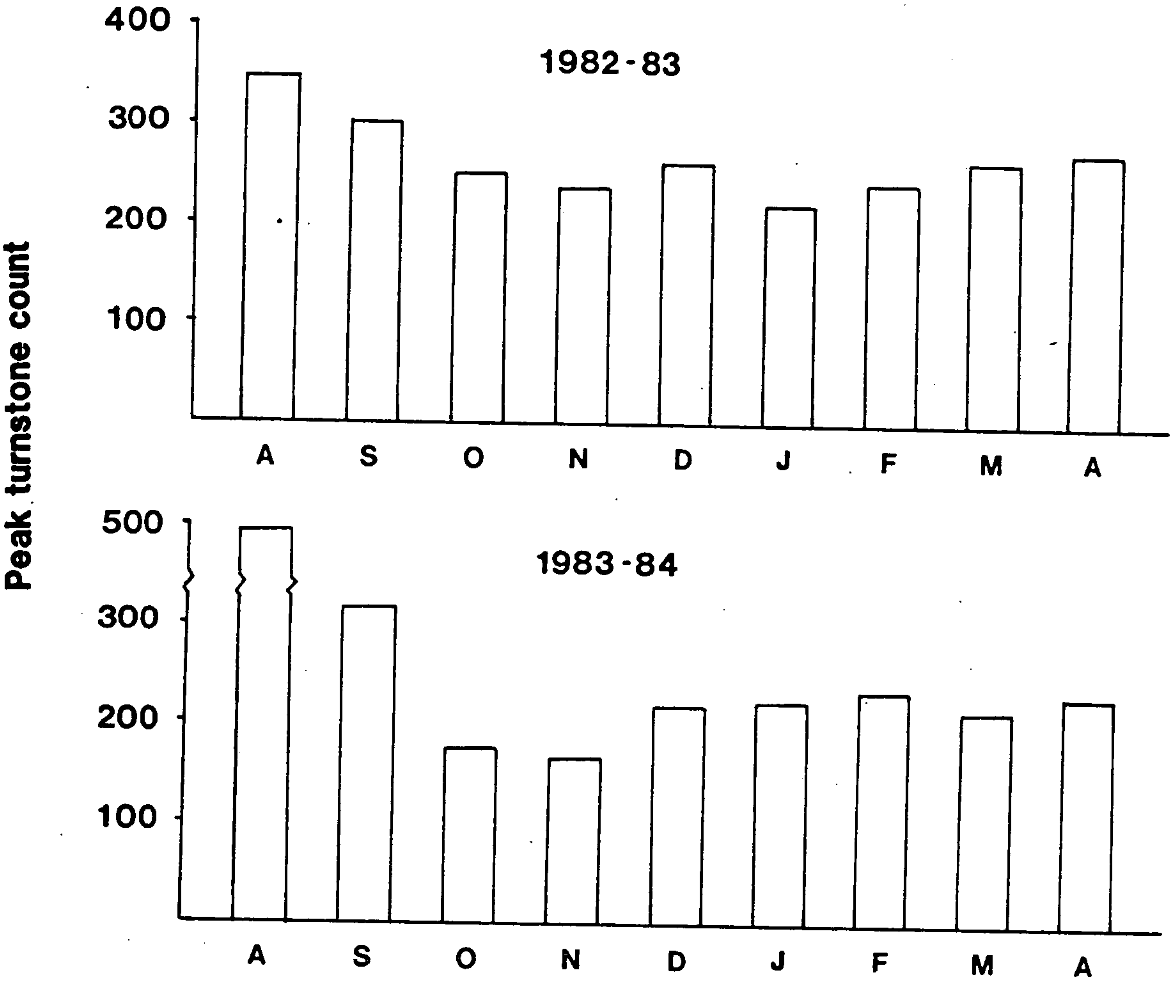

Peak turnstone count
400
300
200
100
1982 - 83
A
S
O
N
D
J
F
M
A
500
300
200
100
1983 - 84
A
S
O
N
D
J
F
M
A

Fig. 2.2. Median estimates of the proportion of adults which were colour-ringed.

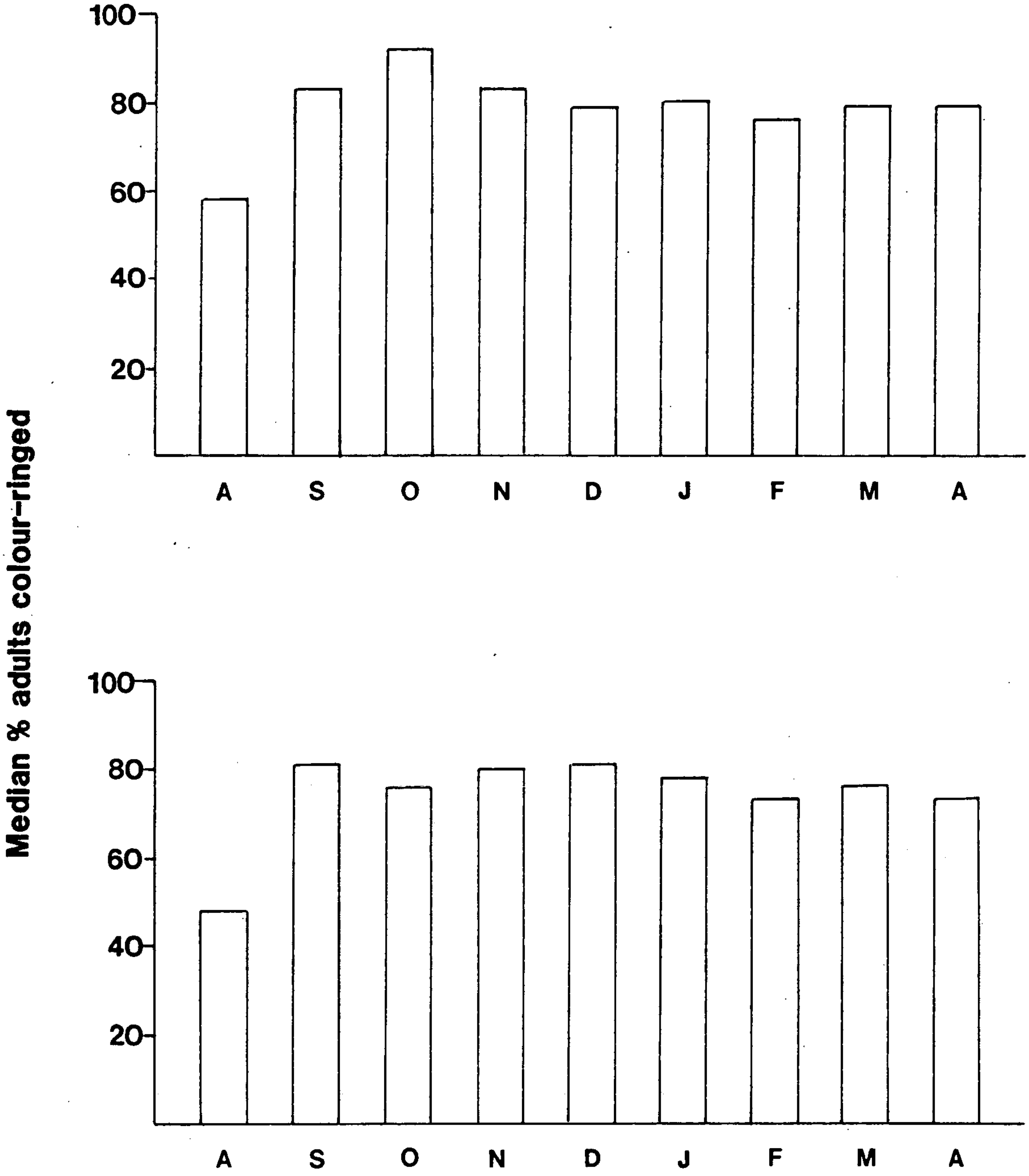

Median % adults colour-ringed
100
80
60
40
20
A
S
O
N
D
J
F
M
A
100
80
60
40
20
A
S
O
N
D
J
F
M
A

TABLE 2.1

Summary of main breeding plumage differences in male and female turnstone.

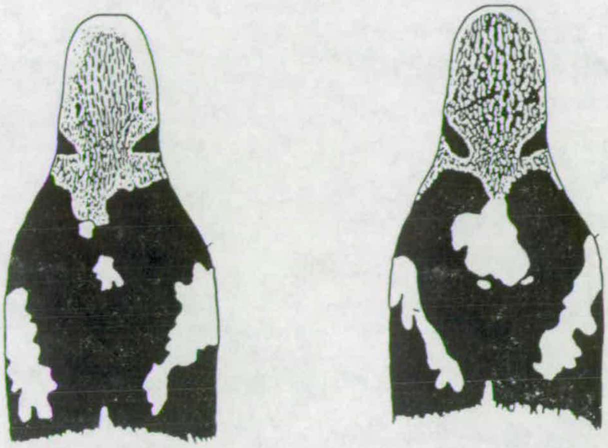
	MALE	FEMALE
CROWN:	Evenly streaked with black and white, forming a distinct cap.	Black and buff streaks, very little white. Cap often indistinct from the buff nape.
NAPE:	White, sometimes with buff or ginger suffusion.	Buff, with occasional white mottling.
MANTLE & SCAPULARS:	Velvet black, with small central ginger mantle patch and distinct ginger scapular patch formed by extensive ginger on several feathers.	Dull black, with indistinct ginger and and grey-brown mantle and scapular patches. Ginger less extensive than in male, usually restricted to margins of feathers.

Several authors have described sexual differences in the breeding plumage of the turnstone (e.g. Witherby et al, 1940; Nettleship, 1967; Prater et al, 1977; Cramp & Simmons, 1983) and the object of this section is to point out which plumage characteristics are of greatest value in sexual discrimination (Table 2.1 & Fig.2.3). Since it is virtually impossible to sex turnstone by winter plumage differences (Chapter 5 and, e.g. Cramp & Simmons, 1983) or by biometrics due to the large overlap between the sexes (section 2.3.2.1.), sexing colour-ringed individuals by breeding plumage as they returned to the study site in late July or August was the method I used to sex members of the study population.

Measurements of several plumage characteristics of male and female turnstone sexed by behavioural differences at Valassaaret, Finland (see Whitfield in press: Appendix 2 and Chapter 6 for details of methods) are presented in Fig.2.4. Whilst there were sexual differences in most of the plumage variables, the most pronounced were in the size of the ginger scapular patches and the amount of white on the nape. A combination of these two plumage variables allowed almost complete separation of the sexes (Fig 2.5). Whilst I normally used a combination of several characteristics, I found that the best plumage characteristics for sexing birds as they returned to Scoughall in August was the size of the ginger scapular patches. Although it was also very useful, the amount of white on the head and nape was not as valuable as were the ginger scapulars because the post-nuptial moult first became apparent on the head and nape, causing rapid attenuation of sexual differences. Ferns (1978) also noticed that the onset of post-nuptial moult in some birds on the breeding grounds was most apparent on the head.

Fig. 2.3. Dorsal views of male and female turnstone in breeding plumage.

Males



Females

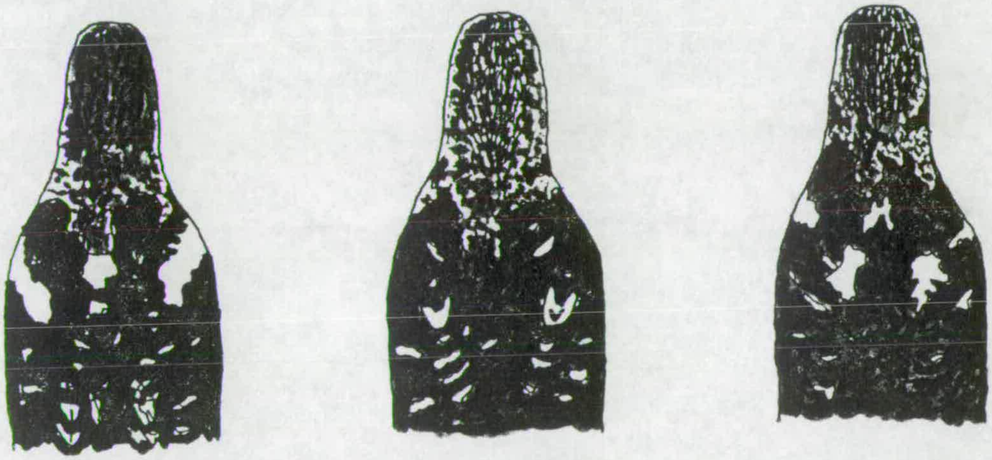


Fig. 2.4. Plumage variable indices of breeding male and female turnstone from Valassaaret, Finland.

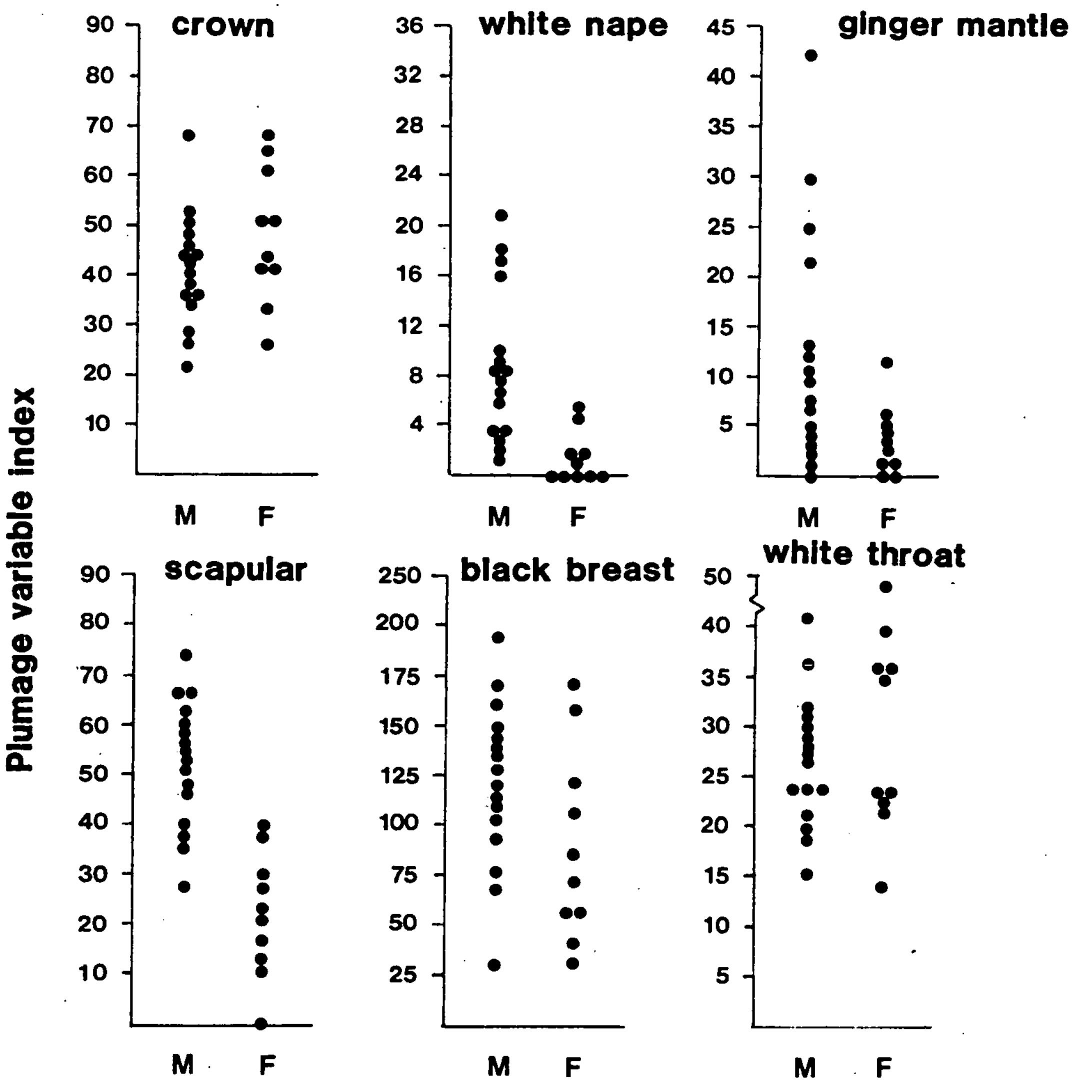
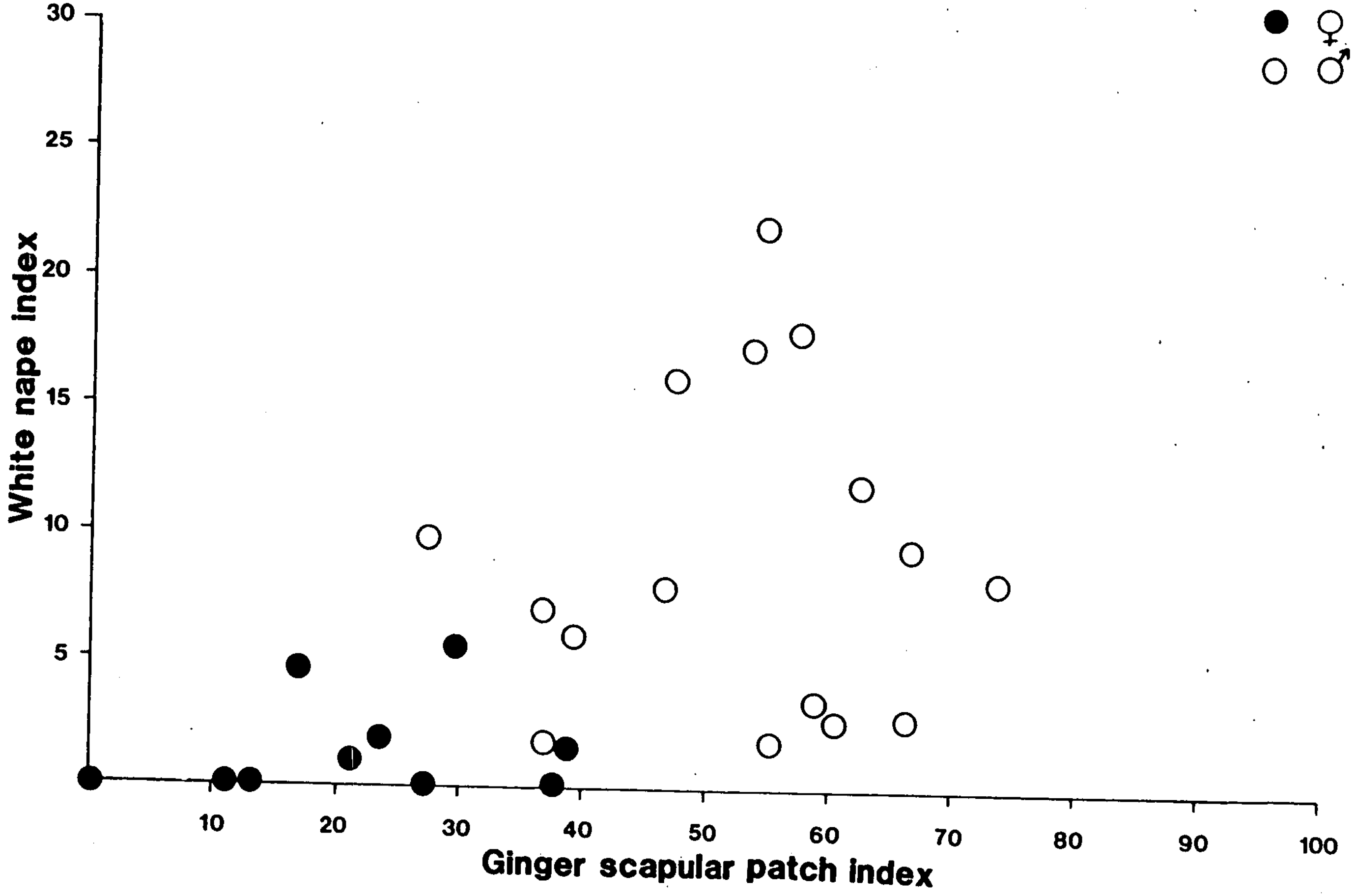

Plumage variable index
crown
90
80
70
60
50
40
30
20
10
M
F
white nape
36
32
28
24
20
16
12
8
4
M
F
ginger mantle
45
40
35
30
25
20
15
10
5
M
F
scapular
90
80
70
60
50
40
30
20
10
M
F
black breast
250
200
175
150
125
100
75
50
25
M
F
white throat
50
40
35
30
25
20
15
10
5
M
F

Fig. 2.5. White nape plotted against ginger scapular patch indices of breeding male and female turnstone from Valassaaret, Finland.


● ♀
○ ♂
White nape index
30
25
20
15
10
5
Ginger scapular patch index
10
20
30
40
50
60
70
80
90
100

suggestion.

For adults, the sexual differences between all body measurements are significant (t-test $p<0.05$) but there is considerable overlap, particularly in tarsus+toe, making simple two character discrimination between the sexes on biometrics virtually useless (Fig. 2.6, 2.7). For example, discriminant analysis performed on wing and bill length, which show the best separation between the sexes, results in the sex of only 66% of individuals being correctly predicted (N=99). Considering that 50% would be correctly predicted by chance alone, the sex of only 16% of birds can be correctly predicted on the basis of wing and bill length. Engelmoer (1984) also found that when discriminant analysis was applied to turnstone, the sex of only around 68% of individuals was predicted correctly, the exact figure varying in different populations. There appears to be similar sexual overlap in the biometrics of juveniles (e.g. wing and bill length, Fig 2.8).

Finally, it is worth noting that there are differences between the measurements presented here and those presented for the turnstone by Cramp & Simmons (1983) and Engelmoer (1984); the published measurements (taken by the same technique) being about 1-4mm lower in wing length and about 0.4-1mm lower in bill length, despite being from the same population (i.e. breeding N.E.Canada/Greenland, wintering W.Europe). Whilst these discrepancies may represent genuine "sub-population" differences, it is more likely that the discrepancies are due to problems, e.g shrinkage, caused by measurements from museum skins which may not have been adequately compensated for, particularly for bill length where there should be negligible inter-observer measurement differences. In species such

TABLE 2.3

Comparison of biometrics of juvenile and adult turnstone captured at Scoughall.

	ADULT			JUVENILE			RATIO
	x	SE	N	x	SE	N	(J/A)
Wing length (mm)	159.5	0.1	152	155.6	0.5	52	0.98
Bill length (mm)	23.0	0.1	139	21.3	0.6	56	0.93
Total head (mm)	51.7	0.1	139	48.1	1.6	56	0.93
Tarsus+toe (mm)	53.6	0.1	79	53.7	0.2	33	1.00

TABLE 2.2

Summary of biometrics of sexed turnstone captured at Scoughall; x± SE(sample size).

(a)

	ADULT		ADULT RATIO
	MALE	FEMALE	MALE/FEMALE
Wing length (mm)	157.6 0.6 (48)	161.4 0.6 (39)	0.98
Bill length (mm)	22.6 0.1 (48)	23.4 0.2 (39)	0.97
Total head (mm)	51.4 0.2 (48)	51.9 0.2 (39)	0.99
Tarsus+toe (mm)	53.2 0.3 (34)	54.0 0.2 (28)	0.99

(b)

	JUVENILE	
	MALE	FEMALE
Wing length (mm)	154.3 0.8 (11)	159.4 1.5 (5)
Bill length (mm)	22.5 0.2 (11)	22.5 0.1 (5)
Total head (mm)	51.2 0.2 (11)	51.6 0.3 (5)
Tarsus+toe (mm)	53.6 0.5 (5)	54.2 1.0 (3)

Since skins shrink with age (e.g. Green, 1980) I have compensated for this by adding 3mm to measured wing length and 0.4mm to measured bill length. These figures were based on the results of Summers (1976), Green (1980), Engelmoer *et al* (1983) and on measurements taken from a collection of turnstone skins.

2.3.2 RESULTS AND DISCUSSION

2.3.2.1 SEX AND AGE DIFFERENCES IN BIOMETRICS

Mean values for the biometrics of aged and sexed turnstone caught on the study site are presented in Table 2.2. There is a slight sexual dimorphism in all measurements, with adult females being slightly larger than males (male/female ratio about 0.98). Other studies of turnstone biometrics show the same degree of dimorphism (Prater *et al*, 1977, Cramp & Simmons, 1983, Engelmoer, 1984), and the same dimorphism is also found in the closely related black turnstone *Arenaria melanocephala* (Handel, 1982). Although sample sizes are small, there appears to be similar sexual dimorphism in juveniles, and juveniles in the sample appear to be slightly smaller than adults in all measurements apart from tarsus+toe. A larger sample, however, confirms that juveniles are smaller than adults in all measurements apart from tarsus+toe (Table 2.3), and this agrees with similar age-related differences presented by Cramp & Simmons (1983). The results suggest that the legs of young turnstone attain adult size first, then the wings, followed by the bill and possibly the skull. Unfortunately, there has been no study on the relative growth rates of turnstone body parts to confirm or refute this

Wing length was measured according to the maximum chord method 3 of Svensson (1975) and taken to the nearest millimetre using a stopped wing rule. Tarsus plus toe was also measured using a stopped rule. This measurement involves placing the tibio-tarsal joint at right angles against the stopped end of the rule, straightening the middle toe, and reading off the value to the nearest 0.5mm underneath the end of the middle (=longest) toe. The claw is not included (see Anderson 1975). Bill length was measured form the tip of the upper mandible using a pair of CAMLAB calipers (Clark 1983). CAMLAB calipers were also used to measure total head length, which was taken by measuring from the tip of the upper mandible to the back of the skull, pressing the feathers flat against the skull. Different people took these measurements on different occasions, but on each catch the measurer´s name was noted on the recording sheet. Each measurement was corrected to take account of consistent differences in measures taken by different people; these differences were quantified by each person measuring the same sample of birds. In addition to measuring individuals in the field, I also took measurements of captive birds in the Department aviary.

Birds were aged using the method outlined in Prater et al (1977). The main discriminatory character was that juveniles had a well defined buff fringe to the wing coverts. Birds were assigned to a sex on the basis of their breeding plumage (see section 2.2.1.1).

Since turnstone do not normally attain full breeding plumage until after their second winter (e.g. Prater et al, 1977) this limits my sample size for sexed juveniles, as does the small number of juveniles which were caught. Therefore, I measured a sample of sexed juveniles from the collection of the Royal Scottish Museum.

I attempted to assess my accuracy in sexing turnstone on breeding plumage differences by three methods: (a) by assigning cannon-netting casualties or skins held in the Royal Scottish Museum, Edinburgh, to a sex and subsequently checking my conclusions either by autopsy or by examination of museum record cards; (b) by assigning individuals photographed in the field at Valassaaret, Finland to a sex and subsequently checking my conclusions against my records made two years previously; (c) by assessing my consistency in sexing colour-ringed individuals in the field at Scoughall whilst they were in breeding plumage.

By method (a), sexes assigned to five cannon-netting casualties on plumage characteristics were in all cases confirmed by autopsy, and 27 (93%) of 29 museum species in full or partial summer plumage were correctly assigned to sex. By method (b), of 36 individuals photographed at Valassaaret 35 (97%) were correctly assigned to sex two years later. By method (c), in August 1983 at Scoughall, 90% of birds which were sexed five times and over were assigned to a sex with 100% consistency (N=112) and 96% of birds which were sexed five times and over were assigned to a sex with over 85% consistency (N=112). Of 142 individuals assigned to a sex in August 1983, 140 (99%) were assigned to the same sex in August 1984. For all future purposes, a colour-ringed bird was considered as being of a given sex if it had been assigned a sex on at least two occasions with over 85% consistency. On average, if a bird was sexed at all, it was sexed on 7.6 ± 0.3 ($x \pm$ S.E.) occasions (N=127).

2.3.1.2 BIOMETRICS

Fig. 2.6. The relationship between bill length and wing length for adult male (Scoughall ○, captive birds □) and female (Scoughall ●, captive birds ■) turnstone.

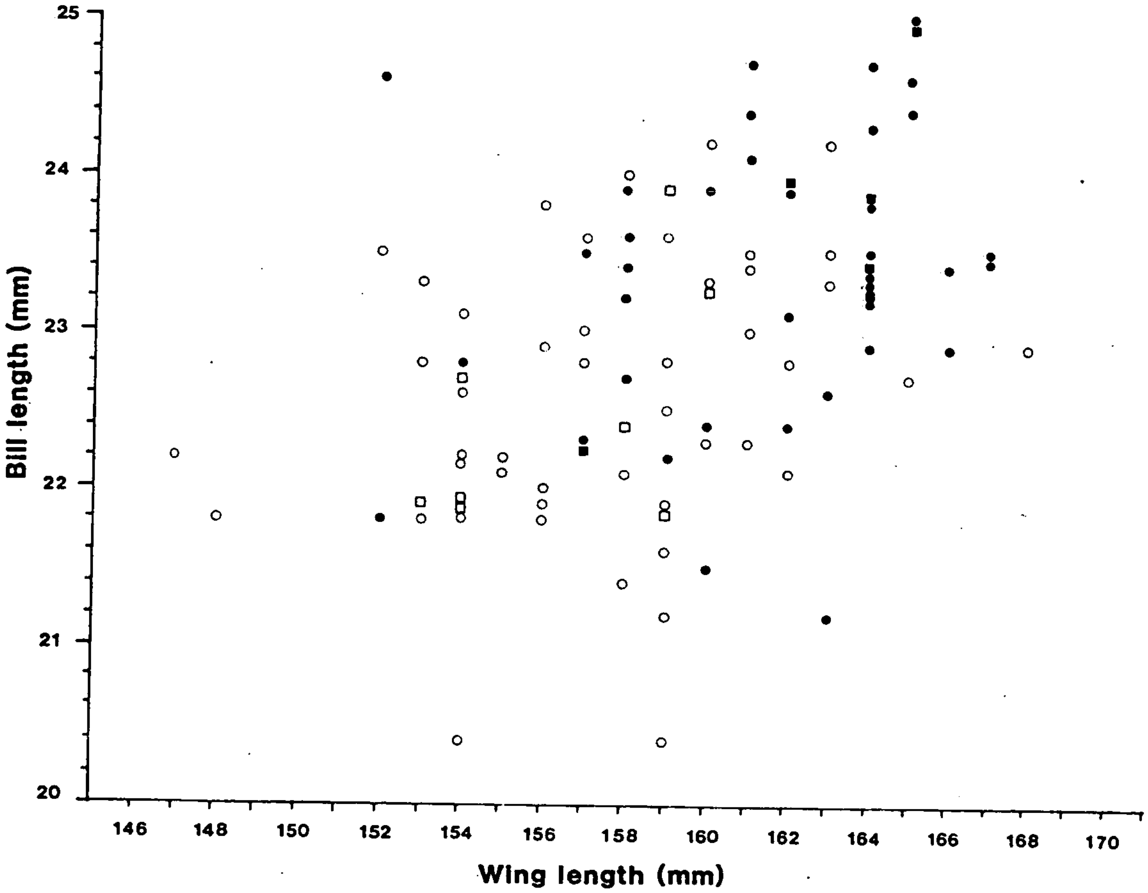

25
24
23
22
21
20
Bill length (mm)
146
148
150
152
154
156
158
160
162
164
166
168
170
Wing length (mm)

Fig. 2.7. The relationship between total head length and wing length for adult male (Scoughall○, captive birds□) and female (Scoughall●, captive birds■) turnstone.

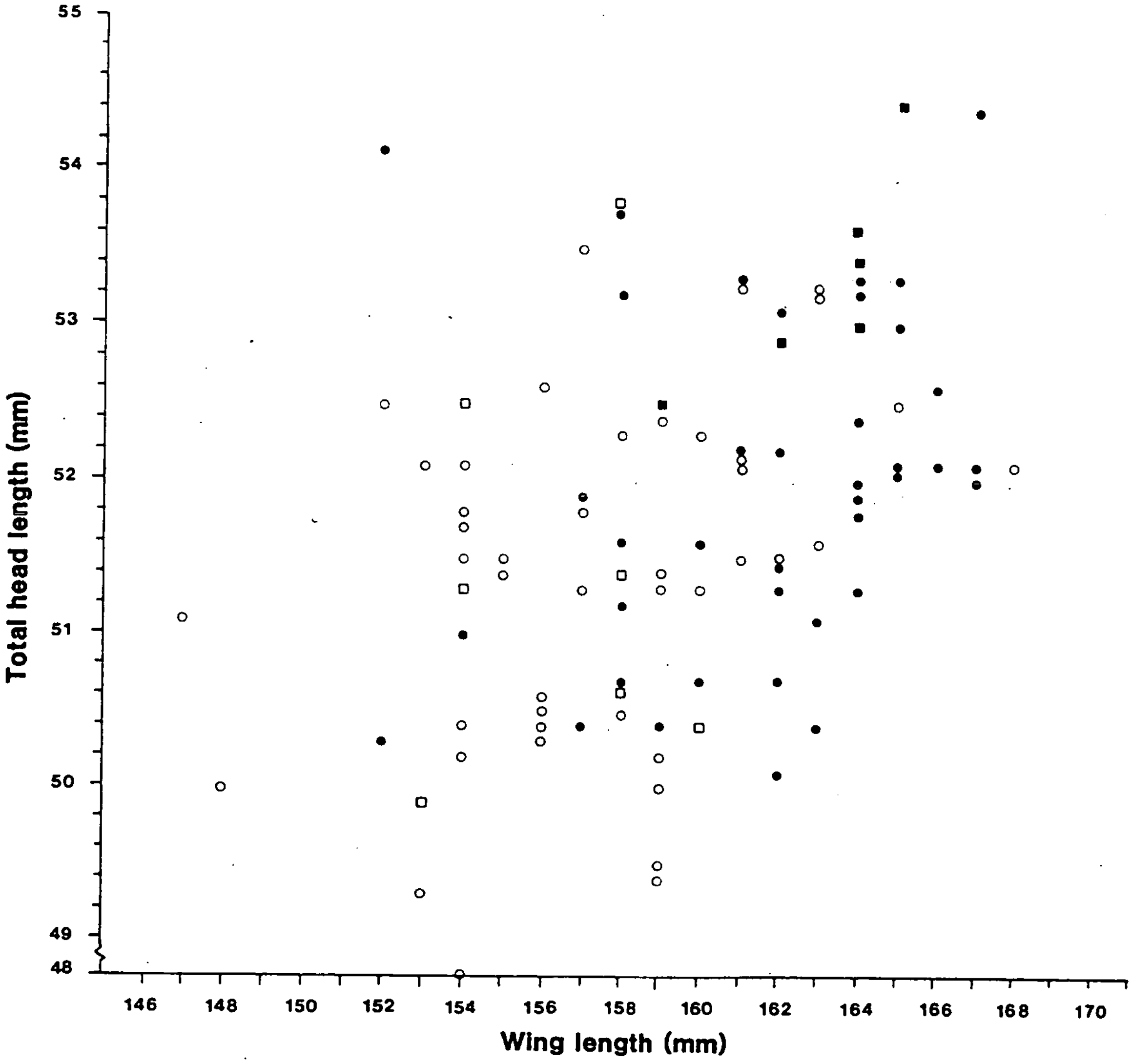
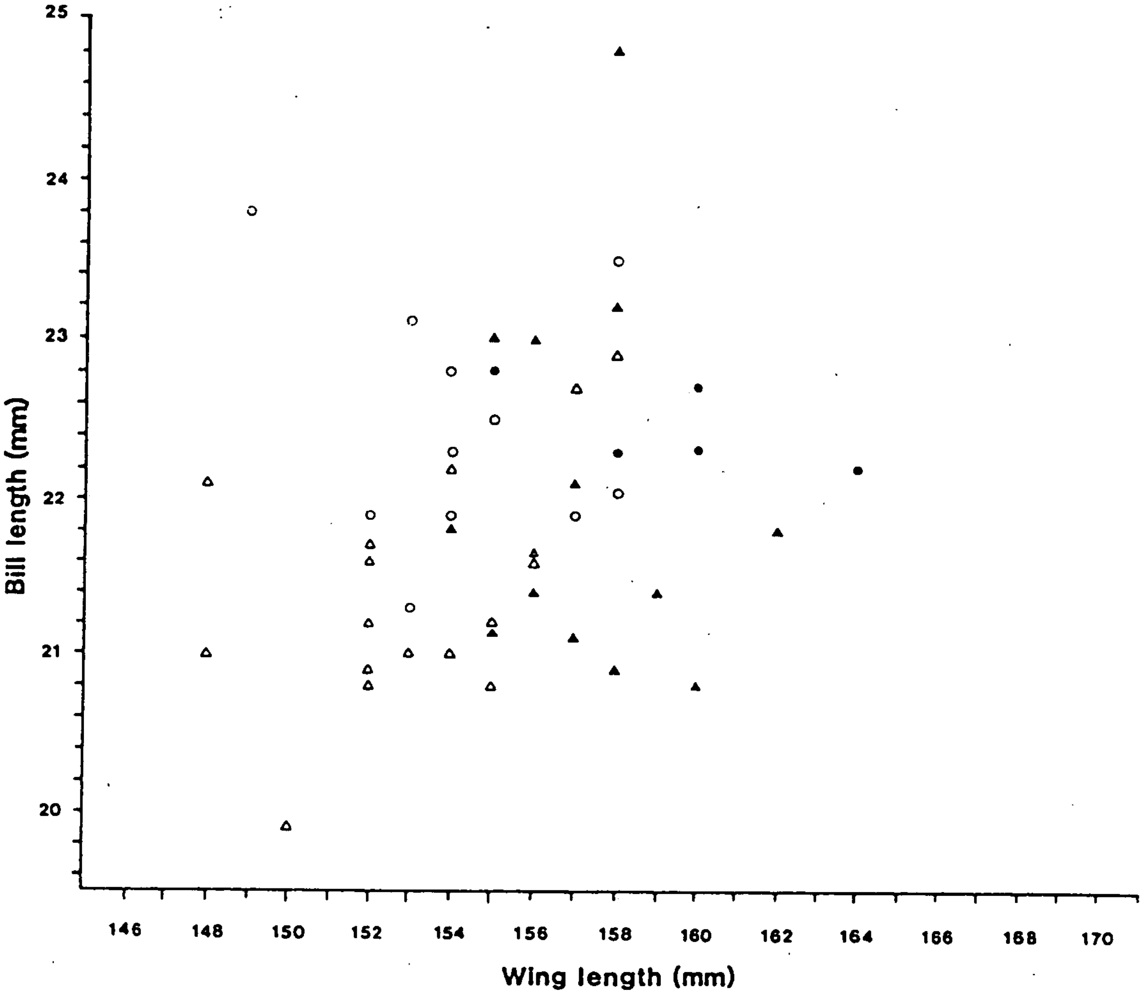

55
54
53
52
51
50
49
48
Total head length (mm)
146
148
150
152
154
156
158
160
162
164
166
168
170
Wing length (mm)

Fig. 2.8. The relationship between bill length and wing length for juvenile male (Scoughall ○, RSM △) and female (Scoughall ●, RSM ▲) turnstone.


25
24
23
22
21
20
Bill length (mm)
146
148
150
152
154
156
158
160
162
164
166
168
170
Wing length (mm)

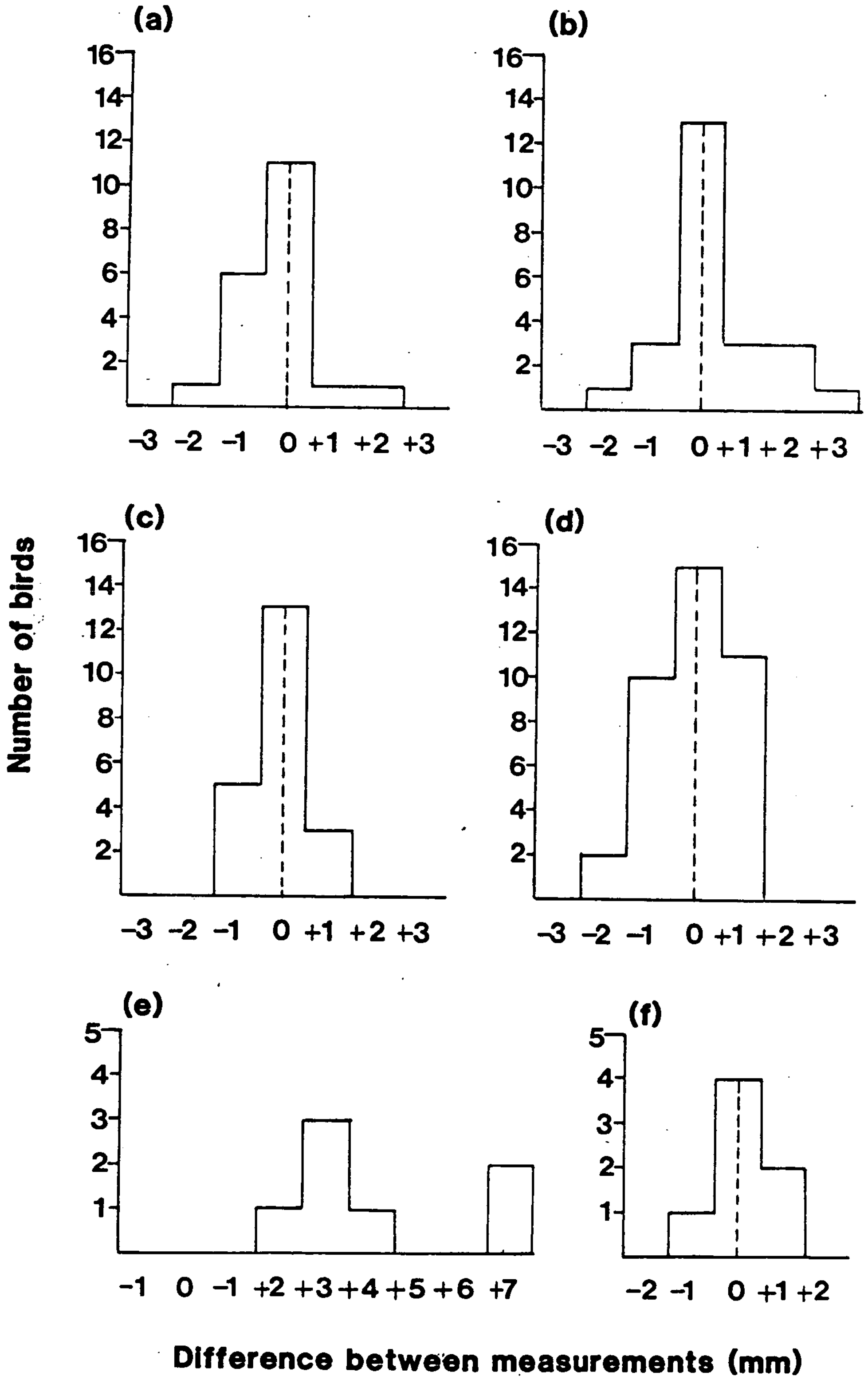
as the turnstone where the geographical variation is slight (Cramp & Simmons, 1983), the problems associated with applying measurements from museum skins to live birds make the difficulties of determining geographical origin of individuals even more exasperating. Since different museum conditions produce different degrees of shrinkage (M. Nicoll pers. comm.) it is preferable to use measurements from live birds wherever possible in looking for geographical differences between populations.

2.3.2.2 SEASONAL AND ANNUAL CHANGES IN BIOMETRICS

In this section I have considered only bill and wing lengths. There appears to be negligible decrease in adult wing length due to abrasion within a winter, which is in agreement with the findings of Cramp & Simmons (1983) (Fig. 2.9a). Clark (1983) found that adult dunlin *Calidris alpina* also showed little decrease in wing length due to abrasion. Although Pienkowski & Minton (1973) reported a noticeable inter-moult reduction in the wing length of knot *Calidris canutus*, the reduction appeared to increase with the age of the feathers so by treating the reduction as a linear function they overestimated the reduction in winter but underestimated the decrease in spring and summer (Clark, 1983). My sample size for juveniles is too small to make any comment on wing length reduction in this age class.

For birds at Scoughall the bill length of adults stays more or less the same within a winter; although variations do occur, there is no tendency for bill length to either increase or decrease (Fig. 2.9c). However, the birds in captivity showed a significant increase

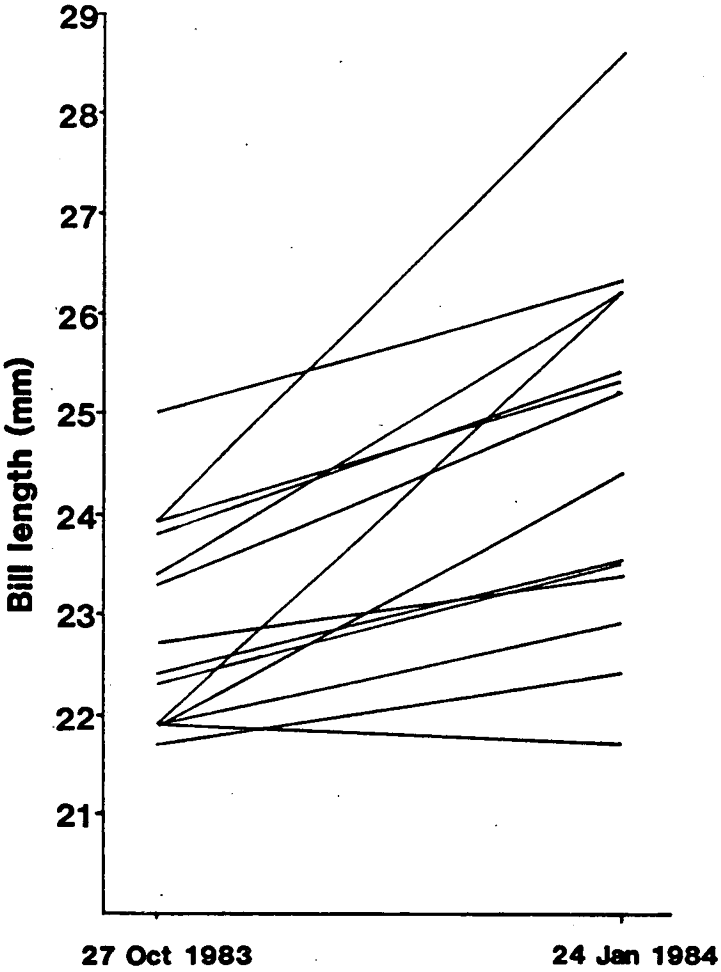
Fig. 2.9. Seasonal and annual differences in wing and bill lengths of individual Scoughall turnstone. (a) Adult wing length within winter; (b) adult wing length consecutive winters; (c) adult bill length within winter; (d) adult bill length in consecutive winters; (e) wing length of juvenile retrapped in following year; (f) bill length of juvenile retrapped following year.


(a)
(b)
(c)
(d)
(e)
(f)
16
14
12
10
8
6
4
2
5
4
3
2
1
−3 −2 −1 0 +1 +2 +3
−1 0 −1 +2 +3 +4 +5 +6 +7
−2 −1 0 +1 +2
Number of birds
Difference between measurements (mm)

in bill length over three months (Wilcoxon matched pairs signed ranks test, N=14, T=1, p<0.001) (Fig 2.10). In contrast to most other waders, the rhampotheca (the horny sheath surrounding the bone) of the bill of turnstone and oystercatchers extends well beyond the bone (Burton, 1974; Pienkowski, 1976; Summers, 1976). This is probably because both turnstone and oystercatchers employ feeding techniques where the bill is frequently in contact with abrasive materials e.g. hammering open barnacles or opening mussels, and the hypertrophic rhampotheca serves to protect the bill from damage. Such feeding techniques will also tend to cause excessive wear on the bill and must be compensated for by comparatively rapid growth of the rhampotheca: the rhampotheca of the oystercatcher grows continuously (Hulscher, 1983; Swennen <u>et al</u>, 1983). The rhampotheca of turnstone probably grows continuously too, and in captive turnstone where the birds fed mainly from soft food in open bowls, the rhampothecal growth did not appear to have been held in check by wear. Any seasonal or annual variations in bill length in birds in the field are probably due to changes in the balance between rhampothecal growth and abrasion. Between-winter variations in bill length appear to be greater than within-winter variations (Fig. 2.9d). This is probably because between winters the growth-abrasion balance is more likely to be affected; possibly due to a simple time factor (longer period between measurements leading to a greater chance of there being differences) and possibly due to different feeding conditions encountered during the intervening breeding season.

As mentioned earlier, juveniles have shorter wings than adults, and juvenile wing length increases when they become adults i.e. wing length increases between their first and second winters (Fig. 2.9e).

Fig. 2.10. Changes in the bill length of turnstone kept in captivity.


Bill length (mm)
29
28
27
26
25
24
23
22
21
27 Oct 1983
24 Jan 1984

It is surprising is that there was no evidence for an increase in bill length between a bird's first and second winter, despite juveniles having shorter bills than adults (Fig. 2.9f). This may be a result of the small sample size of retraps.

2.3.2.3 SEX RATIO OF THE POPULATION

Birds were considered to be members of the population if they were seen on at least ten separate days within each winter, and the sex ratio was defined as the number of males in the population divided by the number of sexed individuals in the population x 100%. Since turnstone do not adopt full summer plumage until after their second winter (Prater et al, 1977; Cramp & Simmons, 1983) each winter's sex ratio estimate applies only to birds over two years old as only these individuals could be sexed. The sexed colour-ringed birds were a subset of the total population, so the estimate assumes that this subset was a random sample. There was no reason to suspect that this assumption was invalid, particularly in view of the relatively high proportion which was colour-ringed.

In the 1982-83 winter the sex ratio was 50% (N=148), in 1983-84 the sex ratio was 51% (N=149). These values clearly indicate an equal proportion of the sexes in the turnstone at Scoughall.

2.4 AUTUMN MIGRATION OF TURNSTONE AT THE STUDY SITE

2.4.1 METHODS

In 1982, 1983 and 1984 I counted the number of turnstone on the study site at or near to high tide on several days from mid July to the end of August. At high tide most birds congregated on the roost at the Great Car and they were counted from a hide on the roost or as they left the roost for the feeding areas when the tide dropped. Any birds feeding on the strandline elsewhere were also counted when possible. Birds were sexed and aged using plumage characteristics, and this allowed me to estimate the sex and age composition of the population on several days. The identity of colour-ringed birds was noted whenever possible, as was the ratio of unringed:ringed birds. Thus by assuming 25% of residents were unringed, an estimate of the proportion of migrants on the study site could be made.

2.4.2 RESULTS AND DISCUSSION

The data for 1982, 1983 and 1984 are shown in Figs. 2.11, 2.12 and 2.13 respectively. The pattern of arrival and influx of adults occurred between 2 and 5 August in 1982, but between 6 and 8 August in 1983. I suspect that this first influx consisted of a large number of birds arriving more or less simultaneously. Individuals of both sexes were involved in this influx but females predominated, and about 65% of the birds were migrants. At least some of these migrants appeared to leave the study site in the next two or three days, at the same time as a small influx of predominantly migrant males. About four or five days after the first major influx of birds, a second large influx of birds occurred, composed almost entirely of migrant males. Counts and changes in the population sex ratio indicate that these migrant males possibly left the study site

Fig. 2.11. Summary of return of colour-ringed birds and autumn migration at the study site in 1982. (a) Total population parameters: population counts, sex ratio, age ratio. (b) Colour-ringed population parameters: sex ratio, cumulative numbers of first sightings of males and females. The dotted lines represent an equal sex ratio.

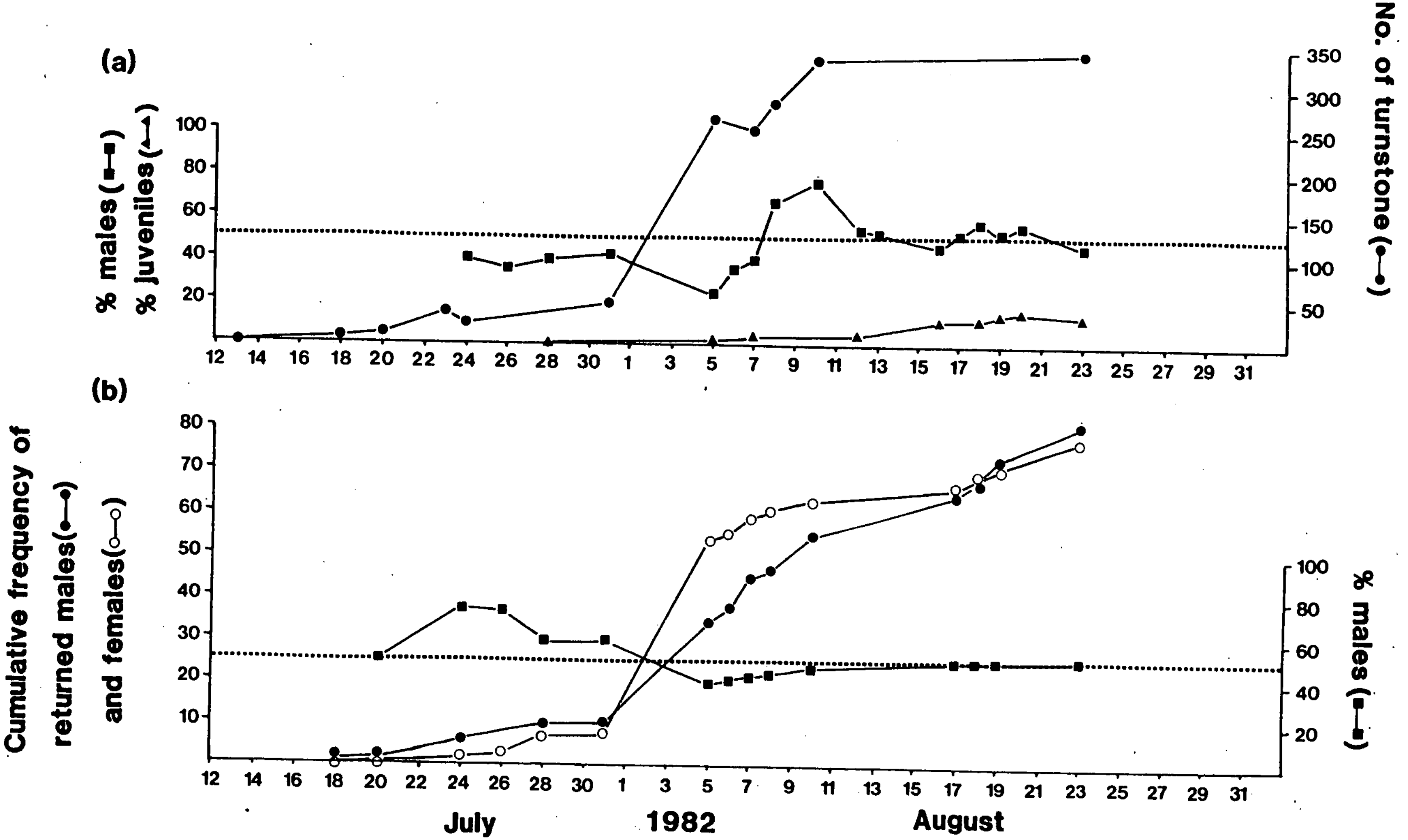

(a)
% males (■—■)
% juveniles (▲—▲)
100
80
60
40
20
No. of turnstone (●—●)
350
300
250
200
150
100
50
12 14 16 18 20 22 24 26 28 30 1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31
(b)
Cumulative frequency of
returned males (●—●)
and females (○—○)
80
70
60
50
40
30
20
10
% males (■—■)
100
80
60
40
20
12 14 16 18 20 22 24 26 28 30 1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31
July
1982
August

Fig. 2.12. Summary of return of colour-ringed birds and autumn migration at the study site in 1983. (a) Total population parameters: population counts, sex ratio, age ratio. (b) Colour-ringed population parameters: sex ratio, cumulative numbers of first sightings of males and females. The dotted lines represent an equal sex ratio.

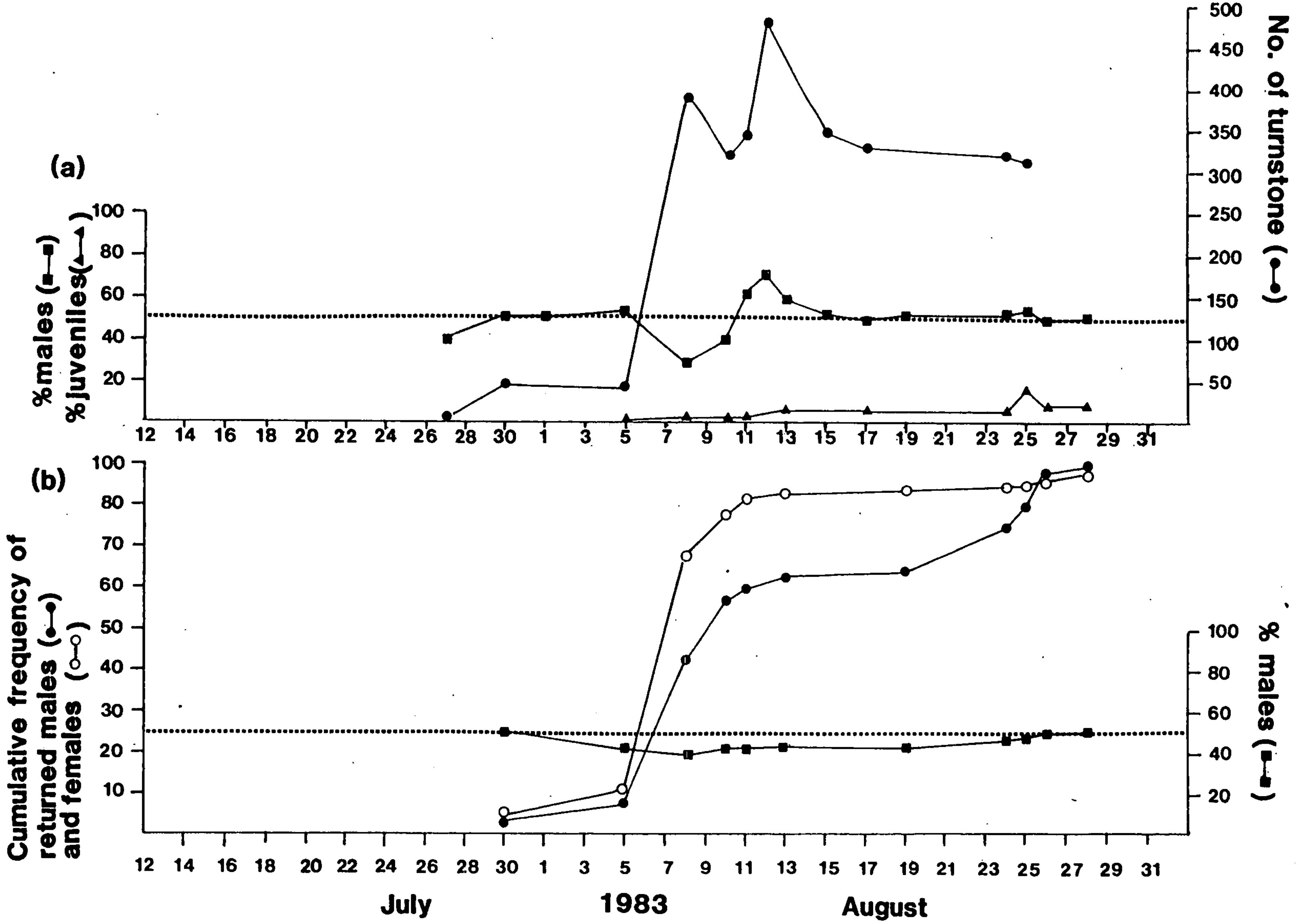
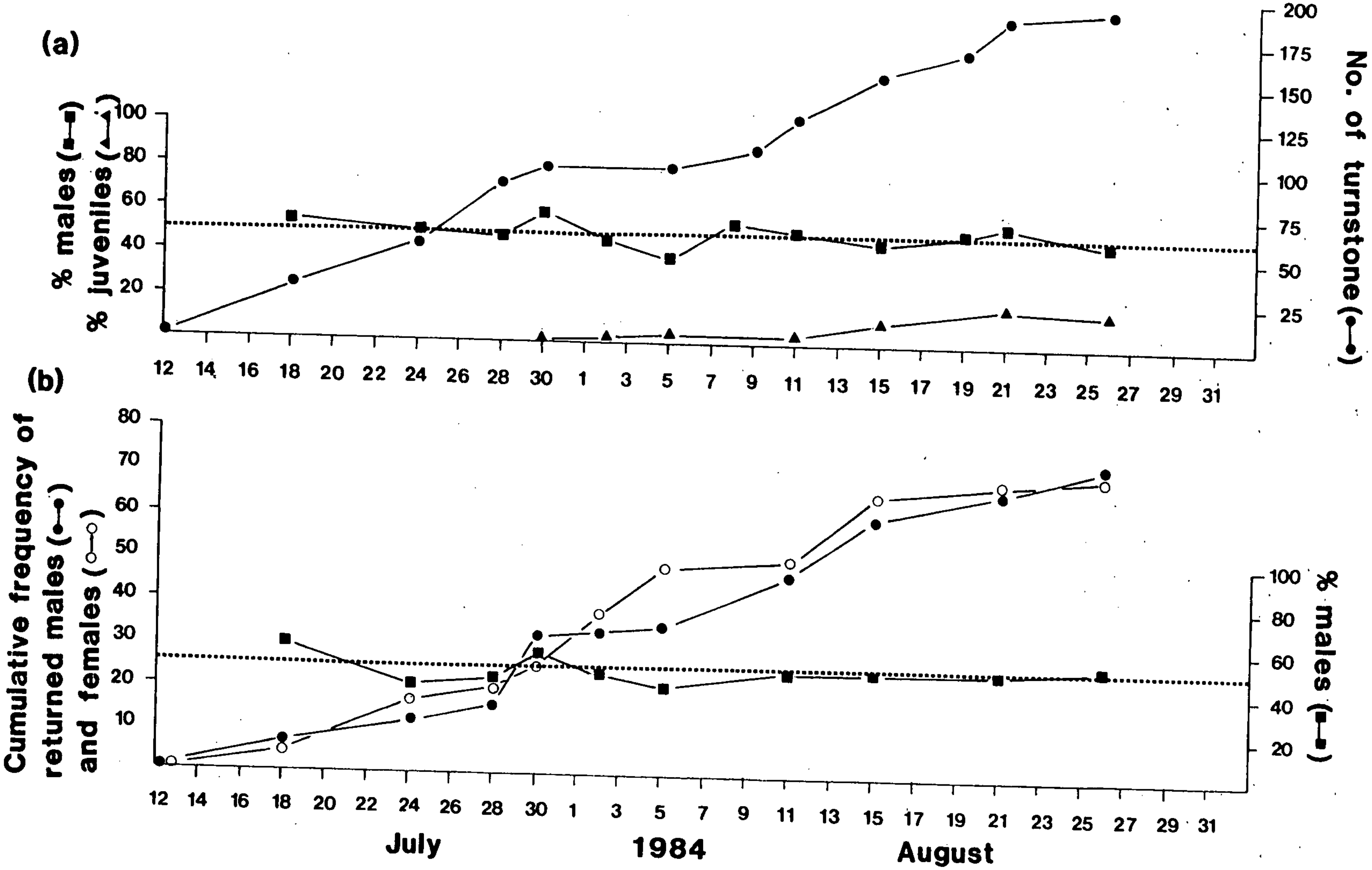

(a)
%males (■—■)
%juveniles (▲—▲)
100
80
60
40
20
No. of turnstone (●—●)
500
450
400
350
300
250
200
150
100
50
12 14 16 18 20 22 24 26 28 30 1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31
(b)
Cumulative frequency of returned males (●—●) and females (○—○)
100
90
80
70
60
50
40
30
20
10
% males (■—■)
100
80
60
40
20
12 14 16 18 20 22 24 26 28 30 1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31
July
1983
August

Fig. 2.13. Summary of return of colour-ringed birds and autumn migration at the study site in 1984. (a) Total population parameters: population counts, sex ratio, age ratio. (b) Colour-ringed population parameters: sex ratio, cumulative numbers of first sightings of males and females. The dotted lines represent an equal sex ratio.


(a)
% males (■—■)
% juveniles (▲—▲)
100
80
60
40
20
No. of turnstone (●—●)
200
175
150
125
100
75
50
25
12
14
16
18
20
22
24
26
28
30
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
(b)
Cumulative frequency of returned males (●—●) and females (○—○)
80
70
60
50
40
30
20
10
% males (■—■)
100
80
60
40
20
July
1984
August

within two days of their arrival. From mid-August to the end of August the population sex ratio remained at parity and the number of birds on the site appeared to remain more or less constant. During this period I regularly saw the arrival and, particularly, the departure of migrant flocks, which suggests that there was a steady passage of birds of both sexes through the site rather than there being relatively sedentary group of migrants. Most or all of the winter residents stayed to moult at Scoughall, and by mid-September the passage of migrants through Scoughall had stopped.

In 1982 and 1983 the pattern of arrival of the resident adults was different from that of migrant adults. In migrants there were two waves of arrivals, the first mainly of females, the second almost entirely of males. In residents a second large influx of males did not occur, as after the single large influx males returned gradually. The pattern of arrival of female residents was similar to males´ except that more females arrived in the large influx, and therefore, on average, females tended to arrive slightly earlier than males. The pattern and timing of the arrival of female residents was even more similar to males´ in 1984.

1984 was strikingly different from the preceding two years in the virtual absence of any migrant adults using Scoughall as a stopover point. I suspect that this was due to a lack of recovery of the substantial barnacle population at the Great Car after being totally decimated by storms in February and March 1984: the vast majority of migrants fed on the Great Car barnacles in preceding years. Because there were very few migrants in 1984 the total population counts and total population sex ratio estimates were essentially a reflection of these same parameters of the resident population.

As a further contrast to 1982 and 1983, there was no single large influx of resident birds in 1984. It is possible that this difference is related to the greater breeding success in 1984 compared with 1982 and 1983 (section 2.5). It could be argued that the major influx of residents in 1982 and 1983 consisted of failed males, failed females and successful females, which leave the breeding grounds before successful males (Nettleship, 1973): certainly the sex ratio of the influx fits this interpretation. With an increased breeding success in 1984 there was less evidence of a single large influx as a result of fewer failed breeders. However, because successful females leave before successful males, with a greater breeding success in 1984 it would be expected that there should be an even more pronounced difference in the arrival times of the sexes, not a reduced difference as was found (see also Holmes 1960). Whether there is any connection between increased breeding success and the timing and pattern of the residents' arrival at Scoughall is difficult to decide, as other factors, notably weather (Richardson, 1978, 1979) may affect the timing of migration. The main conclusion that can be drawn is that females precede males on migration and, to a lesser degree, on arrival at the wintering site; this is to be expected since females leave the breeding grounds before males (Nettleship, 1973; Meltofte, 1985).

Turnstone can be classified, therefore, as having a Type 2 parental care system according to the scheme of Myers (1981a), since both sexes incubate, but one sex (in this case the female) leaves the brood. Several reasons have been suggested for the early departure of one sex. It may reduce competition for food resources, primarily for the young, but also for the remaining parent (the ´food competition´ hypothesis, e.g. Pitelka <u>et al</u>, 1974). On the other hand, Ashkenazie & Safriel (1979) have speculated that through early departure an individual can decrease the costs of long-distance migration (the ´cross-seasonal´ hypothesis), and although empirical evidence is non-existent, in Calidridine sandpipers increasing emancipation of one sex correlates with migration distance (Myers, 1981a). The work of Schneider & Harrington (1981) indicates that it may be beneficial to arrive at migration stopover points early to forestall prey depletion by other waders. Other available evidence tends to favour the second, cross-seasonal interpretation of early departure of one sex, although several factors are probably involved (Myers, 1981a).

As mentioned above, in turnstone breeding in high arctic Ellesmere Island and Greenland the female leaves the breeding grounds soon after the young have hatched, whereas the male remains until around the time the young fledge, and failed breeders of both sexes leave early (e.g. Meltofte 1985). In Finland, however, I found that in successful pairs females remain with males until the young fledge. Failed females left the breeding grounds early, as did failed males who possessed low quality territories. Failed males who held high quality territories, however, remained on their territories until late in the season. Clearly, conditions on the breeding grounds were implicated in departure dates, at least in males. Since Finnish females stayed longer than high arctic females the food competition hypothesis would predict higher food resources on the Finnish breeding grounds compared with the high arctic. However, Finnish turnstone were confined to their islet breeding territories, whilst high arctic turnstone move their young to areas with extremely high prey densities (e.g. Ferns & Mudge, 1976), so the food resources available to young turnstone in the high arctic are probably as abundant, perhaps more so, than those in Finland. This casts some doubt on the prediction derived from the food competition hypothesis of Pitelka _et al_ (1974). Finnish turnstone probably do not migrate further away from their breeding grounds than do Greenland birds (Branson _et al_, 1978), and I suspect that factors other than cross-seasonal considerations may be most important in prolonging Finnish females' stay on the breeding grounds. The co-ordinated defence of young by both parents against predators, the large amount of time spent in attacking predators and the large numbers of potential predators (Whitfield unpubl. data) suggests that an increased predation risk of young may have selected for females to remain longer on the breeding grounds. Increased intrusion pressure on high quality sites (Whitfield, in press: Appendix 2) probably forced failed males which possessed high quality territories to remain longer than low quality territory holders, as intruders continued their attempts to secure high quality territories well into the post-hatching period.

My results also show that juveniles migrate and/or arrive at Scoughall after the adults, which again is expected from observations on the breeding grounds (summarised in Meltofte, 1985). The staggered migration times of sex and age classes is perhaps a hint that families and/or mated pairs do not winter together (see also Myers, 1983).

2.5 AGE COMPOSITION OF THE POPULATION

2.5.1 METHODS

I estimated the age composition of the population by ageing birds in the field whilst flocks were feeding or roosting on the strandline. The main criteria used in ageing turnstone were the presence or absence of distinct buff fringes to the wing coverts and leg colour (see Prater et al, 1977; Cramp & Simmons, 1983; Whitfield, 1985: Appendix 1 for further details). Assessment of the age of colour-ringed turnstone agreed in 92% (N=236) of instances with those made in the hand when the birds were caught. These checks on my ability to age birds in the field occurred after colour-ringing, but individuals were aged before I could see their colour-ring identity, because their legs were often out of view when they fed. Because of the close agreement between the assessment of age in the field and in the hand I am confident that the majority of birds were aged accurately.

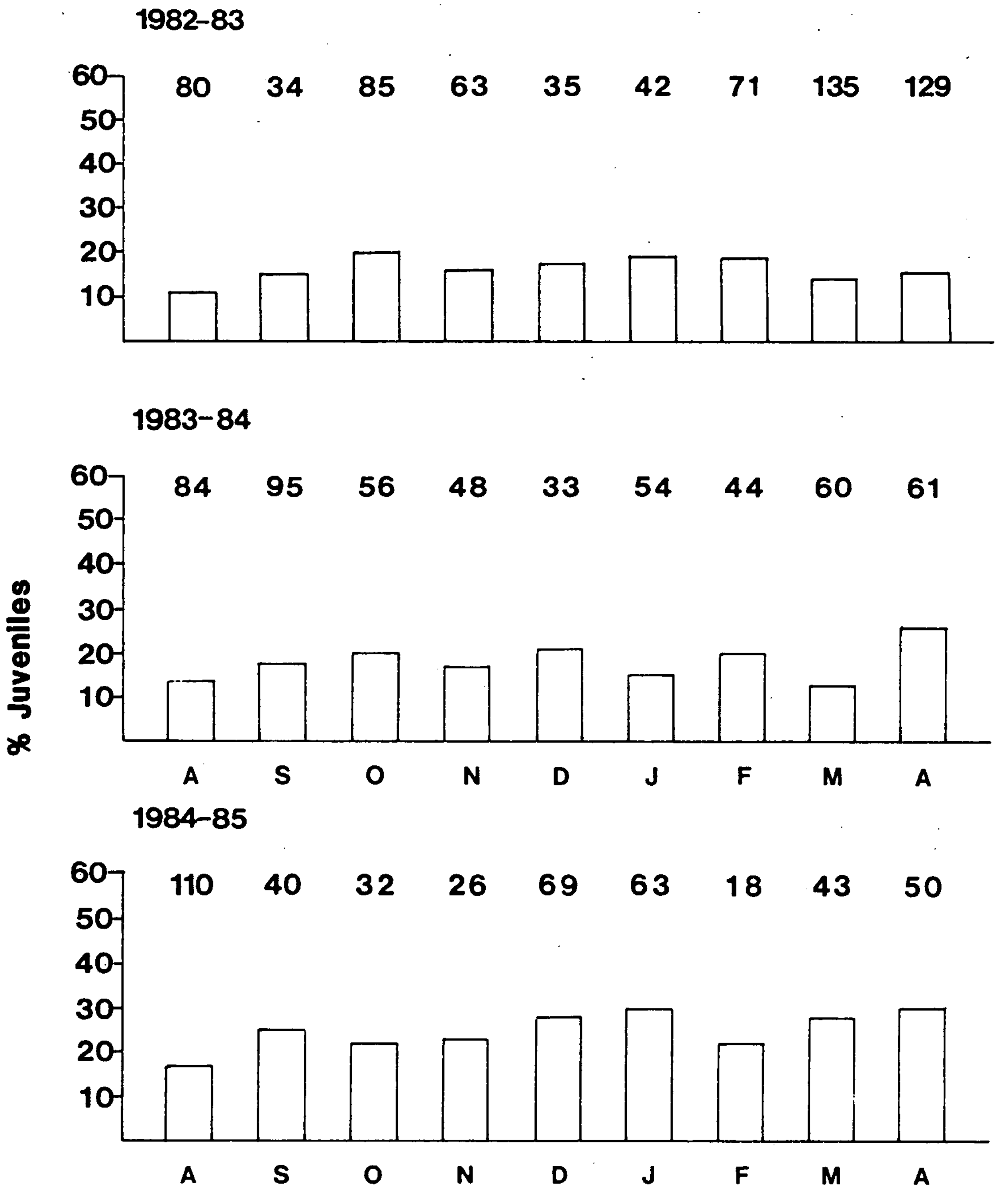
There is some evidence that samples of waders which are caught are biased towards juveniles (Pienkowski & Dick, 1976; Goss-Custard et al, 1981a). To discover if cannon-netted samples of turnstone at Scoughall were biased in favour of juveniles, I compared the proportion of juveniles in catches with the proportion of juveniles in the field (based on estimates made within one week of each catch).

2.5.2 RESULTS AND DISCUSSION

2.5.2.1 ESTIMATES FROM AGEING IN THE FIELD

For the three winters in which samples of birds were regularly aged the proportion of juveniles in the population appeared to remain about the same throughout each winter (Fig. 2.14). Excluding periods

Fig. 2.14. Field estimates of the proportion of juveniles in the population. Figures above columns indicate the number of birds aged. Estimates are median values for each month.


1982-83
60
50
40
30
20
10
80
34
85
63
35
42
71
135
129
1983-84
60
50
40
30
20
10
84
95
56
48
33
54
44
60
61
% Juveniles
A
S
O
N
D
J
F
M
A
1984-85
60
50
40
30
20
10
110
40
32
26
69
63
18
43
50
A
S
O
N
D
J
F
M
A

of possible migration, mean values of % juveniles in the population were as follows: 1982-83, 17%; 1983-84, 18%; 1984-85 26%. Branson et al (1979) and R. Summers (pers. comm.) suggest that the 'normal' proportion of juveniles is about 15%. Since the proportion of juveniles in wintering populations of waders can be used as a broad indicator of the succcess of the preceding breeding season (Prater 1981), the data from Scoughall suggest that in 1982 and 1983 the breeding success of turnstone in N.E.Canada/N.Greenland was about average whilst breeding success in 1984 was comparatively good. As I will discuss in the following section, I regard the % juvenile estimates (about 6% juveniles) derived from the large catches of turnstone in the 1981-82 winter as probably being reasonably accurate: these estimates suggest that there was comparatively poor breeding success in 1981. Such relatively large variations in year to year breeding success are typical of high arctic breeding waders (e.g. Evans & Pienkowski, 1984; Meltofte, 1985).

2.5.2.2 ESTIMATES FROM CANNON-NETTING SAMPLES

Where comparisons were possible, the proportion of juveniles in the population as estimated from cannon-netted samples was usually higher than as estimated in the field (Table 2.4). These discrepancies were significant (Sign test, $p<0.002$) indicating that a disproportionate number of juvenile turnstone were caught by cannon-netting. Some possible reasons why juveniles may be caught more easily than adults are discussed by Pienkowski & Dick (1976) and Goss-Custard et al (1981a). Whitfield (1985: Appendix 1) showed that juvenile turnstone on the strandline at Scoughall were less likely than adults to respond to the appearance of a sparrowhawk Accipiter

TABLE 2.4

Comparison of estimates of the proportion of juveniles in the population as derived from cannon-netted samples and samples of birds aged in the field.

Date of catch.	N	% juveniles in cannon-netted catch.	% juveniles based on field estimate taken within one week of catch.
14.11.81	55	7	--
27.01.82	157	5	--
09.02.82	183	4	--
27.02.82	28	18	--
03.10.82	12	42	20
18.10.82	20	0	20
14.11.82	23	26	16
13.02.83	20	25	18
29.03.83	4	25	14
05.11.83	8	25	18
05.02.84	7	57	14
27.10.84	8	100	25
24.11.84	19	26	23
21.12.84	39	10	25
23.01.85	14	36	22

nisus by flying out to sea: such behaviour would also make juveniles more likely to be caught by cannon-nets.

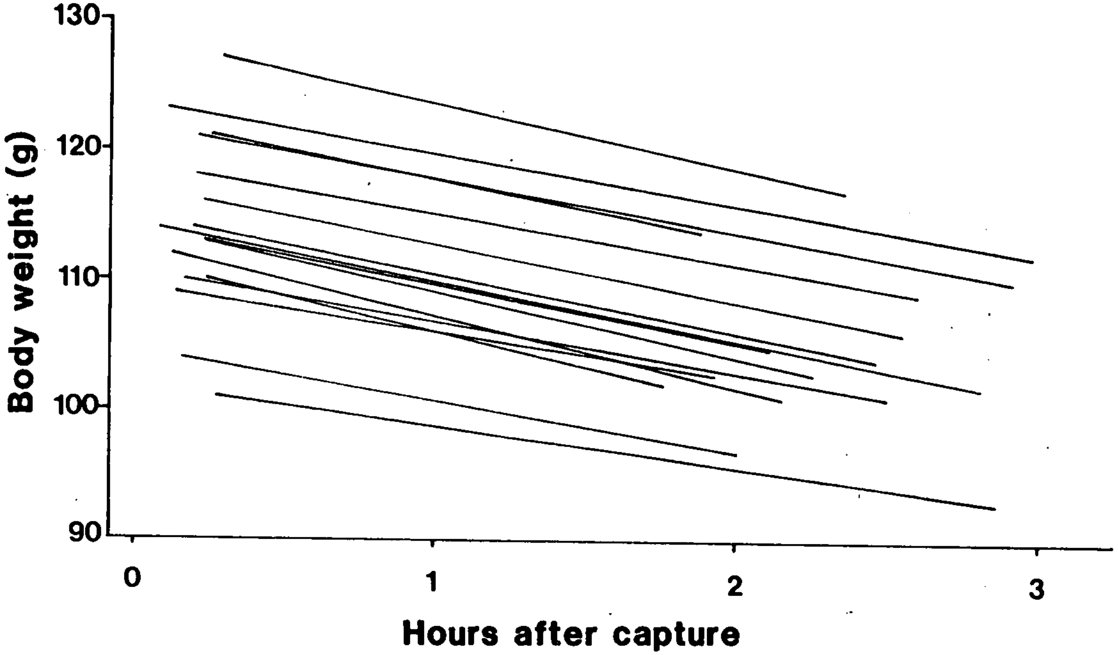
In all but the last catch of the 1981-82 winter a comparatively large section of the population was captured. As the proportion of any population which is captured increases, an increasingly representative sample should be obtained, so I regard the estimate of around 6% juveniles in the population, as calculated from the first three catches, as probably being accurate. This figure of 6% also agrees with my estimates made in the field towards the end of February and March 1982.

2.6 SEASONAL WEIGHT CHANGES

2.6.1 METHODS

After each catch of turnstone at Scoughall, and following a temporary period in captivity, every bird was weighed to the nearest 1g using a Pesola spring balance. Loss of weight by birds whilst in captivity prior to processing has been recorded in several waders (OAG Munster, 1975, 1976; Lloyd et al, 1979; Goede & Nieboer, 1983; Schick, 1983; Davidson, 1984). Weight loss is due to dehydration, fat catabolism and loss of lean dry muscle (Davidson 1984). These studies have obvious implications for the accurate measurement of body weight, so I attempted to calculate the rate of weight loss in turnstone whilst being held temporarily in captivity at Scoughall on 9 Feb 1982. Sixteen turnstone were weighed immediately after removal from the cannon-net, and then placed in hessian keeping cages before being weighed again about two hours later. Weight loss of these sixteen birds is shown in Fig. 2.15. Mean weight loss was 4.5g/hr,

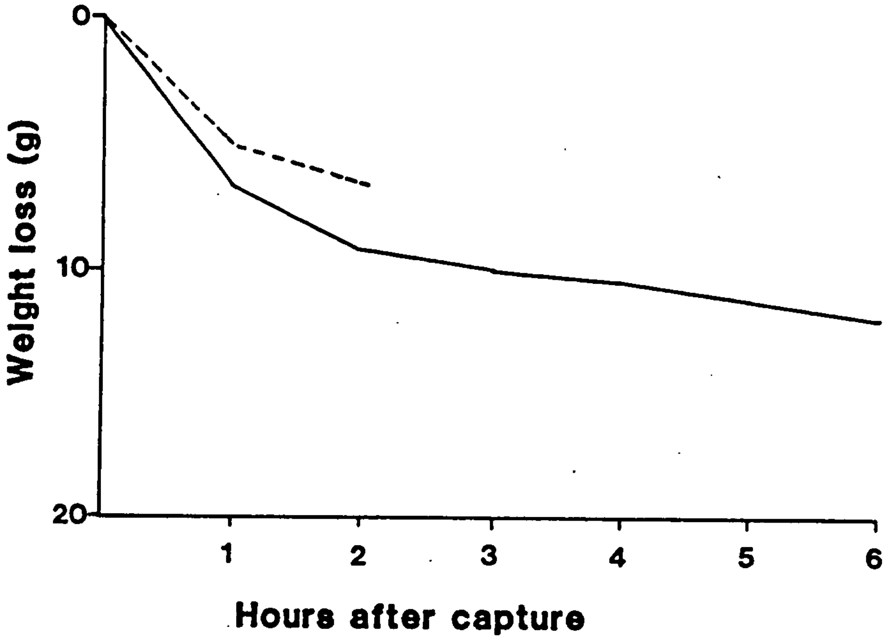
Fig. 2.15. Weight loss of Scoughall turnstone after capture.


130
120
110
100
90
Body weight (g)
0
1
2
3
Hours after capture

and there appeared to be no sex or age differences in weight loss although the small sample size precluded statistical testing. However, several studies have indicated that weight loss is not a linear function of time in captivity as depicted in Fig. 2.15 (e.g. Lloyd et al, 1979; Schick, 1983; Davidson, 1984), so in catches of turnstone made at Portobello and Joppa, Mid Lothian , I reweighed two and 22 turnstone, respectively, at hourly intervals after their removal from the cannon-net. Mean hourly weight loss for these two samples is depicted in Fig. 2.16. As in most other studies weight loss rate was greatest during the first hour of captivity. Although the sample size from Joppa was very small I have used the curve derived from this catch in applying corrections to weight data because the rate of weight loss was very similar to that from the Scoughall catch. No turnstone were held in captivity for longer than five hours, so the possibility of a second phase of increased weight loss (Davidson, 1984) was not important. Since the time after capture could be calculated for weighings from field sheets (see Clark, 1983 for details) it was possible to correct the weight of each bird from every catch by reading off values from the weight loss curve.

To provide a comparison with the field results the turnstone in the Department roof aviary were weighed at the same time of day (16.00 GMT) about every three weeks throughout their term in captivity. No corrections were made to these data as the time between catching and weighing was negligible.

Fig. 2.16. Mean weight loss of turnstone after capture, Joppa (----) N=16, Portobello (——) N=2.


0
10
20
Weight loss (g)
1
2
3
4
5
6
Hours after capture

2.6.2 RESULTS AND DISCUSSION

Attempts to catch turnstone at Scoughall were frequently either unsuccessful or difficult to carry out if the birds were on the roost at high tide, so I have included weight data from several other sites on the S. Forth (Joppa, Portobello and Musselburgh) to provide a more complete picture of seasonal weight changes. Adults tended to have low weights in September and October rising to a peak in late January, followed by a steady decline thereafter (Fig. 2.17). Mid-winter peaks in weight arise principally as a result of peak fat reserves (Davidson, 1981) and are typical of several waders wintering on northern European coastlines (e.g. Smit & Wolff, 1981; Davidson, 1981; Johnson, 1985). The pattern of seasonal weight change presented here for S. Forth turnstone populations is extremely similar to that for populations on the Wash, eastern England (Johnson 1985), although is is more difficult to compare absolute weight differences as the Wash data were not adjusted for weight loss in captivity. However, it is probably reasonable to assume that on average, weight loss in captivity was around 8g, which if correct, suggests that on the Wash turnstone do not have lower weights than on the Forth, in contrast to dunlin (Pienkowski _et al_, 1979). Weight changes of the captive turnstone in the aviary were also very similar to those of field populations on the Forth, showing a peak weight in late January (Fig. 2.18).

There did not appear to be any consistent weight differences between adults and juveniles (Fig. 2.17). Whilst this may be a genuine effect, it may be a result of small juvenile samples as

Fig. 2.17. Corrected weights of turnstone captured at Scoughall (circles), Musselburgh, Joppa and Portobello (triangles). Closed symbols are mean adult weights, open symbols are mean juvenile weights: lines are standard errors.

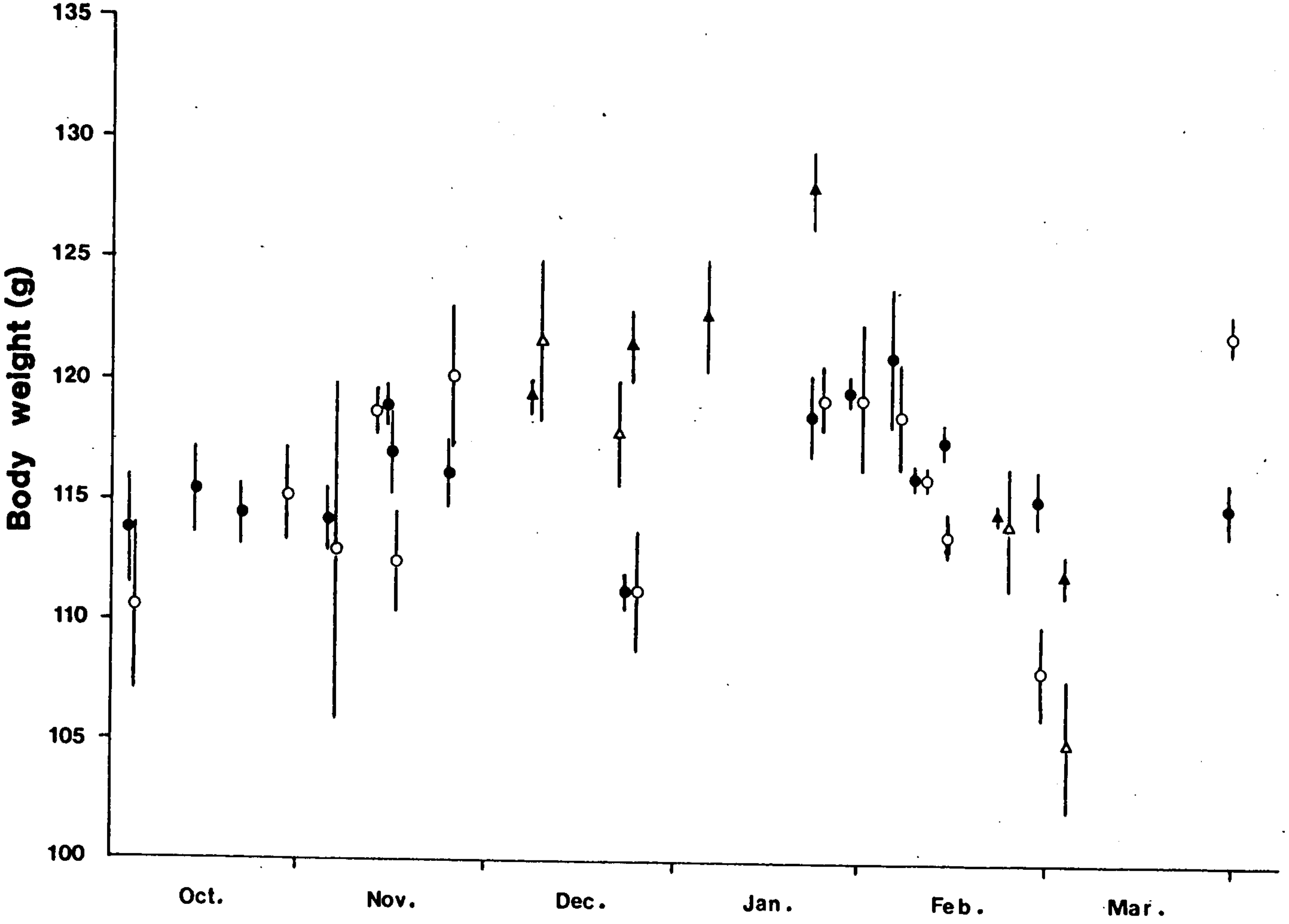
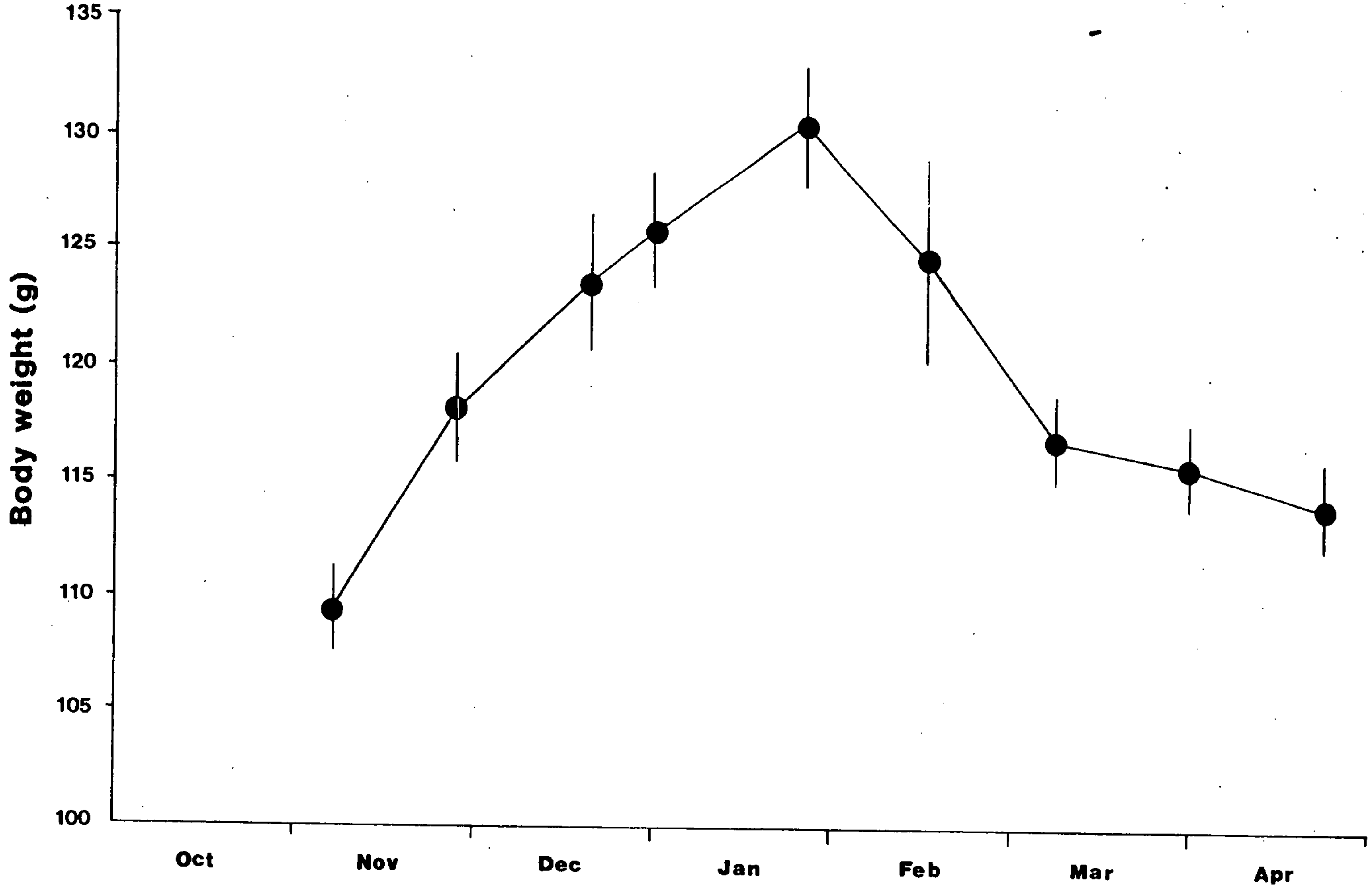

Body weight (g)
135
130
125
120
115
110
105
100
Oct.
Nov.
Dec.
Jan.
Feb.
Mar.

Fig. 2.18. Means and standard errors of weights of the captive turnstone.


Body weight (g)
135
130
125
120
115
110
105
100
Oct
Nov
Dec
Jan
Feb
Mar
Apr

Johnson (1985) found that juveniles had consistently higher weights than adults. At Scoughall, during the relatively severe winter of 1981-82 the ratio of mean adult male weight/mean adult female weight was 0.98 for each catch made on four separate occasions: this suggests that there were no sexual differences in weight, and therefore fat reserves, beyond those expected from sexual dimorphism in body size (see section 2.3.2.1).

The mid winter increase in fat reserves is usually interpreted as an insurance against the probability of increased difficulty in obtaining food due to adverse environmental conditions (e.g. Evans & Smith, 1975; Clark, 1983; for reviews of the factors producing increased mid-winter feeding difficulties see Pienkowski _et al_, 1983 and Puttick, 1984). In addition, it appears that levels of reserves are regulated so that late winter weight loss is not due to food shortages (Pienkowski _et al_ 1979; Clark 1983), and weights are maintained at lower levels in mild winters (e.g. Clark, 1983). This implies that there is a cost to maintaining as a contingency measure, fat reserves which may not be required. Possible costs are usually considered in terms of the disadvantages in carrying extra weight, such as increased energy expenditure during flight or a decrease in manoeuvrability in avoiding predators (e.g. Dick & Pienkowski, 1979; Clark, 1983). On the latter issue, if heavier birds are slower to take flight in response to a raptor they may be more vulnerable to being killed, as Whitfield, (1985: Appendix 1) found that waders which were slower to respond to sparrowhawk attacks were probably more likely to be caught by hawks. However, it is also possible that there is a cost to accumulating fat reserves as well as maintaining them, the cost being a reduction in the chances of detecting predators. If a bird is to increase its fat reserves it must increase its food intake, which may be achieved by either a) increasing the time spent feeding and/or b) increasing feeding rate, and/or c) feeding in more productive sites or on more productive prey. There is evidence which shows that at times when waders are attempting to lay down increased fat reserves they may employ both option a) (e.g. Goss-Custard, 1979a; Baker, 1981; Chapter 6) and option b) (Metcalfe & Furness, 1984). Both options can reduce the amount of time spent looking out for predators and, consequently, may increase the chances of being taken (Metcalfe & Furness, 1984; Chapter 6-Fig. 6.16). In mid and late winter option c) is probably not open to many waders given the reduction in prey availability at this time of the year (reviewed in Chapter 3) or if it is , it may involve feeding in areas or on food which involve a greater predation risk (Whitfield, 1985: Appendix 1). Avoiding death due to predators and avoiding death due to severe weather and starvation may produce conflicting selection pressures of which variability in feeding behaviour and fat reserves are manifestations.

2.7 MORTALITY

2.7.1 METHODS

Two methods of estimating mortality were used: (1) searching for corpses and remains of corpses, and (2) equating the disappearance of colour-ringed birds with their death.

(1) Searching for corpses. Details of this method are given in Whitfield (1985: Appendix 1) for the winters of 1982-83 and 1983-84.

The same method was used to investigate aspects of turnstone mortality in the 1984-85 winter. The study site was searched regularly for corpses and other remains, and each set of remains was ascribed to one of several categories according to their state and position. These categories were used to identify the probable cause of death of each corpse. For example, Category A encompassed all corpses eaten in cover, on or near to the ground, with cleanly plucked feathers and with any bones picked clean of flesh. This category typified the appearance of remains resulting from sparrowhawk depredation, and the number of remains placed in Category A effectively represented the number of birds eaten by sparrowhawks. Categorising remains allowed me to produce estimates of the number of birds (a) killed by sparrowhawks, (b) killed by peregrines Falco peregrinus or merlins F.columbarius, (c) killed by owls, probably tawny owls Strix aluco, (d) killed by mammalian predators e.g. foxes Vulpes vulpes or stoats Mustela erminea, (e) dying from natural causes, or starvation and/or severe weather effects. The date of death was estimated from the state of the remains and the date of the preceding search at the site of the find. There was a possibility that some predators removed corpses from the study site, thus affecting the accuracy of the method. The age of turnstone which died could usually be discovered by examining feathers amongst the remains or by referring to ringing records. Details of the calculations used to estimate mortality are given in Appendix 1.

(2) Disappearance of colour-ringed birds. This method can be used to estimate mortality both on the wintering grounds and away from the wintering grounds (e.g. Evans & Pienkowski, 1984). In the present analysis the winter component of annual mortality was taken to be that occurring between 1 August and 1 April (the latter date was used because it represented the earliest normal departure date of individuals that survived until the following August- Fig. 2.19). Thus the number of birds dying on the wintering grounds in winter x is given by:- number of birds seen after August 1 in winter x, last seen before April 1 in winter x, but failing to return to Scoughall in winter (x + 1). The number of birds dying away from the wintering grounds following winter x is given by:- number of birds seen after August 1 in winter x, last seen after April 1 in winter x, and failing to return in winter (x + 1).

Mortality can be overestimated if individuals which are prone to move away from the study site during a winter are included in the cohort of colour-ringed birds from which the estimate is derived (see Townshend, 1982 for grey plover). If only those birds which are seen regularly and frequently on the study site are included in the cohort then this problem of overestimation can be minimised. I have included, therefore, only those birds with a past history of regular and frequent sightings, i.e. at least ten sightings per month, in the analysis. The price of increasing the accurracy of mortality estimates by using this criterion is that the estimates will apply only to the more site faithful individuals.

2.7.2 RESULTS

2.7.2.1 WINTER MORTALITY AS REVEALED BY SEARCHING FOR CORPSES

Sparrowhawk predation was the major cause of winter mortality of turnstone on the study site (Table 2.5). Predation by raptors (Falconiformes and Strigiformes) accounted for 100% of winter

Fig. 2.19. Percentage of colour-ringed adult turnstone departing in two-weekly periods from Scoughall, in spring 1984 (N=138).

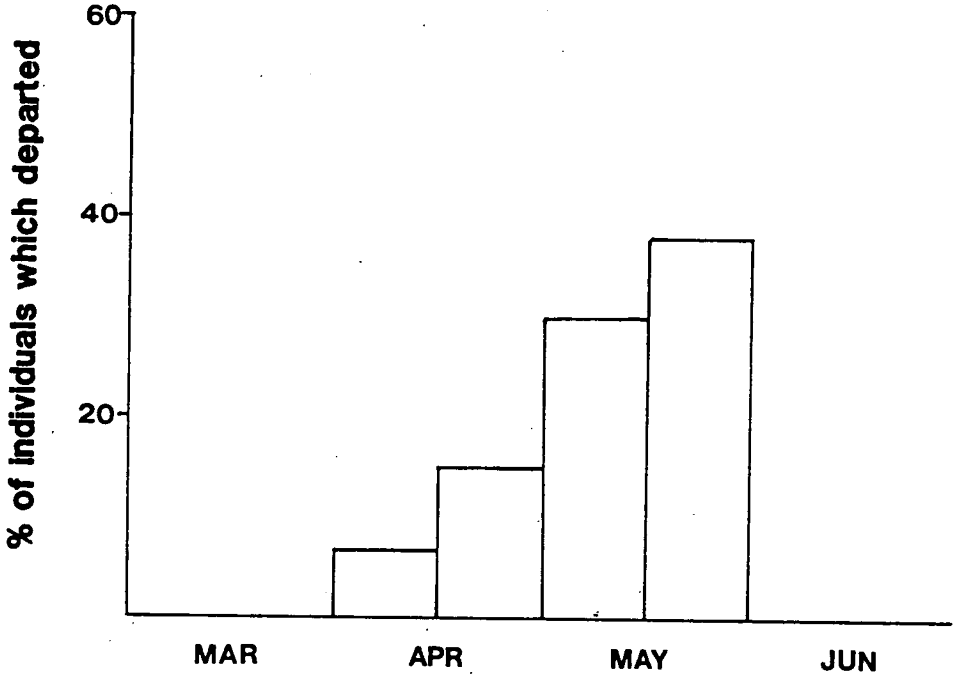

% of individuals which departed
60
40
20
MAR
APR
MAY
JUN

TABLE 2.5

Sources of winter mortality.

	Predation					Severe
	peregrine/ merlin	sparrowhawk	owl	kestrel	stoat/ fox	weather/ starvation
1982-83	1	7	1	1	0	0
1983-84	0	10	0	0	0	0
1984-85	1	14	0	0	0	0
Total	2	31	1	1	0	0
%	6	89	3	3	0	0

mortality in the three winters in which systematic searches were made. Although two birds (1 adult, 1 juvenile) probably died as a result of adverse weather in the winter of 1981-82, no such evidence was found in the following three winters. Whilst in 1981-82 I searched only the strandline for corpses, two juveniles which had been killed by raptors were discovered by chance and many more kills were undoubtedly missed because I did not search appropriate areas. Raptor predation was the major source of winter mortality in other waders at the study site in 1982-83 and 1983-84 (Whitfield, 1985: Appendix 1) and in 1984-85 (Whitfield, A.Evans & P.Davison, unpubl. data).

Winter mortality was, on average, 5% for the turnstone population, with juveniles experiencing heavier mortality than adults (Table 2.6). Significantly more juveniles were killed in each winter than was expected by their representation in the population (see Appendix 1).

More turnstone were killed in January than in other months (Table 2.7a), and assuming a more or less constant population size (section 2.2) this indicates peak mortality occurred also in January. At least six adult male turnstone and five adult females were known to have been killed during the study period, which, given an equal population sex ratio (section 2.3.2.3), suggests that there were no sexual differences in winter mortality. Based on body part measurements taken from kills, six juvenile turnstone which were killed could be assigned to a sex with a reasonable degree of confidence: three were probably male and three were probably female.

Of those turnstone which were killed, I could be certain that eleven adults were colour-ringed and that three were unringed: there

TABLE 2.6

Estimates of % winter mortality based on searches for corpses.

	Population	Adult	Juvenile
1982-83	4	2	13
1983-84	5	3	14
1984-85	6	4	12

TABLE 2.7

(a) Seasonal changes in the numbers of turnstone found dead; (b) numbers of adult and juvenile turnstone found dead.

	(a) OCT	NOV	DEC	JAN	FEB	MAR	(b) TOTAL	AD	JUV	?
1982-83	4	2	0	3	0	1	10	3	6	1
1983-84	2	1	2	4	0	1	10	5	5	0
1984-85	1	2	4	3	4	1	15	7	8	0
TOTAL 1982-85	7	5	6	10	4	3	35	15	19	1

was no significant difference between the proportion of dead adults which were colour-ringed and the proportion of colour-ringed adults in the population (Fisher's exact probability test, $p>0.05$). The numbers of colour-ringed (2) and unringed (8) juveniles which were killed did not differ significantly from expectations based on the numbers of colour-ringed and unringed juveniles in the population (Fisher's exact probability test, $p>0.05$). There was no evidence, therefore, which suggested that colour-ringing affected a bird's likelihood of being killed by predators.

2.7.2.2 WINTER MORTALITY AS REVEALED BY RETURN RATES

Estimates of adult winter mortality rates, based on the disappearances of colour-ringed birds, were between 5 and 6% (Table 2.8). These estimates were slightly higher than those derived from the discovery of corpses. This is perhaps to be expected, as searching for corpses probably underestimates the number of deaths because some remains are missed, whereas the return rates method probably overestimates mortality, particularly in more itinerant species or populations (cf Townshend, 1982). The true adult mortality level probably lay somewhere between the estimates.

Summer mortality may have been a little lower than winter mortality, but it is difficult to compare the two seasons on such a small sample size. There was also a possibility that males suffered heavier summer mortality than did females (2 females, 4 males), but that females had lower survival in winter (7 females, 5 males). Annual adult mortality appeared to be similar, at about 10%, to the estimates produced for turnstone at Teesmouth, N.E.England (Evans & Pienkowski, 1984).

TABLE 2.8

Estimates of % annual, winter and summer mortality based on return rates of colour-ringed birds. N=number of colour-ringed birds from which estimate was derived.

	ADULT				JUVENILE	
	ANNUAL	WINTER	SUMMER	N	WINTER	N
1982-83	10	5	5	125	11	9
1983-84	8	6	2	124	--	-

CHAPTER 3

MOVEMENTS, HOME RANGE AND FLOCK STABILITY

3.1 INTRODUCTION

Definitions of the term 'home range' vary from author to author, although commonly they refer to the area over which an animal normally travels in pursuit of its routine activities (e.g. Jewell, 1966). The properties of site attachment or faithfulness to a particular locality without active defence of that locality, together with the pattern of movements made in the course of resource utilisation, are central to the concept of home range. Investigations of home range have been carried out on many mammals (e.g. primates, Clutton-Brock & Harvey, 1977 and references therein), although avian studies are fewer in number and usually restricted to breeding individuals (e.g. Schoener, 1968; Newton, 1979; Marquiss & Newton, 1982; Kenward, 1982).

Observations of marked birds have shown that at least some individuals of many species return to the same wintering area year after year, e.g. sanderling Calidris alba (Evans et al, 1980; Myers & McCaffery, 1980; Myers et al, 1984), curlew Numenius arquata (Bainbridge & Minto, 1978; Townshend, 1979), dunlin Calidris alpina (Clark, 1983), American golden plover Pluvialis dominica fulva (Johnson et al, 1981), willet Catoptrophorus semipalmatus and marbled godwit Limosa fedoa (Kelly & Cogswell, 1979). Individuals frequently remain within the same area for several months within a winter (e.g Page, 1974; Clark, 1983; Johnson et al, 1981; Kelly & Cogswell, 1979; Symonds et al, 1984).

Recent work has shown that site fidelity may vary both between and within species (reviews by Myers, 1984; Pienkowski & Evans, 1984). In Britain, some coastal species are more itinerant than others in winter, different species apparently occupying different sections on a resident-itinerant continuum (Pienkowski & Clark, 1979; Evans _et al_, 1980; Evans, 1981; Symonds _et al_, 1984). The knot _Calidris canutus_ seems to be the most itinerant species yet investigated, often moving many kilometres within a winter, whilst in other species, such as the turnstone, birds appear to remain in the same locale throughout a winter (e.g. Symonds _et al_, 1984).

Individual sanderlings appear to vary markedly in site fidelity (Evans _et al_, 1980; Myers, 1980; Myers & McCaffery, 1980; Evans, 1981; Myers, 1984). Evans (1981) suggested that sanderlings were either resident or itinerant, but Myers (1984) found no evidence of this hypothesised dichotomy. Rather it appears that there is continuous inter-individual variation in sanderling site fidelity (Myers, 1984).

Evans (1981) has suggested that the stability of food supplies may determine such inter- and intra-specific variations in site fidelity. Residents exploit relatively stable food supplies whilst itinerants exploit more unstable food supplies, (see also Tree, 1979; Myers & McCaffery, 1980; Pienkowski & Evans, 1984). This echoed similar arguements attempting to explain the interspecific differences between breeding calidrine sandpipers which were classified as strongly philopatric (conservative breeders) exploiting predictable resources or weakly philopatric (opportunistic breeders) exploiting unpredictable resources (Pitelka _et al_, 1974). Within a species the two strategies may have equal payoffs (cf Swingland, 1984) or may be conditional on, for example, status, with unequal payoffs (cf Gauthreaux, 1978).

Wintering turnstone appear to be very site faithful both within and between years (Summers et al, 1976; Branson et al, 1978; Sutherland, undated; Symonds et al, 1984) and Marshall (1981) has speculated that the turnstone population at the study site is a resident community. This suggested that a study of the home range of turnstone was a realistic proposition, and, this chapter describes the results of such a study. I examined whether individuals differed in their site fidelity and investigated possible factors influencing the degree of site fidelity. I also investigated the possibility that inter-individual associations occurred, as would seem likely given the apparent strength of site fidelity in turnstone.

3.2 METHODS

3.2.1 PLOTTING BIRDS' LOCATIONS AND HOME RANGE ESTIMATION

During the course of collecting observations of feeding behaviour (Chapter 6) the study site was regularly searched for colour-ringed turnstone. When one was located the following information was recorded: date, time, colour-ring combination, feeding technique used, microhabitat feeding in, nearest neighbour identity (colour-ring combination, unringed adult or juvenile, colour-ringed adult or juvenile), nearest neighbour distance in metres and the number of birds in the flock. A group of turnstone was judged to be a flock if all individuals were within 10m of each other: groups which were so dispersed responded as a single unit when moving or when disturbed, whereas groups which were more dispersed did not always respond as a single unit. Due to the nature of the rocky shore habitat I could never be sure that I had accurately counted the number of turnstone in an intertidal flock and so flock size categories were employed: 1-3, 4-7, 8-12, 13-18, 19-25, 26-35, 36-45, 46-60, 61-80, 81-100. On the strandline, flock size could usually be measured more accurately due to the greater openess of the habitat.

The rock formations of the littoral zone as represented on Ord~~i~~nance Survey maps of the study site were in~~n~~accurate. Therefore, they could not be used to plot the location of colour-ringed birds. To overcome this problem photographs of the littoral zone were taken from set observation points along the coastline. These photographic images were converted to line drawn images which were copied onto check sheets. Several copies of these check sheets were taken into the field and a birds' position was denoted by a point on the drawing labelled with a letter. Under the drawing the details of the birds' identity etc. was noted next to the same letter. This method was used only in the 1981-82 winter. By the end of my first winter I had become sufficiently familiar with the study site to enable me to record a bird's location by reference to its position relative to landmarks (e.g. large boulders, pools). Each bird's location could then be converted later to an eight figure Ord~~i~~nance Survey coordinate using a grid superimposed over aerial photographs (obtained from the Scottish Office, aerial photographs division) of the study site, each small square on the grid representing a 10x10m square.

Periodically during a winter I made visits to areas outside the study site to check for colour-ringed birds. Several people also sent records of sightings made outside the study area.

Home range was defined by the area encompassed by the 0.9 probability level which specified the proportion of time an individual turnstone was seen feeding in that area (the 0.9 minimum area probability, MAP (0.9)). This utilisation distribution (UD) was defined by the distribution of the actual coordinates using the nonparametric method of Anderson (1982). I used this method because it was apparent that turnstone frequently had more than one activity centre within their home range, so the UD could not be defined by a bivariate frequency distribution, invalidating the use of a parametric estimate of home range. I did not use the minimum convex polygon (MCP) method (e.g. Odum & Kuenzler, 1955) because it is very sensitive to outlying points. The harmonic mean method of Dixon & Chapman (1980), which has none of the problems of the MCP or probabilistic parametric methods, was not used because the home range computation by this method is laborious in comparison with Anderson's method. Critical reviews of techniques used to estimate home range can be found in MacDonald <u>et al</u> (1980), Schoener (1981), Anderson (1982), Samuel <u>et al</u> (1985) and Wilkinson & Bradbury (in press).

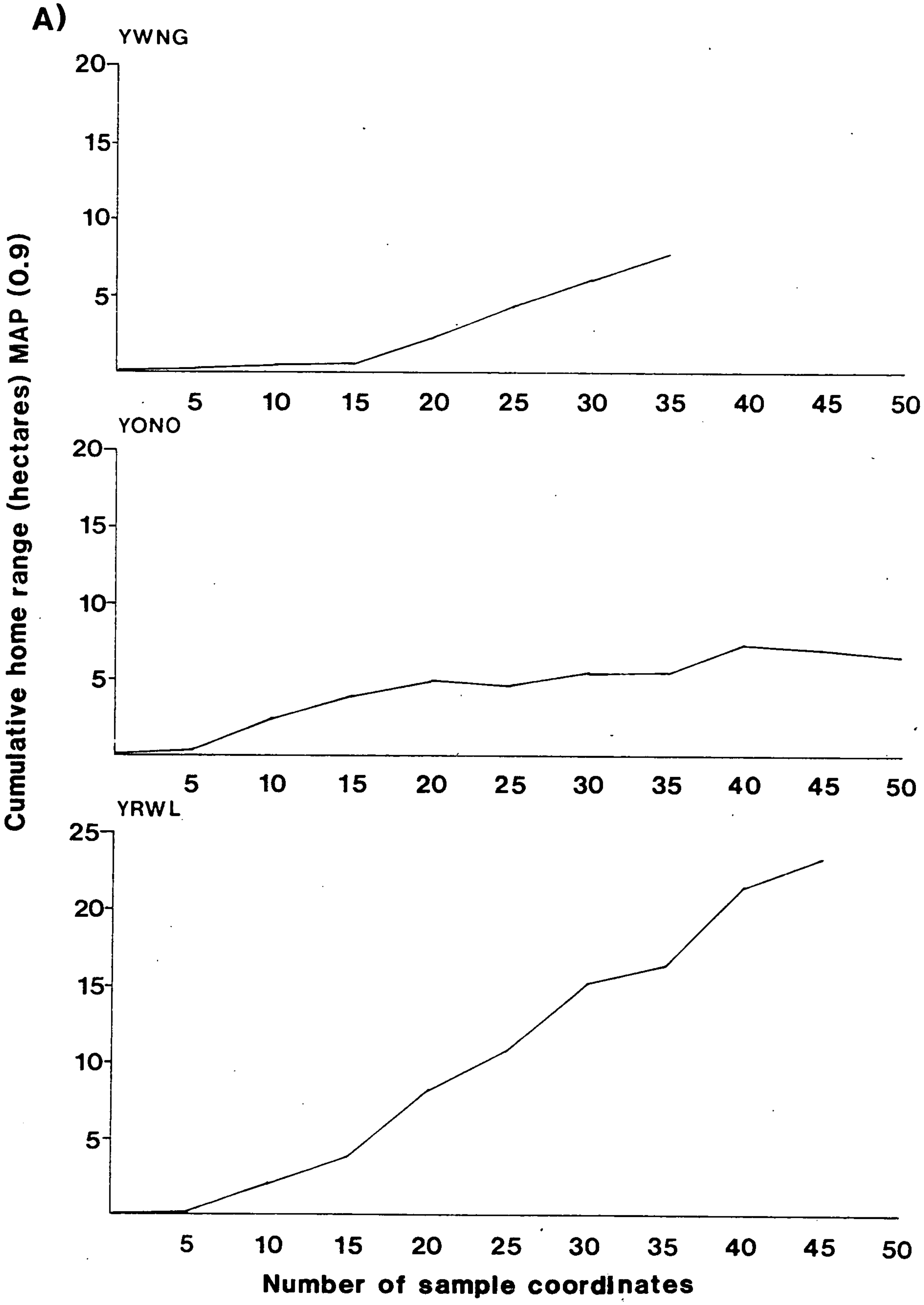
For each bird I discarded each sample coordinate which was recorded less than 15min. from another sample coordinate. I did not test for independence between sample coordinates (Schoener, 1981; Wilkinson & Bradbury, in press), because the large variation in home range area (see Results) meant that the criteria for discarding non-independent observations would probably not have been constant, making tests for serial dependency of observations an extremely time consuming exercise. Instead, I have used 15min as the minimum inter-sample time, since within this period a turnstone could potentially move between any two points on the study site.

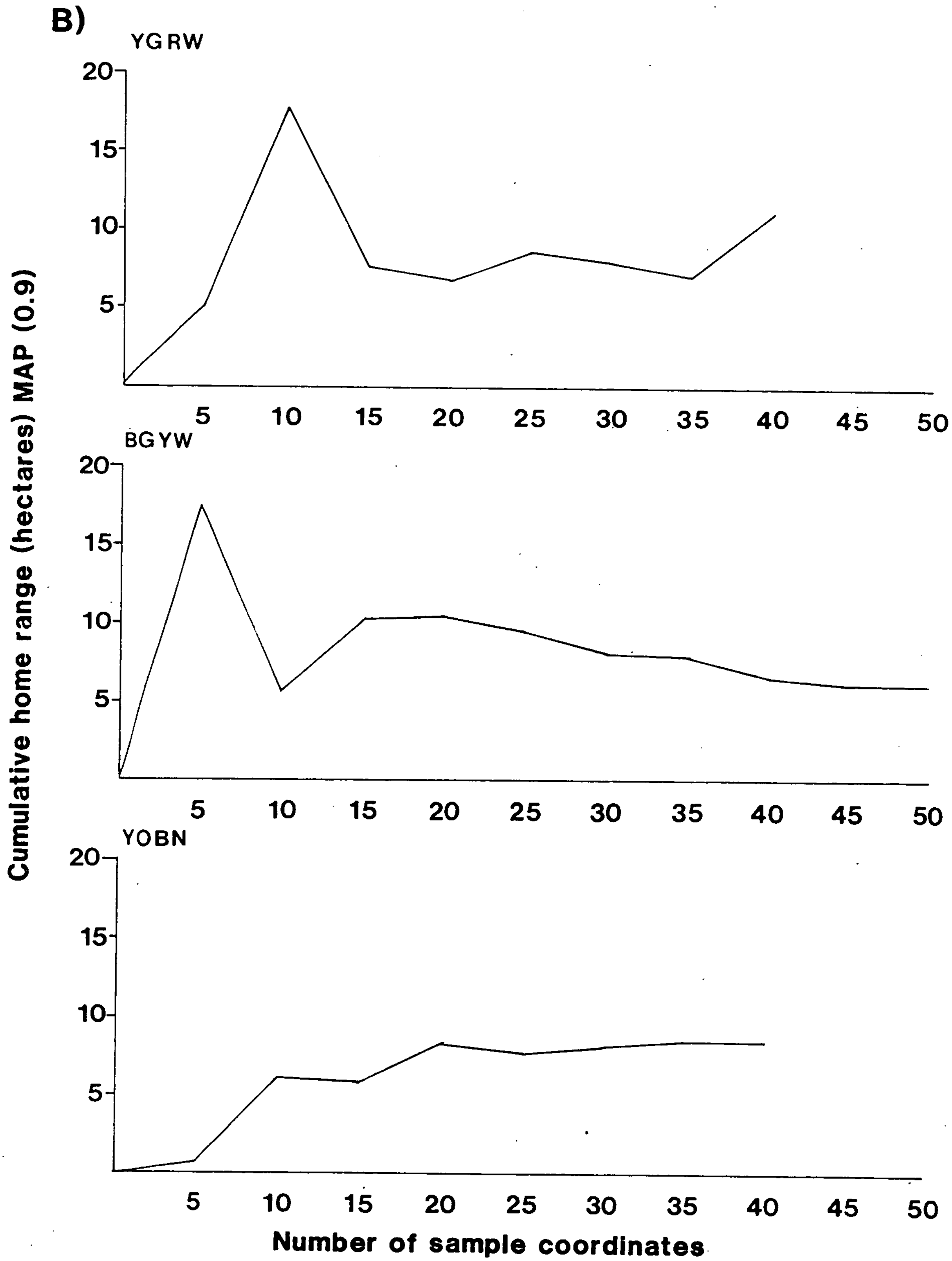
The accuracy of home range estimates depends on the number of samples (e.g. Wilkinson & Bradbury, in press): too small a sample size may underestimate the home range area. The usual method for determining the required number of samples which provides a reasonably good estimate is to assess the number of observations at which home range estimates stabilise (e.g. Odum & Kuenzler, 1955). Cumulative home range estimates for several turnstone showed that although estimates stabilised after varying numbers of observations (because of seasonal expansions in some individuals' home range), the average number of required observations was about 20 (Fig. 3.1). The home ranges of individual turnstone which had less than 20 sample coordinates were therefore not estimated.

Home range referred only to an intertidal feeding area; strandline observations were excluded. Every turnstone residing on the study site used pre-roost sites on the rocks seaward of Chapel Brae cliffs and roost sites on the Great Car. Sometimes turnstone fed at these sites, interspersed between bouts of roosting, and these observations were excluded from the home range analysis because they were probably subject to sampling bias. Turnstone feeding at Tyninghame were frequently so far away that I could not accurately determine their location and so these observations could not be used in home range analysis.

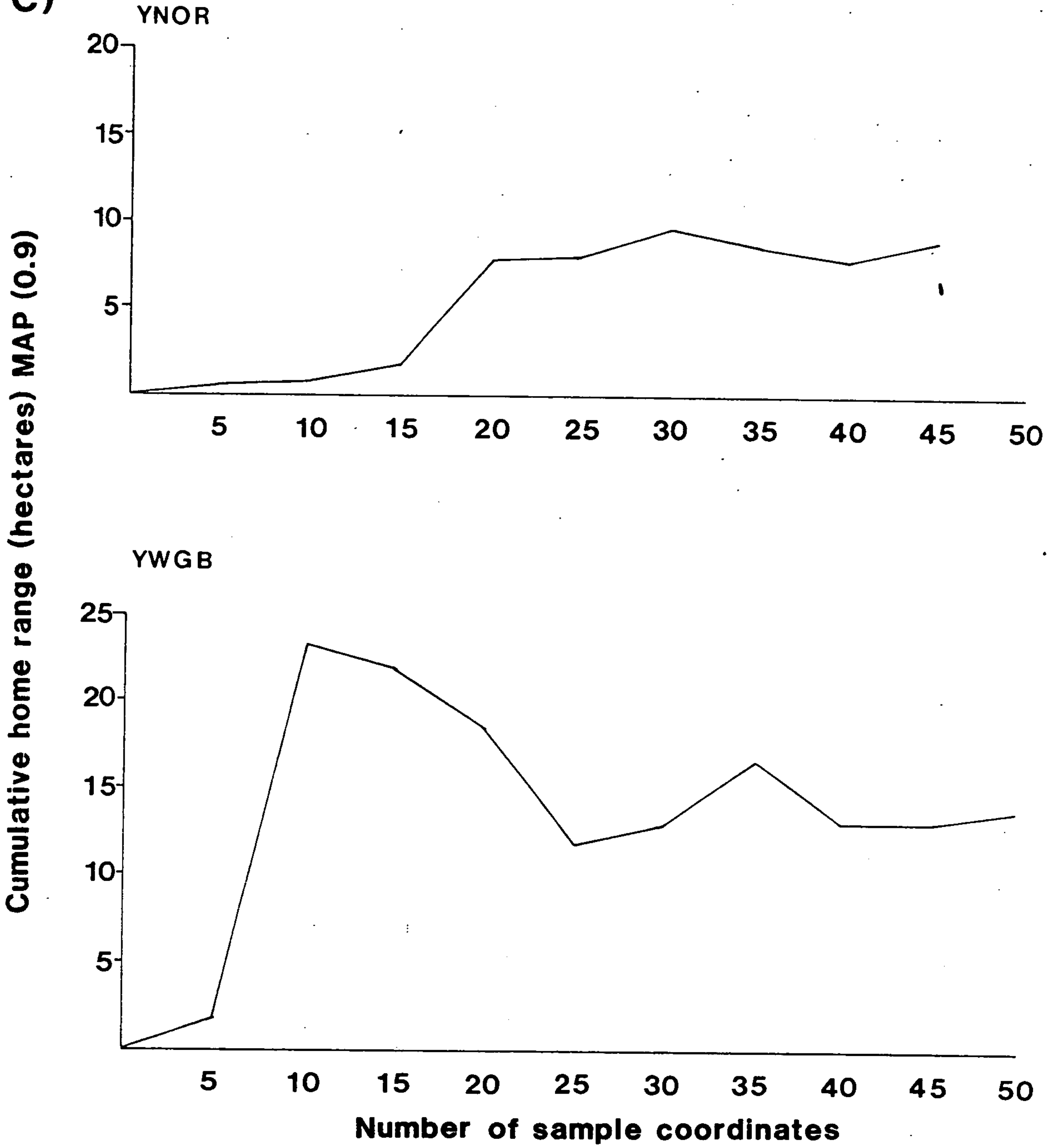
Home range estimates, calculated by using the MAP (0.9) from the Anderson (1982) UDs, were based on observations collected in the 1982-83 winter.

FIg. 3.1a,b,c. Some examples of individual´s cumulative home range area estimates in the 1982-83 winter. The estimates for YWNG and YRWL do not stabilise because the home range areas of these birds increased throughout the winter.


A)
YWNG
20
15
10
5
5
10
15
20
25
30
35
40
45
50
YONO
20
15
10
5
5
10
15
20
25
30
35
40
45
50
YRWL
25
20
15
10
5
5
10
15
20
25
30
35
40
45
50
Cumulative home range (hectares) MAP (0.9)
Number of sample coordinates


B)
YGRW
BGYW
YOBN
20
15
10
5
5
10
15
20
25
30
35
40
45
50
Cumulative home range (hectares) MAP (0.9)
Number of sample coordinates

C)


YNOR
20
15
10
5
5
10
15
20
25
30
35
40
45
50
YWGB
25
20
15
10
5
5
10
15
20
25
30
35
40
45
50
Cumulative home range (hectares) MAP (0.9)
Number of sample coordinates

3.2.2 INVERTEBRATE SAMPLING

Preliminary observations of turnstone in the 1981-82 winter suggested that seasonal differences in turnstone movements occurred. To examine the possible influence of food supplies in seasonal movements I undertook an invertebrate sampling programme in the 1982-83 winter. At three times in the winter, mid-September, mid-December and mid-March I took twenty samples each from three microhabitats (rocks covered with Phaeophycea (brown) seaweed (WR/SWR), pebbles and pool water less than turnstone leg-depth, see Chapter 6 for further details) and from four areas, Car Rocks, Field Space, Scoughall, Coastguard (see Chapter 1). Sampling always took more than one day to carry out, but for each month samples were taken on consecutive days. So far as was possible, I attempted to collect samples from the same microhabitat in different areas at approximately the same stage of the tidal cycle.

The sampling unit was a washing-up bowl with its bottom cut out and encompassed an area of $0.066m^2$. Sampling sites were selected arbitrarily by dropping the sampling unit over my shoulder whilst standing in an apparently suitable microhabitat. Within each area I attempted to sample from sites as widely spread as possible and from places where turnstone fed at some time in the 1982-83 winter.

All living invertebrates and seaweed within the sampling unit were collected and placed in a separate plastic bag for each sample; the bag was then closed with a rubber band and labelled with an indelible marker pen.

Samples were transported back to the Zoology Department where they were stored in a cold room (just above $0^{o}C$) until they were processed. To separate invertebrates from the seaweed the latter was thoroughly washed in a small tank containing warm water; this water was then poured through 1.4mm and 0.425mm mesh sieves. All invertebrates were preserved in formalin and were later counted and classified into size categories (Table 3.1).

On the basis of preliminary observations in the 1981-82 winter I strongly suspected that depletion and wave action caused the number of barnacles in the Great Car area to fall during the course of the winter. A possible corollary of this was that in early winter large numbers of turnstone fed at the Great Car but by late winter very few fed there. To examine possible changes in the abundance of barnacles in the 1982-83 winter in the last week of each month I recorded the proportion of living barnacles (to the nearest 5%) at five sampling stations (each with an area of $0.25m^{2}$) marked out using white road paint on rocks at the Great Car.

3.2.3 INDIVIDUAL ASSOCIATIONS

I had planned to measure the strength of individual associations by calculating the degree of overlap between individuals´ utilisation distributions generated by Anderson´s (1982) home range estimation technique (see Wilkinson & Bradbury, in press). Unfortunately, problems with the computer program, which was necessary to calculate overlap, made it impossible to pursue this form of analysis. A crude measure of inter-individual associations is to calculate the two dimensional mean of each individuals´ sample

TABLE 3.1.

Size categories of the four major invertebrate prey species taken in intertidal seaweed by routing and probing birds (see Chapter 6 for details).

	Size class (mm)					
	small				large	
	1	2	3	4	5	6
Idotea (body length)	<5	5-9	10-13	14-17	>17	
Hyale (curved body length)	<2.5	2.5-3.5	3.5-4.5	>4.5		
Littorina littorea (max. shell height)	<7	7-12	13-16	17-21	22-25	>25
L.obtusata (max. shell height)	<5	5-7.5	7.6-10	10.1-12.5	12.6-15	>15

of coordinates; the distance between two individuals' mean coordinate (or home range centre) gives a measure of the strength of their association (Murray, 1981). I used this method to give a broad picture of individual associations; for example, a cluster of mean coordinates indicate that the birds' represented within the cluster were a reasonably discrete group of individuals which fed in the same locations (cf Murray, 1981).

The only published study of individual associations in waders flocks is that of Myers (1983) on wintering sanderlings Calidris alba. To facilitate comparisons with Myers' work I employed the same method of estimating the strength of associations, Ekman's (1979) coherence index. During the course of gathering data on birds' feeding locations and feeding technique utilisation the flock composition, in terms of colour-ringed individuals present, was recorded for several flocks seen within the Field Space-Coastguard areas in the 1982-83 winter. For each of two colour-ringed individuals, i and j, Ekman's (1979) index, $C_{i.j}$, reflects the strength of their association, so that

$$C_{i.j} = \frac{100T_t}{T_i + T_j + T_t}$$

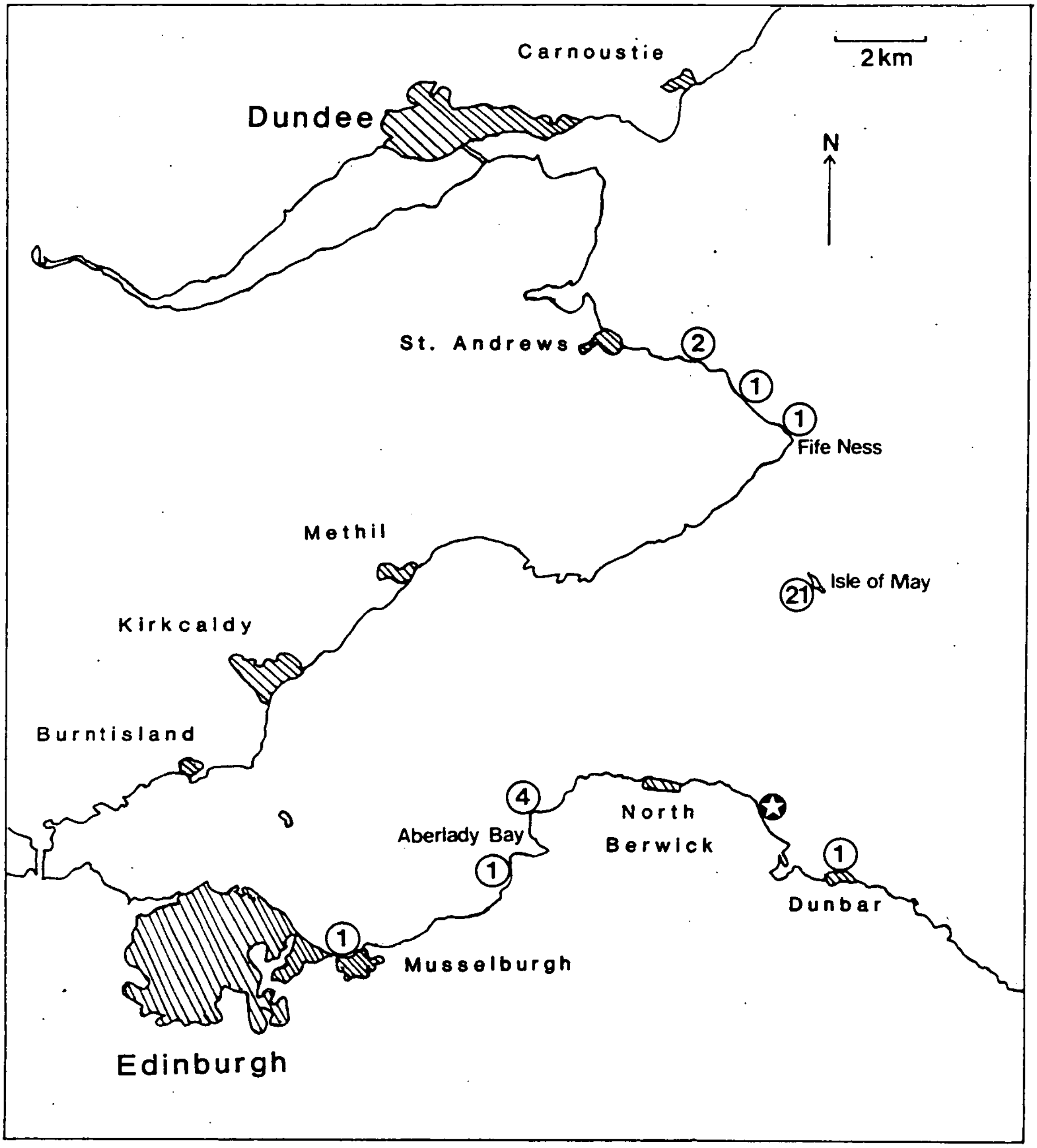
where T_i is the number of observations of bird i without bird j; T_j is the number of observations of bird j without bird i and T_t is the number of observations of bird i and bird j together. Individuals seen on very few occasions may have inaccurate values of C because of sampling error. Therefore, like Myers, I excluded individuals seen fewer than 4 times.

Observed distributions of all possible pairs of birds were compared with expected random distributions obtained by a similar method to Myers (1983). Each bird in the original pool of individuals was assigned a number. For each of the observed flocks the flock composition (but not the number of individuals) was changed by selecting membership in a flock, and any bird could only appear once in any randomly generated flock. As for observed distributions, individuals ´seen´ fewer than 4 times were excluded from the calculations but because all birds in the original pool were considered equally ´available´ for genuinely random flocks, the number of excluded individuals was less in the random data set (cf Myers, 1983).

3.3 RESULTS

3.3.1 SIGHTINGS OUTSIDE THE STUDY SITE

Several turnstone which were caught and colour-ringed on the study site were subsequently seen or caught in areas outside of the study site (Fig. 3.2). The greatest number of individual turnstone were reported as being seen on the Isle of May, which is situated in the mouth of the Firth of Forth. Regular visits were made to Dunbar (by Alistair Clunas) and to the coastline between the study site and North Berwick by myself yet only one colour-ringed bird was seen in these areas. Similarly, regular counts and observations of waders were conducted by several people at other sites on the south Forth coastline but I received comparatively few reports of colour-ringed turnstone which had been seen there. Four different colour-ringed individuals were seen or caught on the north Fife coastline between Fife Ness and St. Andrews, and although I do not know the extent of


Carnoustie
2km
Dundee
N
St. Andrews
2
1
1
Fife Ness
Methil
Isle of May
21
Kirkcaldy
Burntisland
4
Aberlady Bay
1
North
Berwick
1
Dunbar
1
Musselburgh
Edinburgh

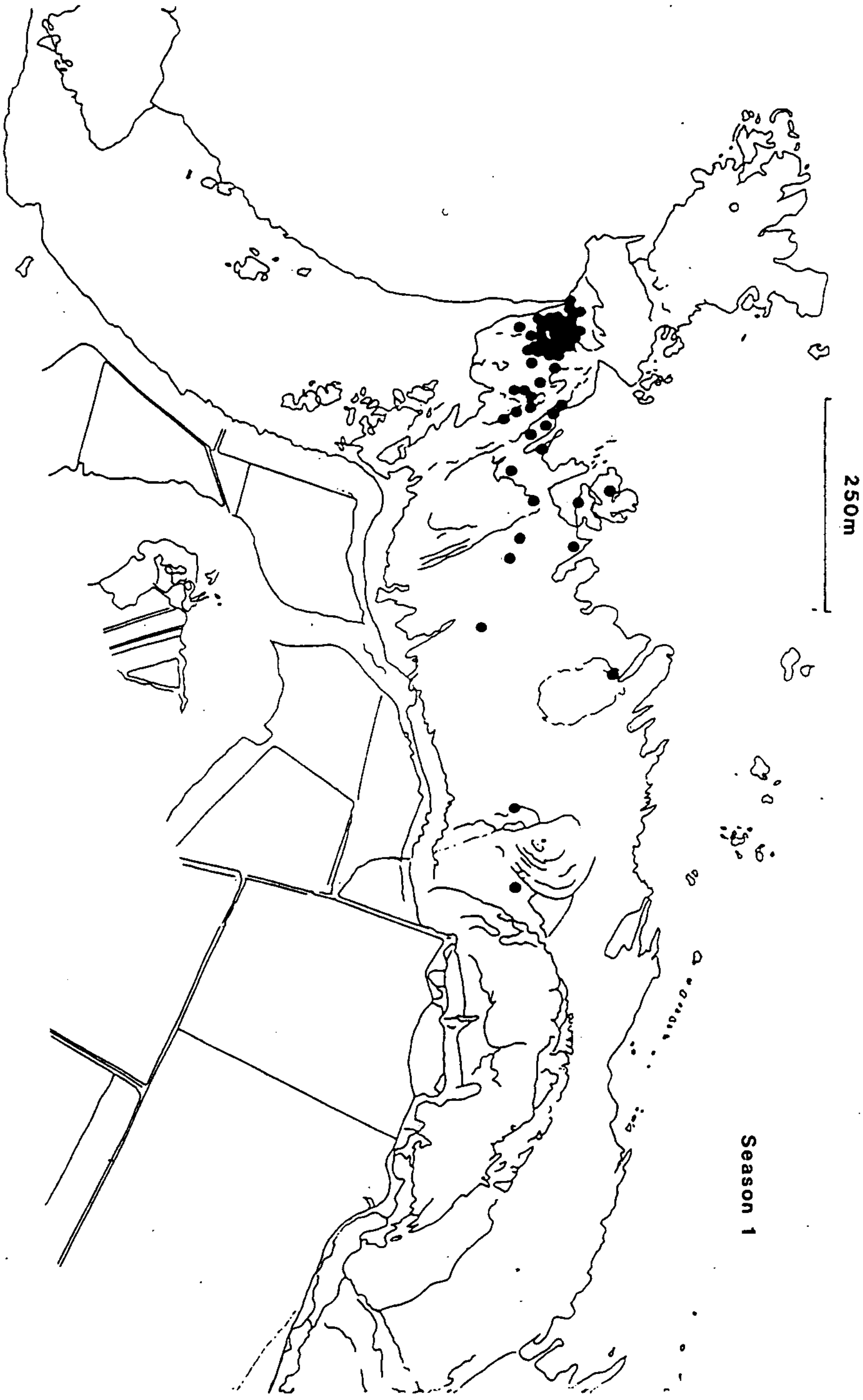
the observer coverage of this area the Tay Ringing Group occasionally made attempts to catch waders there (M. Nicoll, pers. comm.). The Isle of May was regularly visited by bird ringers and professional ornithologists, particularly in early winter, which probaly went some way to explaining the sighting dates and the comparatively large number of reports that I received from the island. Of the twenty-one individual turnstone reported from the Isle of May many were seen there regularly, and it was very likely that more than twenty-one colour-ringed birds used the island (K. Brockie, pers. comm.). One turnstone was seen at five sites: the study site, near Aberlady Bay, Isle of May, Fife Ness and Kingsbarns (between Fife Ness and St. Andrews). Two particularly interesting reports of this bird came from near Aberlady Bay on 13 February 1983 and from Fife Ness a day later!

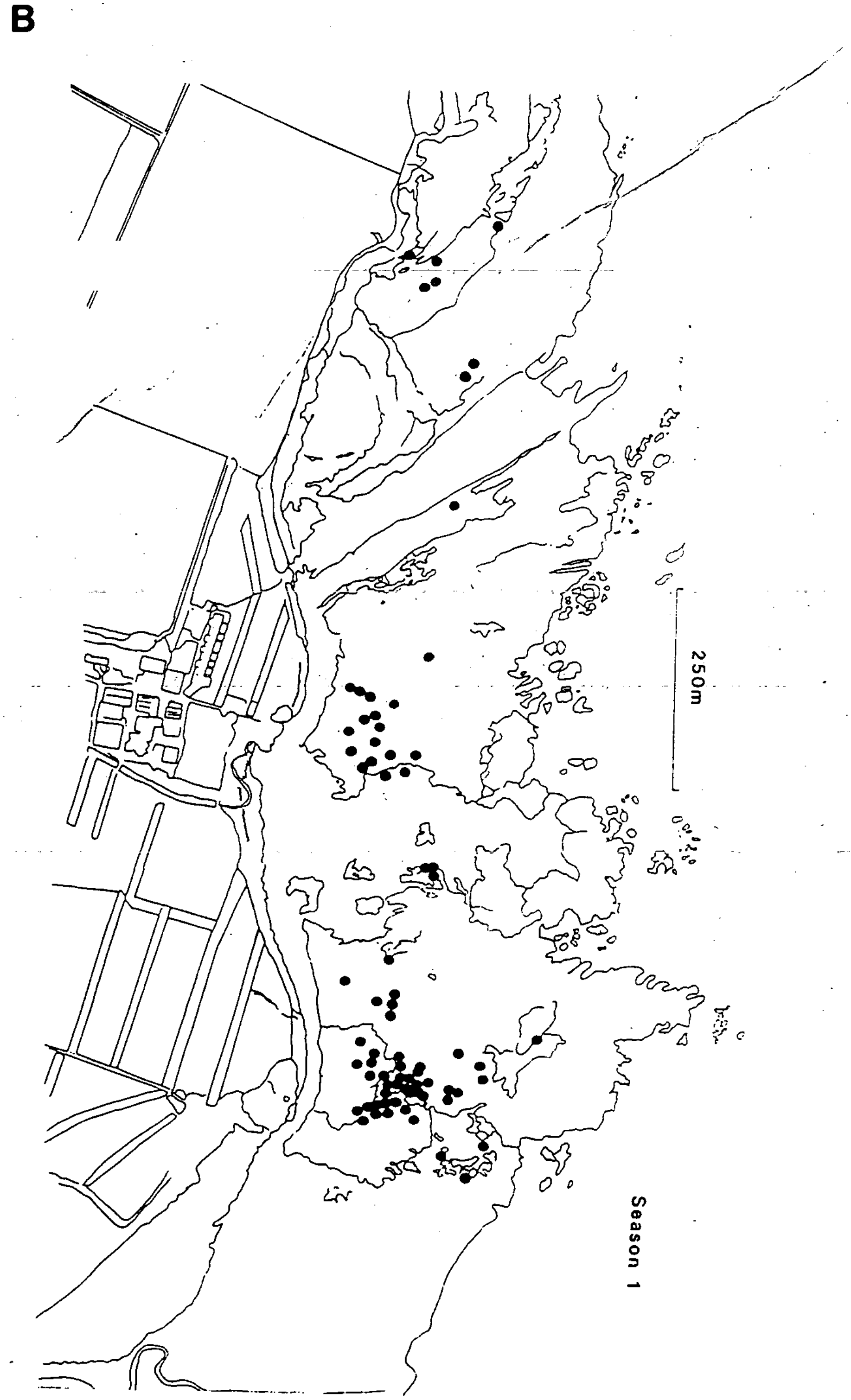
3.3.2 SIGHTINGS WITHIN THE STUDY SITE

From preliminary observations made in the 1981-82 winter it was very obvious that many turnstone were very site faithful, although the degree of itinerancy did appear to vary between individuals, and, as mentioned earlier, seasonal chnages in itinerancy occurred. To facilitate the detection of seasonal shifts in home range I divided each winter (1982-83, 1983-84) into three periods or ´seasons´: (1) August to October, (2) November to January, (3) February to March.

1982-83 winter. When individuals´ mean coordinates for season 1 were plotted onto a map of the study site between Tantallon and the Coastguard it was apparent that turnstone tended to feed in one of three areas: Great Car, Scoughall or Coastguard (Fig. 3.3). (A

A



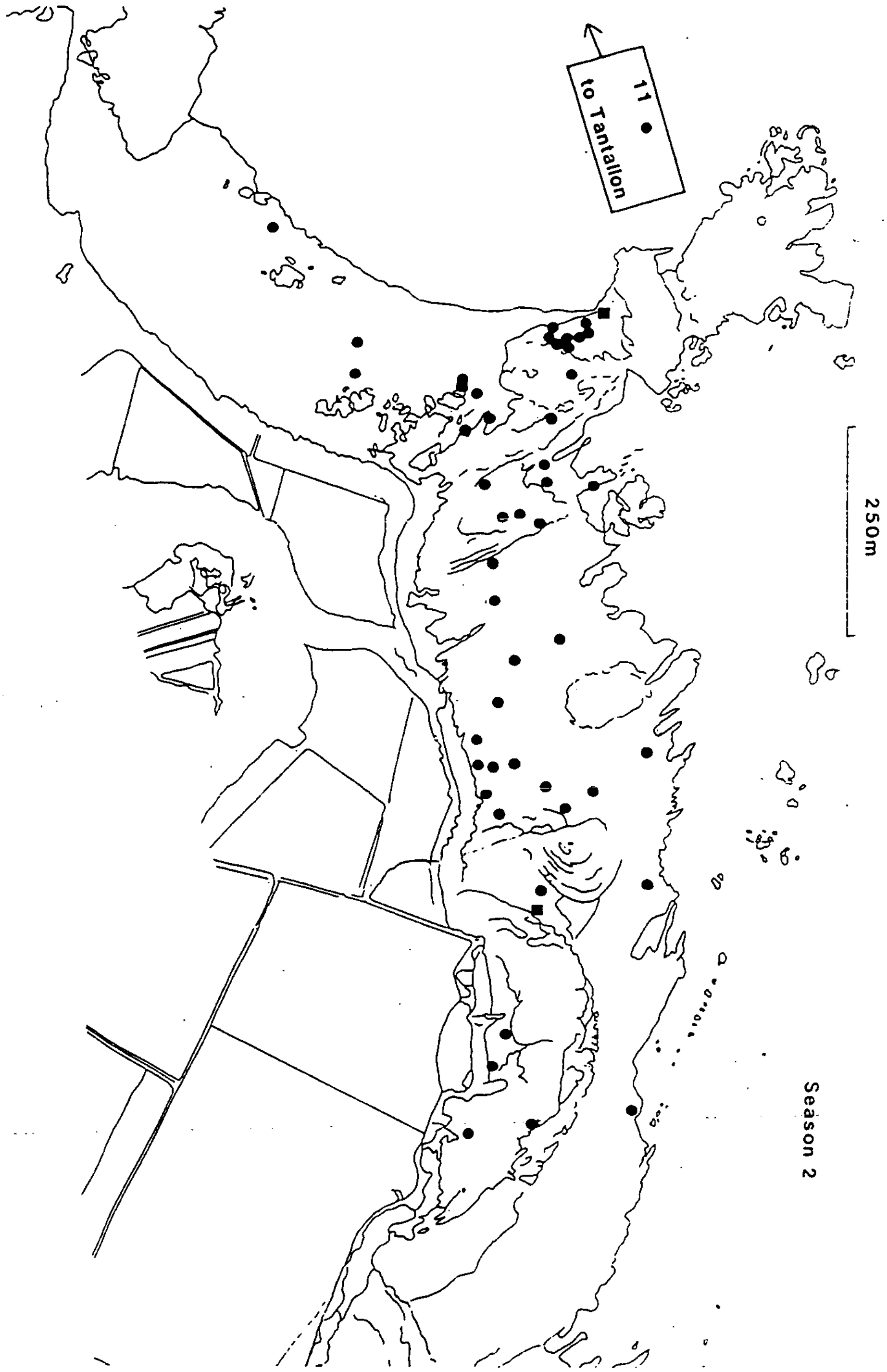

B
250m
Season 1

fourth group of individuals fed at Tyninghame but for the moment these birds will be ignored.) I have called these groups of birds Car Rocks birds, Scoughall birds and Coastguard birds respectively. The strong clustering indicated that turnstone tended to associate with the same individuals by feeding in the same area, the degree of clustering of mean coordinates being a rough measure of the stability of individuals' associations (Murray, 1981). Compared with later seasons (see later) the strong clustering also indicated that in season 1 turnstone utilised comparatively small home ranges. For example, in season 1 Car Rocks birds were seen only occasionally outside a 2 hectare barnacle covered area near the Great Car. Towards the end of season 1 some Car Rocks birds were seen at Scoughall as well as in the Car Rocks area, as evidenced by the position of some birds' mean coordinate between Car Rocks and Scoughall.

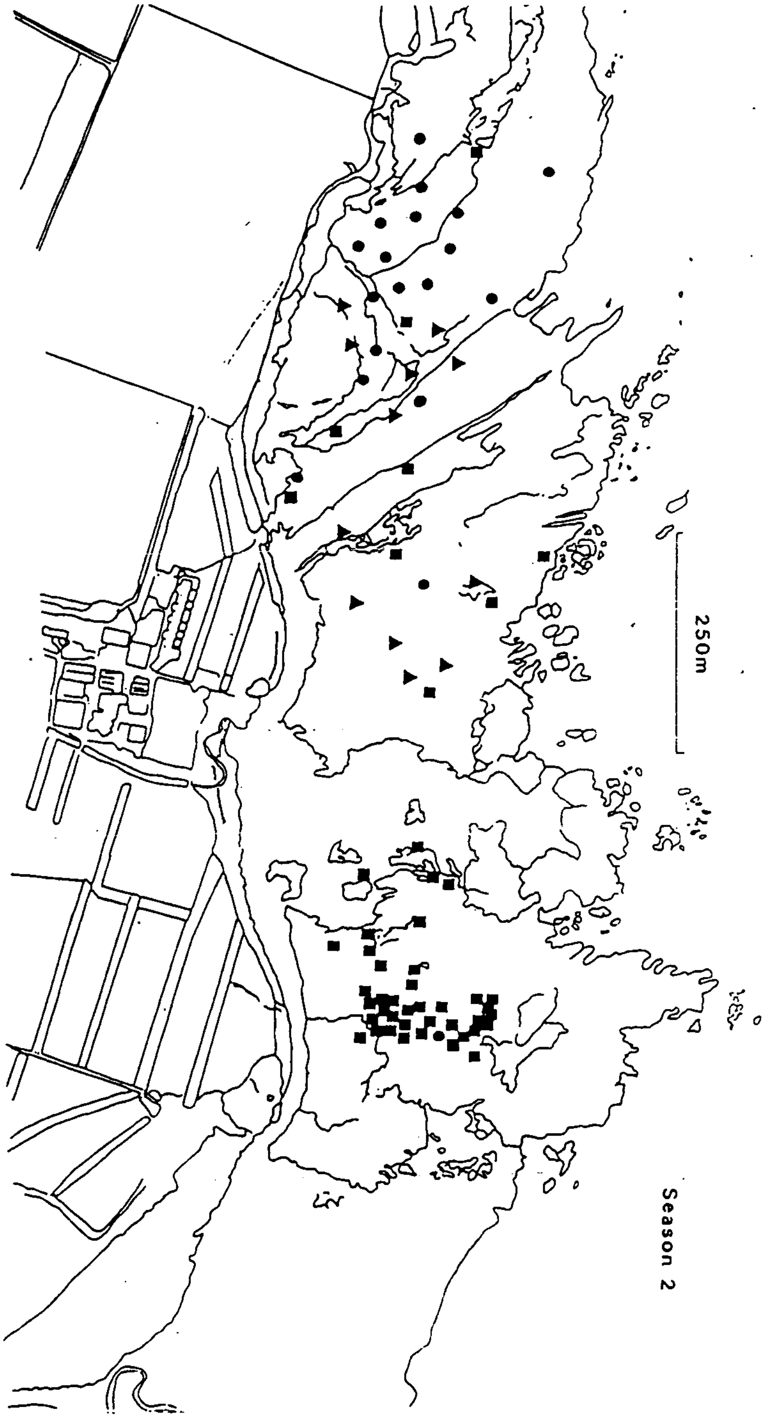
In season 2 many individuals' home range expanded as a result of movements away from their home area in season 1: this is evidenced by the greater spread of mean coordinates (Fig. 3.4). Car Rocks birds showed the greatest shifts in mean coordinates and several patterns of movements appeared to occur. Most Car Rocks birds were still seen at least occasionally in the Great Car barnacles area, indeed, some were seen only in this area. However, others were seen also at Tantallon, another group were seen frequently in the Car Rocks area and a few were observed feeding in both areas. Many Car Rocks birds were seen occasionally at Scoughall and/or the Field Space, particularly towards the end of the season. One further group seemed to feed mainly in the Field Space-North Scoughall area, only occasionally being seen in the Car Rocks area. These birds, as will

Fig. 3.4 a,b. Intertidal activity centres (mean sample coordinates) of individuals in season 2 (November to January). Circles are Car Rocks birds (and Field Space birds-see text), triangles are Scoughall birds and squares are Coastguard birds.

A



B

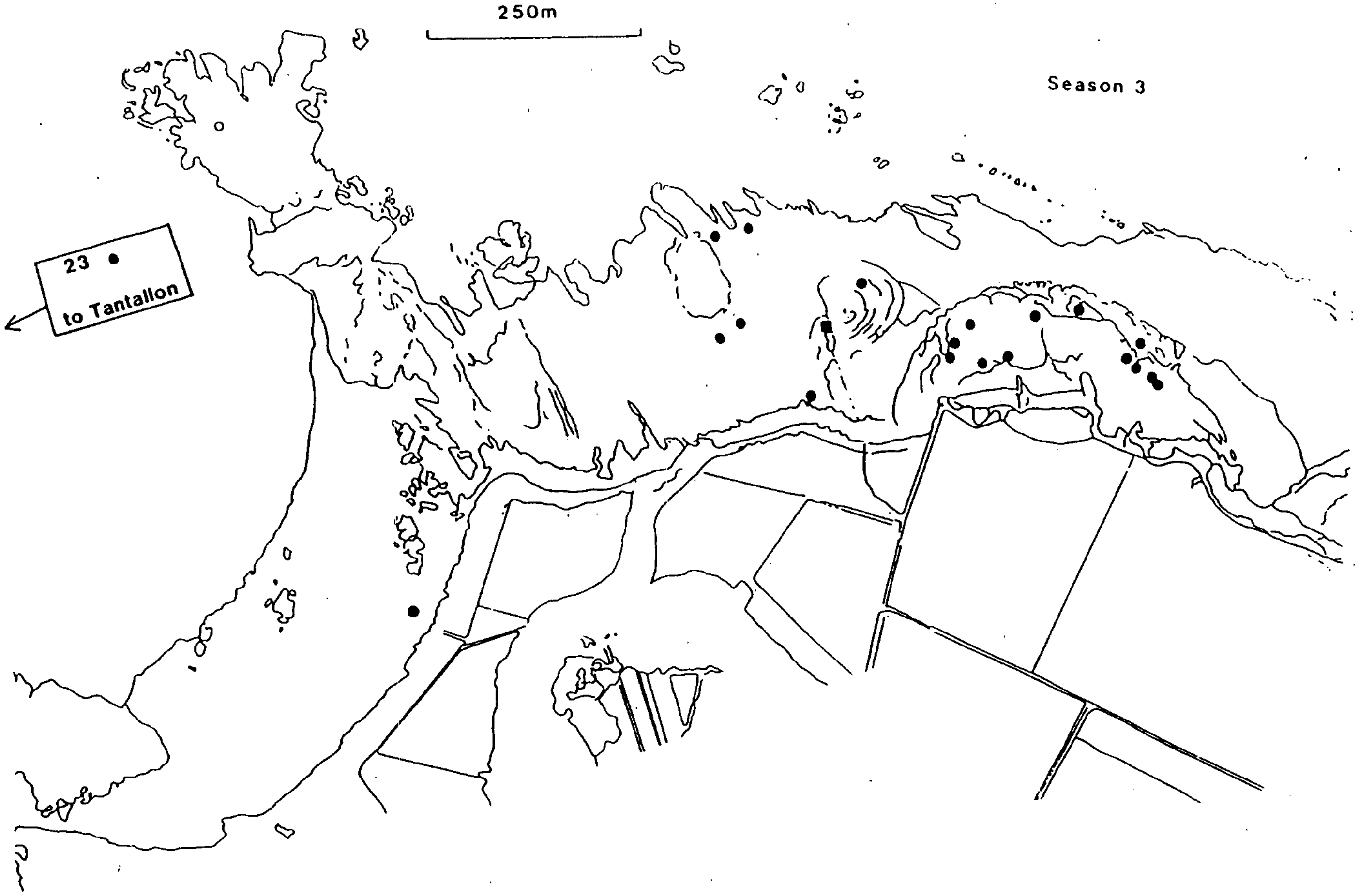


become apparent later, seemed to be a relatively discrete group of birds which I named the Field Space birds. The Field Space birds were usually seen in company with Scoughall birds, particularly Scoughall birds who seemed to favour the northerly section of area in season 1. The expansion of the feeding range of these Scoughall birds can be seen as a shift in their mean coordinates towards Field Space (Fig. 3.4). The Coastguard birds' mean coordinates shifted slightly to the north in season 2, probably as a result of them no longer feeding at sites in the southern part of their area. These sites were primarily Enteromorpha covered rocks which were no longer suitable when the green algae died off in season 2.

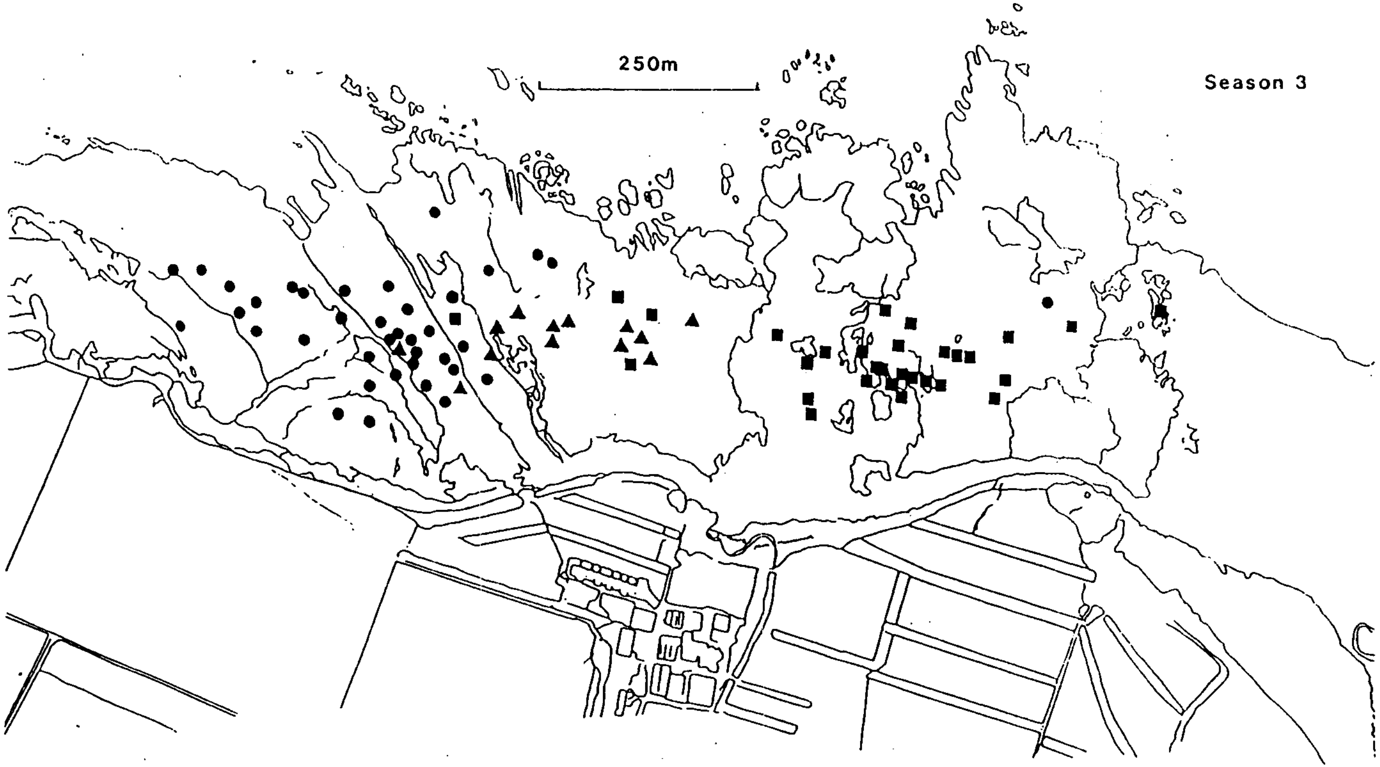
In season 3 the dependence of the Car Rocks birds on the Great Car barnacles area was noticeably weaker, in fact most Car Rocks birds were never seen feeding there (Fig. 3.5). The group of birds which in season 2 fed in both Tantallon and Great Car areas, fed mainly in the Tantallon area in season 3; a few birds fed in both Tantallon and Car Rocks areas and occasionally small numbers of birds fed in the Great Car area. The group of birds which in season 2 fed in both Car Rocks and Great Car areas very rarely fed in Great Car area in season 3; in season 3 they fed in both Car Rocks and Scoughall-Field Space areas. This shift away from Great Car to Scoughall-Field Space is reflected by the southerly shift in mean coordinates of these Car Rocks birds (Fig. 3.5). In season 3 the movements of Scoughall and Field Space birds were very similar to those in season 2, although the Field Space birds were seen even less frequently in the Car Rocks area. The Coastguard birds were seen feeding more often at Scoughall in season 3 compared with the previous two seasons; this is illustrated by the shift of several

Fig. 3.5 a,b. Intertidal activity centres (mean sample coordinates) of individuals in season 3 (February to April). Circles are Car Rocks birds (and Field Space birds-see text), triangles are Scoughall birds and squares are Coastguard birds.

A



B



Coastguard birds' mean coordinates towards Scoughall (Fig. 3.5). In general, season 3 saw many birds feeding at Scoughall/Field Space, away from their hame area.

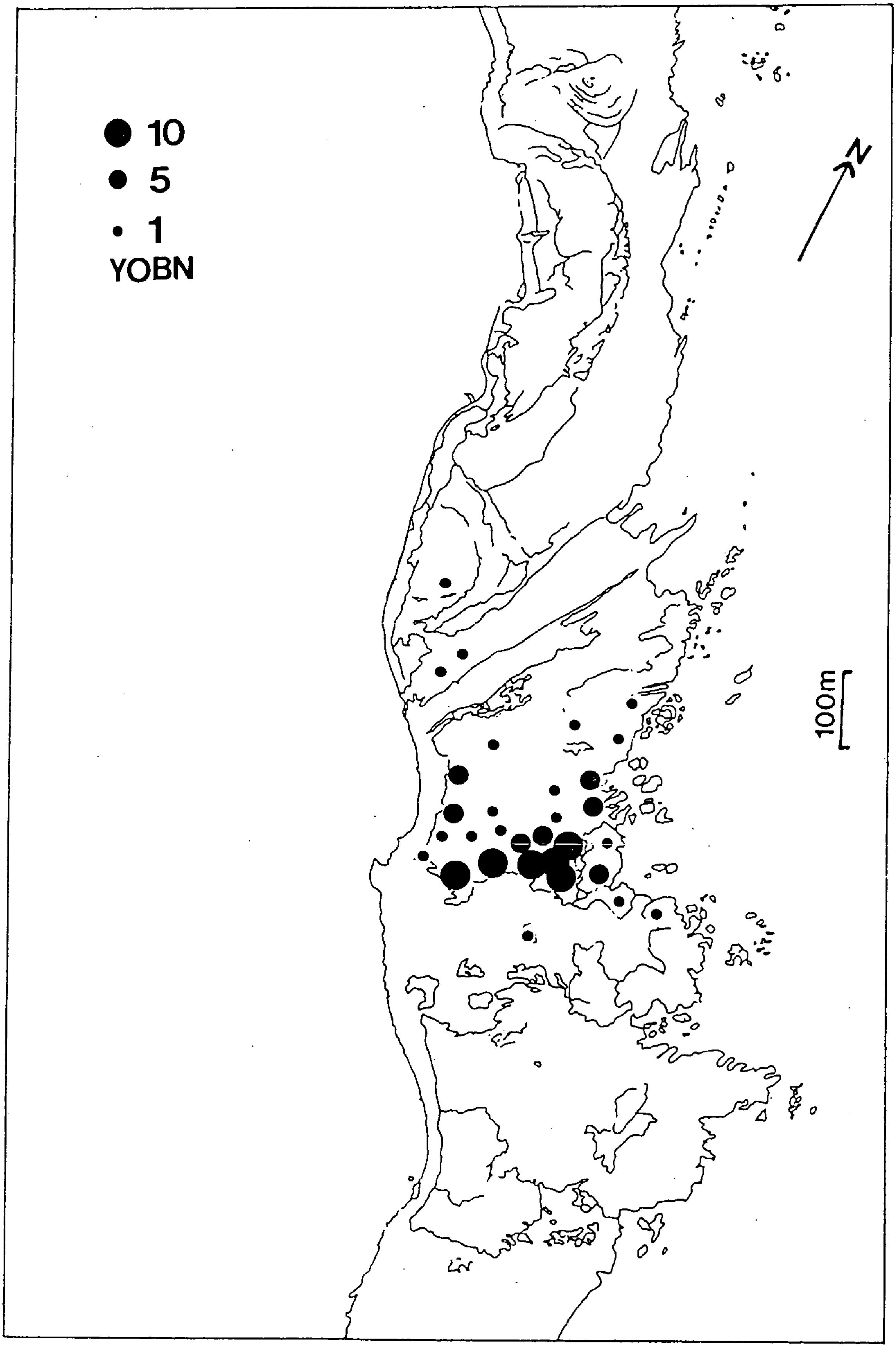
The data on seasonal timing of shifts in the intertidal feeding locations of individual turnstone in the 1982-83 winter were remarkably similar to the data obtained in the 1981-82 winter. Individuals classified as Scoughall birds in 1981-82 were so classified in 1982-83. Similarly, Coastguard birds in 1981-82 were usually Coastguard birds in 1982-83, although several Tyninghame birds appeared to feed at Coastguard, often for two or three months at a time. Since Tyninghame coordinates could not be entered into the analysis, birds which fed mainly at Tyninghame but occasionally at Coastguard would have an erroneus mean coordiante in the Coastguard area. Using sightings of birds at Tyninghame, the problem of distinguishing between Coastguard and Tyninghame birds could be resolved simply. In 1981-82 the movements of Car Rocks birds was also very similar to those noted in 1982-83 i.e. the birds occupied a comparatively small home area around the Great Car barnacles area in early winter, but ranged over an increasing area, away from the Great Car, in the rest of the winter. The movements of the Field Space birds were also similar in 1981-82 and 1982-83.

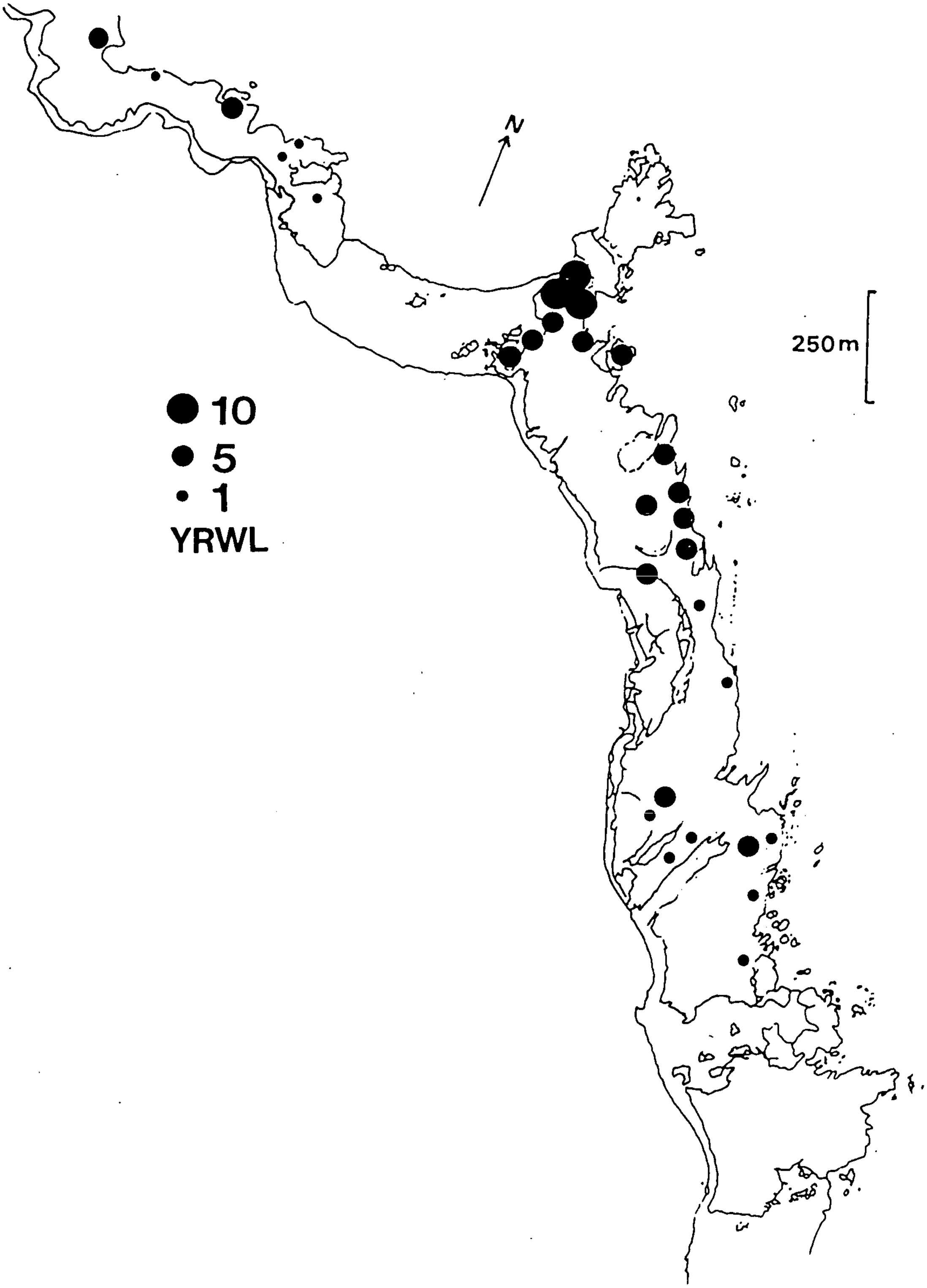
1983-84 winter. The movements of some turnstone in the 1983-84 winter were rather different from those in the previous two winters. In early winter several Car Rocks birds either could not be found on the study site or were seen only occasionally in the Car Rocks area. Regular reports of colour-ringed birds seen on the Isle of May during this period showed that at least some of these 'missing' Car Rocks birds were on the Isle of May. Other Car Rocks birds were seen in the Great Car and Car Rocks areas. In mid-winter the ´missing´ Car Rocks birds apparently returned to the study site, as regular sightings of these birds were made in the Car Rocks and Tantallon area. Interestingly, this group of birds seemed to return to the study site together and were frequently seen feeding in the same flock. The movements of other Car Rocks birds in mid-winter 1983-84 were similar to those made in mid-winter 1982-83, as were the movements of all Car Rocks birds in late winter for both years.

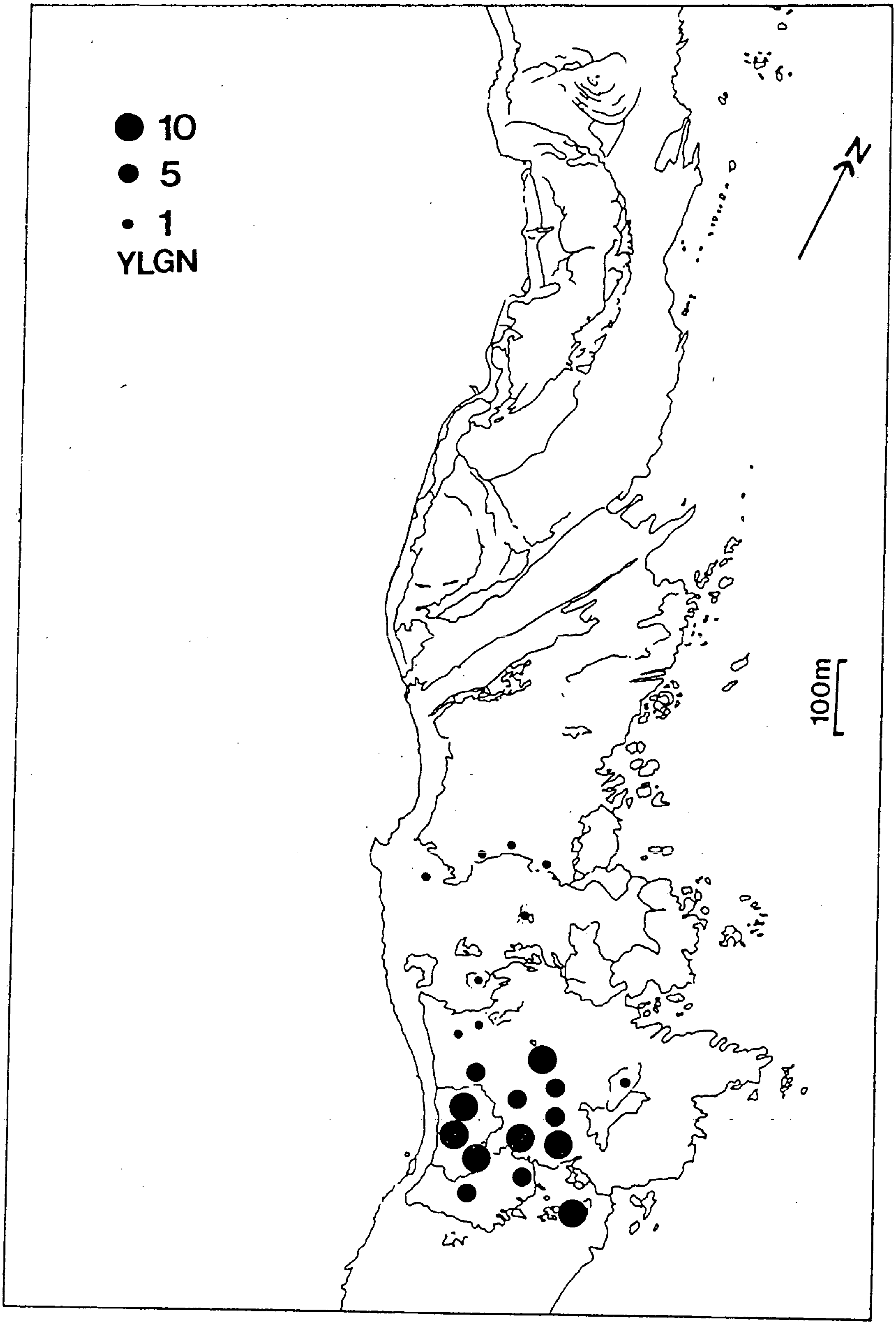
For the whole 1983-84 winter Scoughall and Field Space birds fed in the same areas as they did in season 2 and 3 of 1982-83 winter. Similarly, the intertidal feeding ranges of some Coastguard birds were very similar in 1982-83 and 1983-84, following the same seasonal changes in both winters. In contrast, a few Coastguard birds were seen only rarely on their home area in 1983-84 winter and when they did they were usually seen together; records of feeding birds in the south of the study site indicated they had moved to Tyninghame.

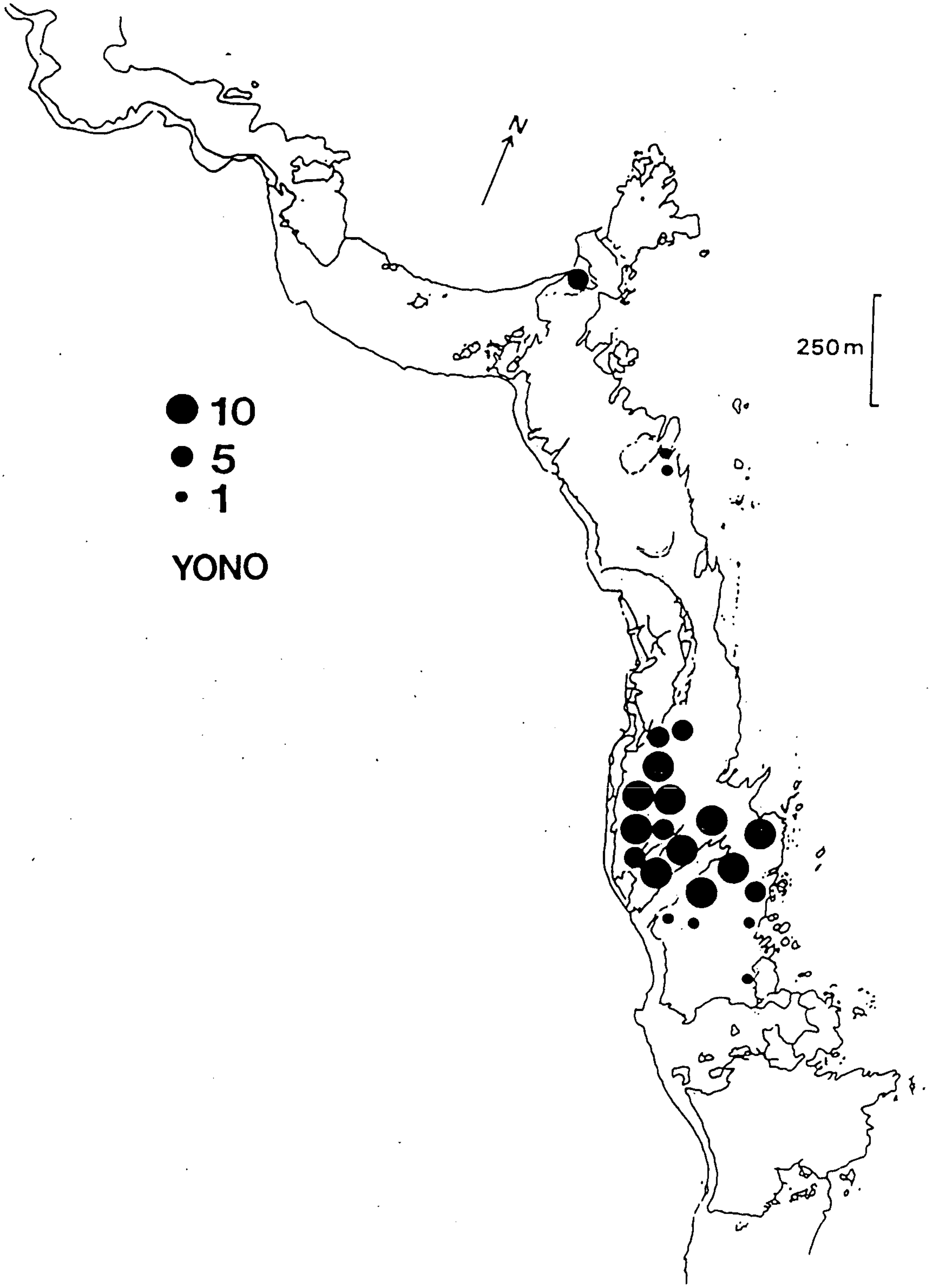
Observations of feeding birds´ locations in the 1984-85 winter were scanty in comparison with the previous winters. They did confirm, however, that birds probably occupied the same intertidal home areas in the 1984-85 winter as they did in the previous three winters. In particular, the surviving Coastguard birds which had moved to Tyninghame in 1983-84 appeared to return to the Coastguard area in 1984-85.

The individual turnstone comprising each home intertidal range ´flock´ are listed in Appendix 4. Some examples of individuals´ sample feeding coordinates are shown in Fig. 3.6.


● 10
● 5
• 1
YOBN
N
100m


N
250m
● 10
● 5
• 1
YRWL

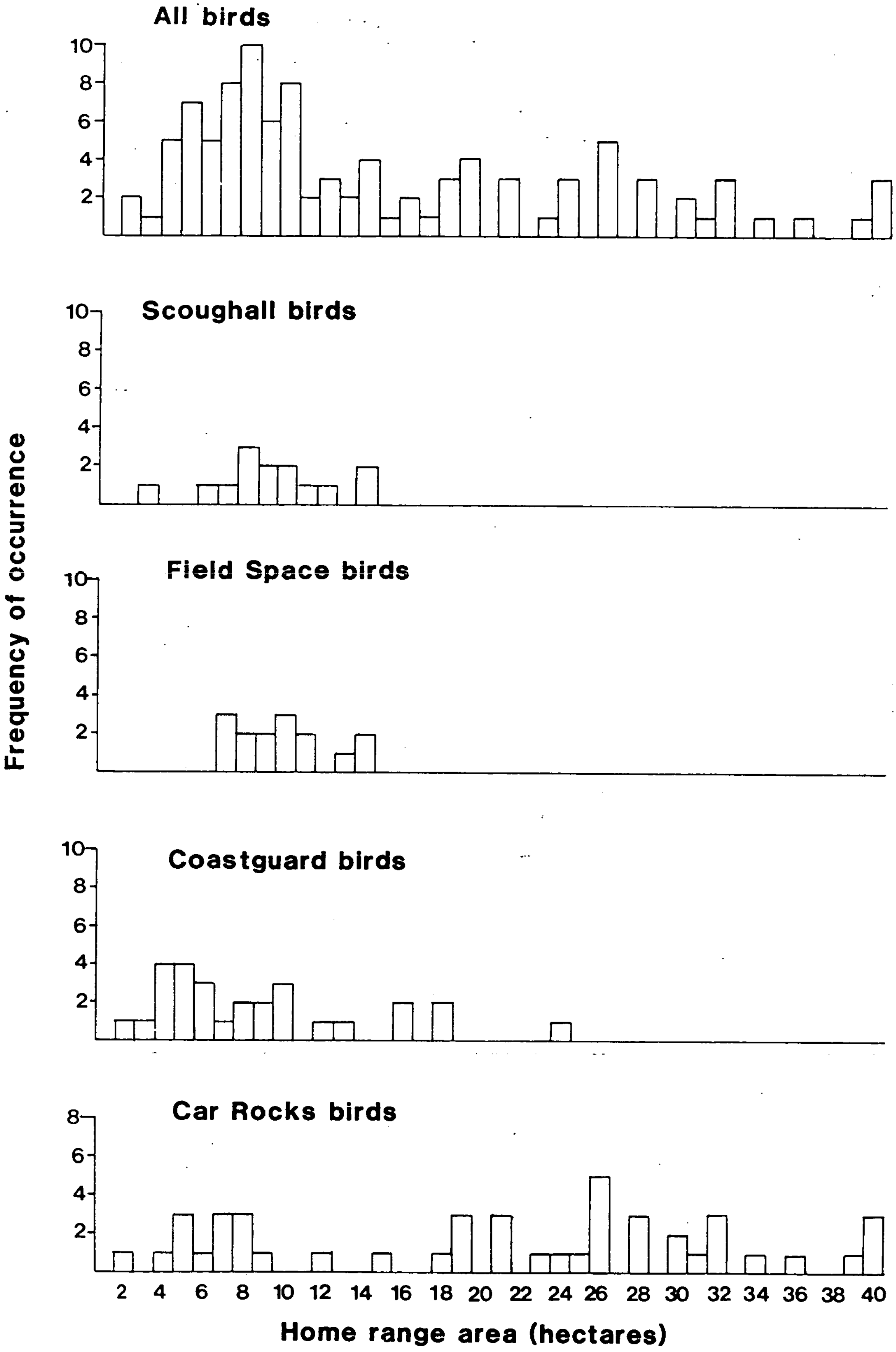

10
5
1
YLGN
N
100m


N
250 m
10
5
1
YONO

3.3.3 HOME RANGE ESTIMATES

Sufficient sample coordinates were recorded to estimate 1982-83 winter home range areas for 101 birds. Mean home range size (MAP (0.9) calculated from Anderson's UD) was 15.1±1.1 SE hectares (N=101). Large differences between individuals' home range size were apparent (Fig. 3.7). Mean (±SE) home range areas (hectares) for birds of each intertidal 'flock' were as follows: Car Rocks, 21.9±2.0; Field Space, 9.9±0.6; Scoughall, 9.2±0.8; Coastguard, 9.2±1.0. Data from other winters were not analysed, but for most birds within-winter home range estimates probably varied little in different winters, due to the year-to-year consistency of many birds' movements. However, since some Car Rocks birds moved to the Isle of May in early winter 1983-84 their home range area over the whole study period will have been larger than estimated from locations within the study site in one winter. Interestingly, of the 29 individuals which were seen outside the study site 11 were Car Rocks birds; only one bird was from another intertidal area. The dates of records of Car Rocks birds seen outside the study area indicated that these birds did not restrict their movements to sites outside the study area to any one time of the winter, although it is difficult to ascertain any pattern in the timing of such movements due to the seasonality of the presence of observers at other sites. Car Rocks birds were seen at sites other than the Isle of May: one was seen at Musselburgh, another was caught at Boarhills, between Fife Ness and St. Andrews (see Fig. 3.2).

The movement of some Coastguard birds to Tyninghame in 1983-84 indicates that these birds' cumulative home range estiamtes for the


All birds
Scoughall birds
Field Space birds
Coastguard birds
Car Rocks birds
Frequency of occurrence
10
8
6
4
2
2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
Home range area (hectares)

whole study period will have been larger than the 1982-83 winter estimates. In contrast, the Scoughall and Field Space birds only rarely moved outside their home areas so their cumulative home range estimates will have been very similar to the within-winter estimates.

Mean juvenile home range area was 11.7±2.2 SE hectares (N=5), mean adult home range area was 15.2±1.1 SE hectares (N=96). The large discrepancy in sample size precluded any statistical testing of age-related differences.

Within the Scoughall-Field Space flock there was no correlation between individuals' agonistic rank (see Chapter 4) and its home range area ($r_s=0.24$, $p>0.05$, N=31). Similarly, within the Coastguard flock there was no correlation between rank and home range area ($r_s=0.11$, $p>0.05$, N=25).

3.3.4 FEEDING LOCATIONS ON THE STRANDLINE

Turnstone were more liberal in their choice of feeding sites on the strandline around high tide than in their use of the intertidal area at lower tidal levels. However, they did still tend to spend more time feeding opposite their home intertidal area (Fig. 3.8, compare with Fig. 3.6).

3.3.5 INVERTEBRATE SAMPLING

The invertebrate sampling programme was undertaken to examine the possibilty that instability in the food supplies available to the Car Rocks birds was responsible for their marked itinerancy compared with other birds. When not hammer-probing for barnacles, Car Rocks

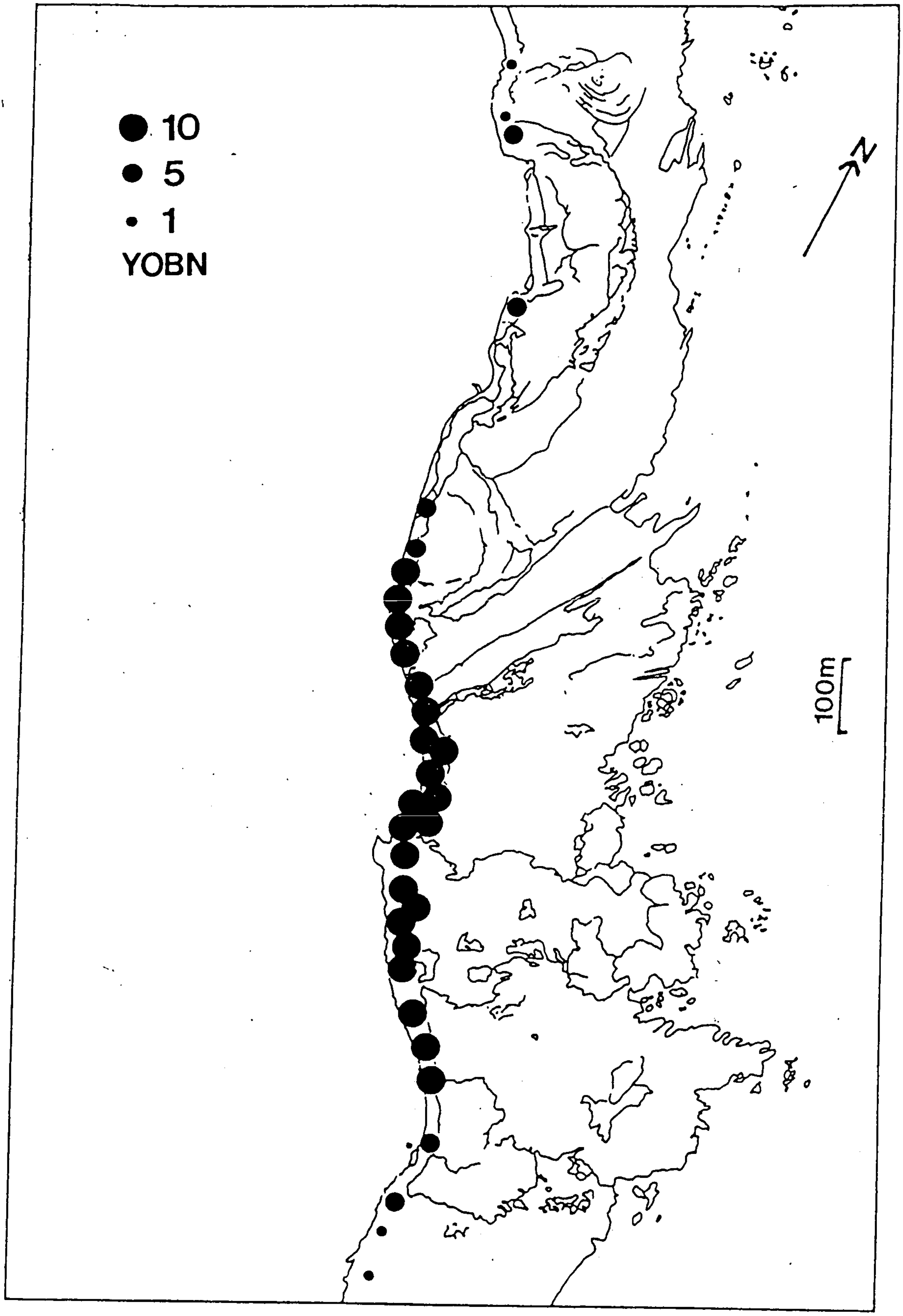
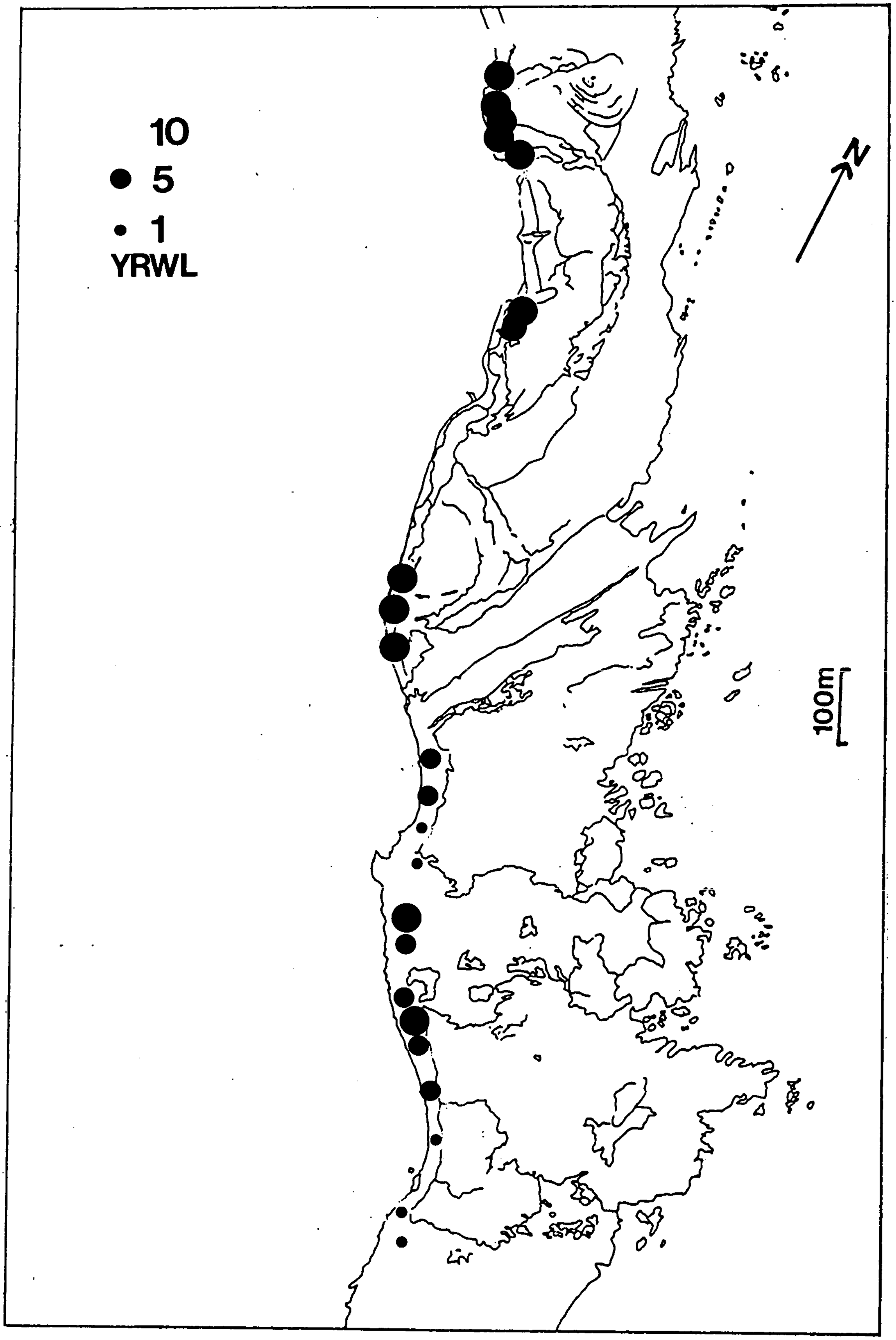
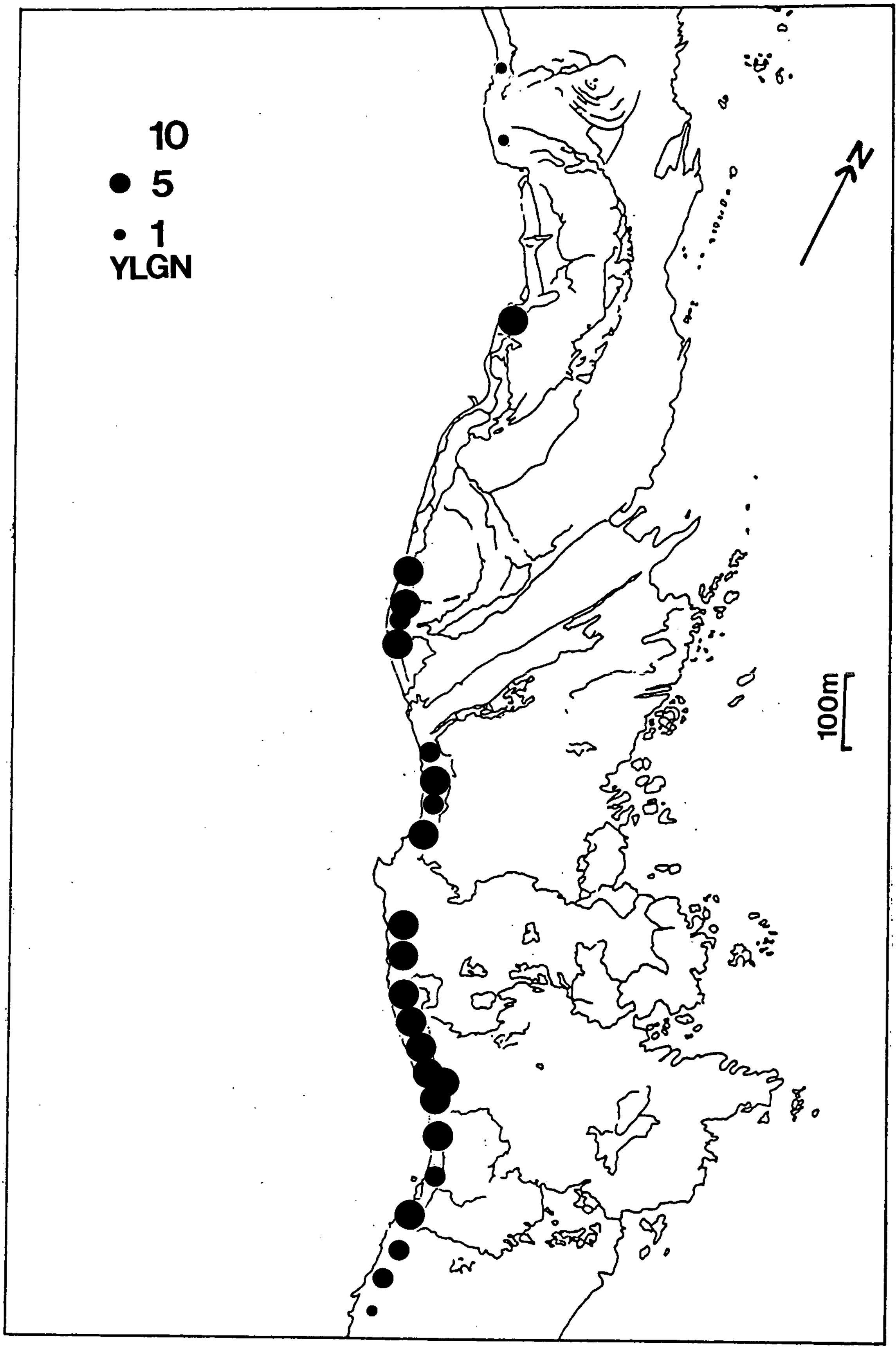
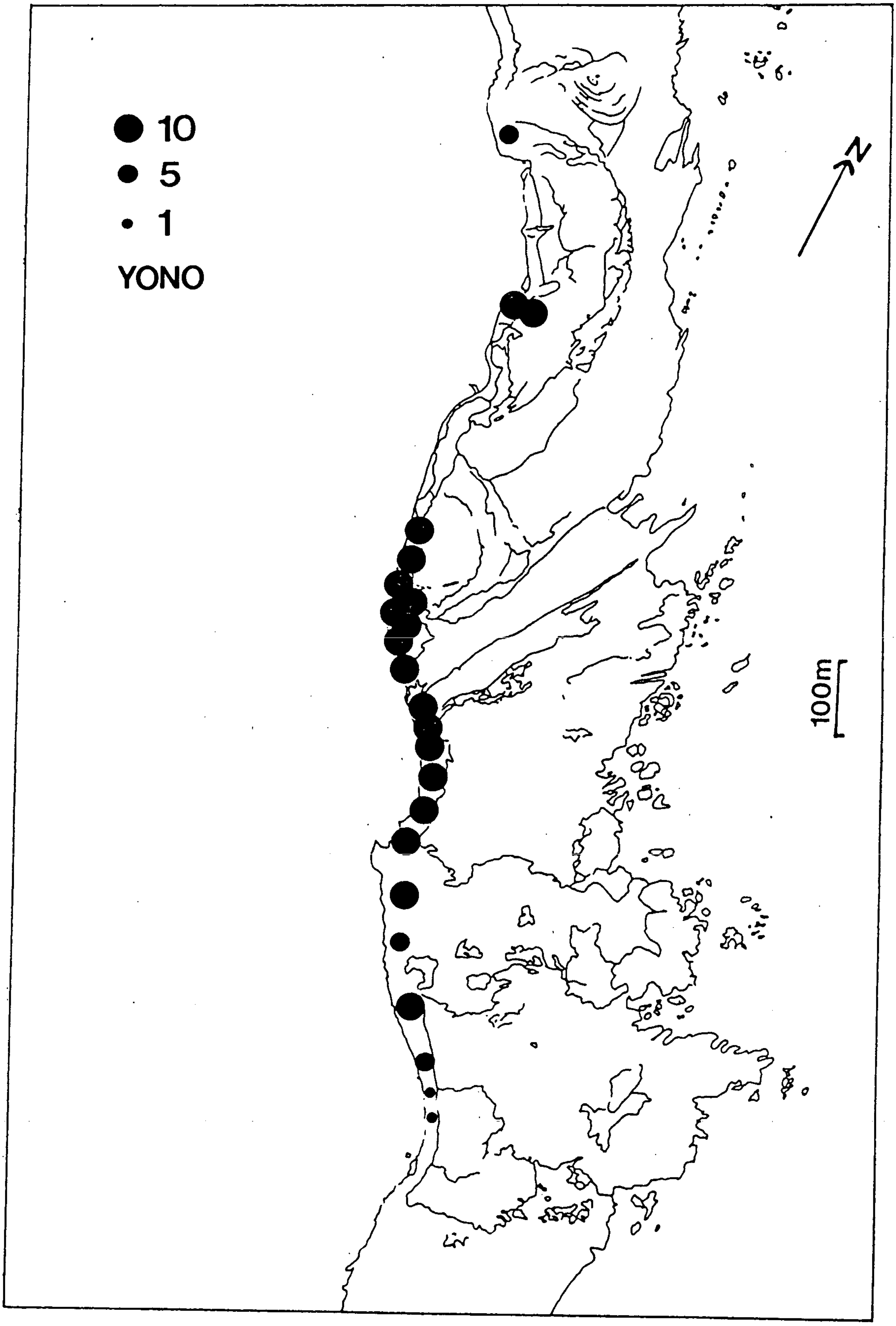

10
5
1
YOBN
N
100m

Fig. 3.8 Some examples of different individual´s strandline coordinates in the 1982-83 winter: (a) YOBN; (b) YRWL; (c) YLGN; (d) YONO


10
● 5
• 1
YRWL
N
100m


10
5
1
YLGN
N
100m


● 10
● 5
• 1
YONO
N
100m

birds fed mainly in brown seaweed on rocks (weed rock-WR, sparse weed rock-SWR; see Chapter 6) therefore I have presented data only for this microhabitat.

The seasonal stability of the total numbers of invertebrate prey collected in the sample periods (as assessed by X^2 heterogeneity tests) was greatest at Scoughall but lowest at Car Rocks: this was evidenced by the differences in the X^2 values, which reflected the magnitude of seasonal differences in prey numbers, between the two areas (Table 3.2). The X^2 values suggested that the areas could be ranked in an order of increasing seasonal instability of prey numbers: Scoughall, Field Space, Coastguard, Car Rocks.

In early winter 1982-83 most Car Rocks birds hammer-probed for barnacles at the Great Car. There was a dramatic reduction in the numbers of living barnacles at the Great Car during the course of the 1982-83 winter (Fig. 3.9) and my impression was that it was mainly the large barnacles which died. Only Car Rocks birds fed on barnacles during early winter so it was not feasible to compare the seasonal stability of barnacle populations of the different areas. However, the decline in the Great Car barnacle population is consistent with the notion that the food supplies of Car Rocks birds was seasonally unstable.

3.3.6 FLOCK STABILITY AND INDIVIDUAL ASSOCIATIONS

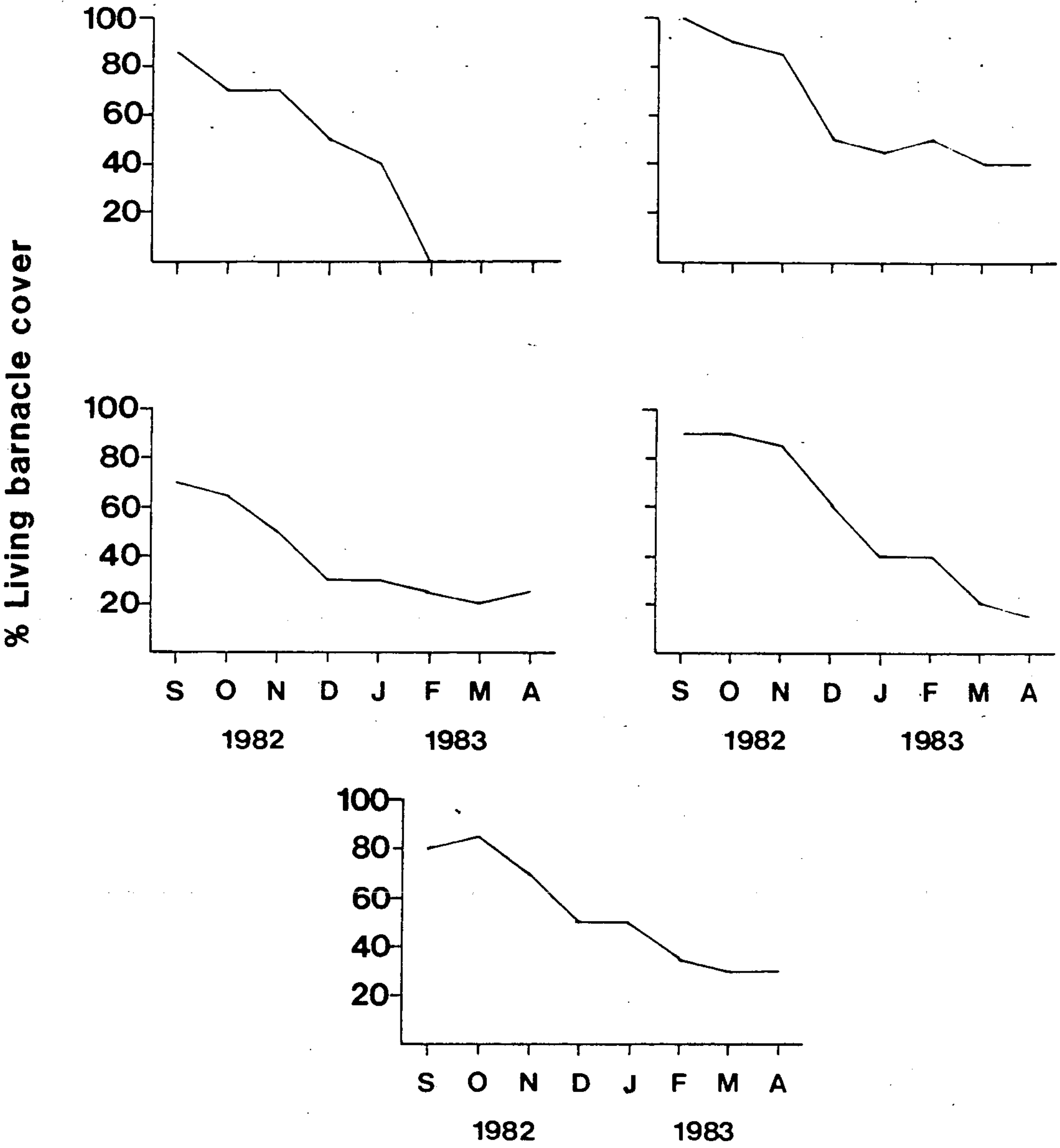
From the results presented in section 3.3.2 it can be seen that relatively discrete groups of turnstone inhabited more or less discrete intertidal areas, since there was a tendency for mean coordinates (home range centres) to be clustered, particularly in

TABLE 3.2.

The total numbers of invertebrate prey collected in 20 0.066m^2 samples from WR/SWR microhabitats in four intertidal areas at three times in the 1982-83 winter. *Idotea*, *Hyale* and *Littorina obtusata* size class 1 are the main prey of routing birds, *L.obtusata* size class 5 and *L.littorea* size classes 3+4 are the main prey of probing birds (see Chapter 6 for details). The magnitude of differences between the numbers collected at different times of the year was assessed for each area by a chi-squared heterogeneity test.

	Idotea	*Hyale*	size classes 3-4 *L.littorea*	size class 5 *L.obtusata*	size class 1 *L.obtusata*
(a) Car Rocks					
SEPT.	75	84	21	7	277
DEC.	63	68	16	6	159
MAR.	49	45	9	4	253
			X^2=27.46 $p<0.001$		
(b) Field Space					
SEPT.	63	712	75	135	428
DEC.	50	526	53	97	322
MAR.	77	604	63	120	450
			X^2=10.52 $p>0.2$		
(c) Scoughall					
SEPT.	69	146	98	59	76
DEC.	59	98	76	44	58
MAR.	67	136	82	53	91
			X^2=4.87 $p>0.7$		
(d) Coastguard					
SEPT.	42	249	23	28	122
DEC.	27	105	12	31	79
MAR.	38	230	16	34	96
			X^2=19.29 $p<0.02$		

Fig. 3.9 Seasonal changes in the % of living barnacles at five semi-permanent stations near the Great Car.


% Living barnacle cover
100
80
60
40
20
S O N D J F M A
1982
1983

early winter. To gain a more quantitative measure of the strength of individual associations the Ekman coherence indices were plotted as frequency histograms for both the observed and expected random data sets (Fig. 3.10). A comparison of the two frequency distributions shows that a greater number of higher indices (indicating stronger individual associations) was present in the observed data set. The differences in the two frequency distributions were highly significant (Kolmogorov-Smirnov two sample test, $p<0.001$), demonstrating that individuals were seen together significantly more often than expected if flock composition was random. Excluding 0% indices (to allow comparison with Myers´ (1983) results) the mean observed coherence index was 23%, and the mean expected coherence index was 12.5%.

Within groups of birds which shared a common home intertidal area there also appeared to be a tendency for birds to feed nearest to birds which employed the same or a similar range of feeding techniques (Fig. 3.11). Juveniles were the nearest neighbours of other juveniles more frequently than adults, suggesting that some form of age-related sub-structuring of intertidal flocks existed; possibly because juveniles avoided adults (Table 3.3) (cf Whitfield, 1985: Appendix 1 for strandline flocks). It was difficult to assess whether juveniles tended to occupy any particular position within intertidal flocks due to the topography of the intertidal zone. However, the Field Space area was comparatively flat and sometimes it was possible to see clearly the majority of a flock. Juveniles were usually positioned at the front of these moving intertidal flocks, unlike strandline flocks when juveniles were found most frequently on both ends of a flock (Whitfield, 1985: Appendix 1).

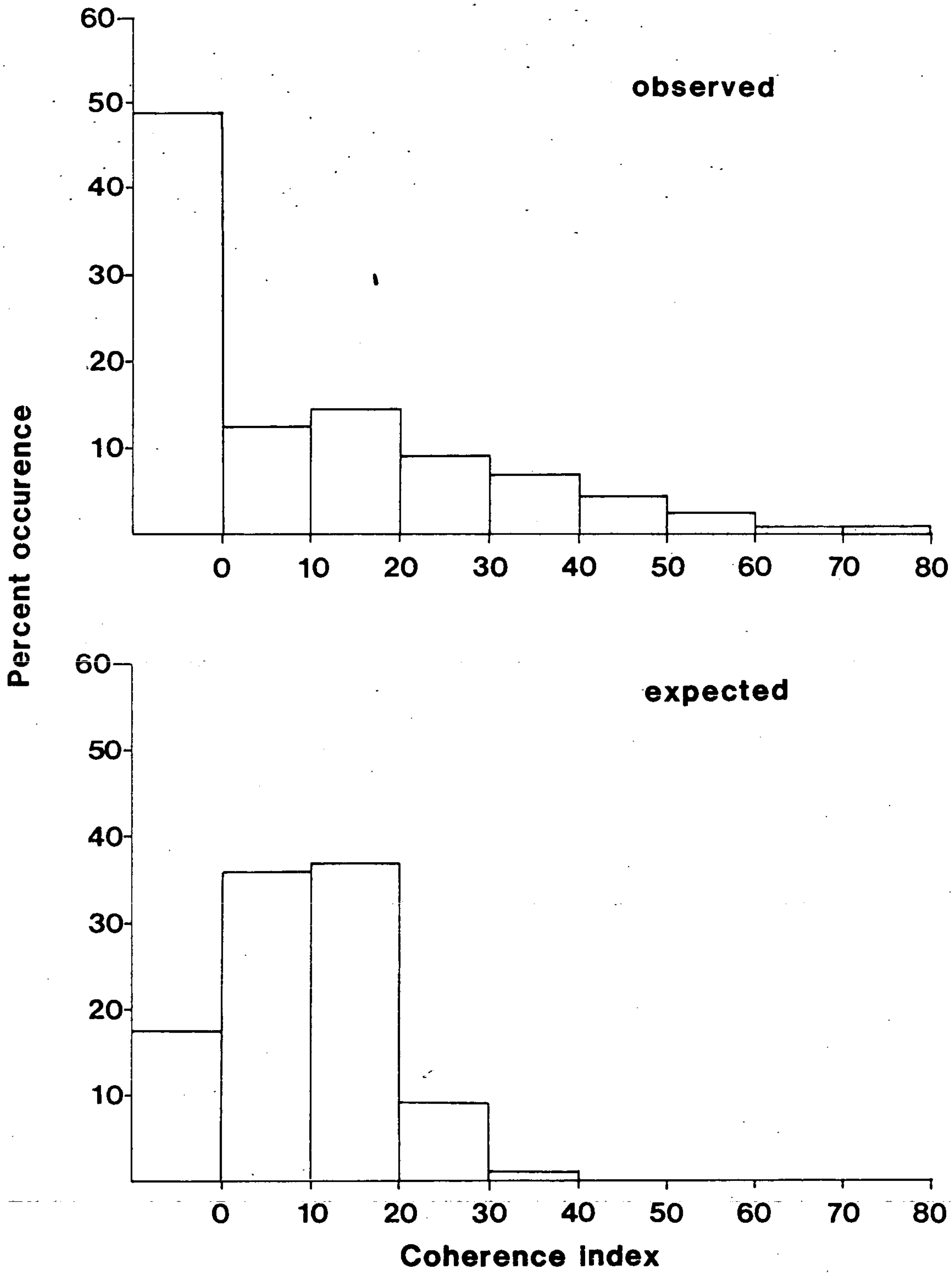

observed
expected
Percent occurence
Coherence index
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80

Fig. 3.11 Matrix showing the number of occasions birds from the Scoughall-Field Space were nearest neighbours. Individuals were ranked in an order with S.Scoughall birds placed above, N.Scoughall-FIeld Space birds below. Within ´sub-flocks´ birds were grouped according to similarity of feeding technique use. Larger numbers of observations clustered around the diagonal suggests that individuals tended to associate with birds which fed in a similar way.

NEIGHBOUR

FOCAL BIRD	YOBN	YLBG	YOWL	YWNR	YWWL	YLLB	YWWR	YWWB	YNLG	YNNG	YWOB	BWWL	YBWL	YGRW	BGYG	YLGR	YWLR	YWGN	YLNW	YNNW	YWWO	YOWO	BWYO	BGYW	YWNL	YWGW	YONO	YLNO	YROL
YOBN		8	9	6	7	9	4		8				1		1	2				1		2			1			1	1
YLBG	10		2	1	2	3		2	6				1		1		1	2	1			1					1		
YOWL	4	4		1		3	2				2				1														
YWNR	1	2	1		7	7	6	3	3			1		1				1		1									
YWWL	3		3	7		9	4		1	1	4			1		1	1				1	1							
YLLB	8	3	1	4	6		5	3	12		3						1	1	1	1									
YWWR		1	1	4	3	4		5	2		1		1	2	1			1								1			
YWWB	2	3	1	3	3	7	4		2								3	2								1			
YNLG	3	3		6	2	11	2			8	10	6	1		1	6		5	2	2	1	3	1			1	1	3	
YNNG					1				4		11	8	12	2	2	2		3		2	1	2		2			1	2	2
YWOB			1		1	2	2	4	5	11		11	3	3		2	1	3	3	2	1		1	1		1	1		1
BWWL		1		1					5	8	7		14	1	1	2				2	3	2	3		5	1	5	4	1
YBWL		1				2			1	10	6	13		1	4	1	1		1	1	2	1	3		1		3	1	
YGRW	1				1		1		4	4	2	1	1		5	1	1	1	1					2	1	1	2	1	
BGYG				1		1	1			1			3	3						1	1		3	4			1	2	1
YLGR	1	1				1	1	1	7	2	1		2	1	1		3	8	3		1	2	1	1		2	1		
YWLR	1	2		1			1	2	2		3		1	2				6	1	2	4	2	1	2		3	1	3	3
YWGN		1		1	1		1	1	5	2	2		1	1		1	7		6	2	2	5	1	2					
YLNW			1			1	2		1	1	6		1	1	1	3	1	7		1	6	1	2		1			1	2
YNNW												3	1				1	1			3	2	2	2	3		4	3	1
YWWO					1				1	1	1	1			2	1	3	1	4	1		14	11	14	2	1	4	5	
YOWO									1	1	2	2	1	1		2	2	2	2	4	13		4	1	1		5	3	1
BWYO					1				1			1	2		2	1	3		2	3	12	5		11	5		7	5	
BGYW	1	1				1					3	2		2	4	1	4	2	1	2	14	6	8		5	2	2	8	
YWNL										1	1	1	4	1	1		1		2	5	2	2	6	5		2	13	2	2
YWGW		1	1						1		2			1		4	1			1	1	1	1	3	4		5	5	
YONO		1			2					1	4	4	1		3		1		1	3	5	6	5	10	14	2		27	1
YLNO									3	3		4	4		2		1	1		4	7	5	6	3	8	5	22		4
YROL										1	1	1	1	2			1		1				3		2		2	6	

TABLE 3.3.

The number of occasions when an adult or a juvenile was the nearest neighbour of a focal colour-ringed adult or colour-ringed juvenile in intertidal flocks. $X^2=932.43$, df=1, $p<0.001$.

		Nearest neighbour	
		JUV	AD
Focal bird	JUV	108	246
	AD	600	4309

3.4 DISCUSSION

There was considerable individual variation in intertidal site fidelity; some individuals were never seen outside a small hectare area whilst others were seen feeding in locations outside the study site. Relatively discrete groups of birds could be recognised, based on common occupancy of intertidal areas, and the mean home range estimates of some groups were enormously different. For example, Scoughall birds had the smallest home ranges (mean 9.2 hectares) while Car Rocks birds had the largest home ranges (mean 21.9 hactares). If the temporal stability of food supplies is the ecological basis of site fidelity in wintering waders, as proposed by Evans (1981) and others, then the food at Scoughall should be more stable over the winter than the food at Car Rocks. This appeared to be the case, as in early winter 1982-83 Car Rocks birds fed in a very small area containing a high density of barnacles but by mid-winter the density of barnacles was substantially lower, probably forcing Car Rocks birds to move further afield and to feed on amphipods and littorinids. The prey that many of the Car Rocks birds fed on in mid-winter was also substantially reduced by late winter, coinciding with Car Rocks birds incorporating feeding sites over a larger area. In contrast, throughout the 1982-83 winter Scoughall birds rarely moved outside an area (Scoughall/Field Space) which contained prey supplies that showed lower seasonal variations. On a year-to-year basis the food of Car Rocks birds also appeared to be unstable. In some years (1981-82, 1982-83) there were extremely high densities of large barnacles at the Great Car in early winter, which supported a high density of resident and migrant turnstone, but in others

(1983-84, and particularly 1984-85) there were very low densities of barnacles and the density of residents and migrants was also lower. A positive relationship between wader density and prey density has been noted on several occasions (see Puttick, 1984).

The differences between the areas in the stability and density of prey supplies may have been due to area differences in topography and exposure to wave action. The feeding sites at Car Rocks were open to the sea and breaking waves whereas feeding sites in other areas tended to be more protected by rocks seaward of the main feeding sites. This was particularly noticeable at Field Space: at low tide this area was basically a relatively flat ´plain´ separated from the sea by several craggy ridges. The differences in exposure to wave action were reflected by differences in seaweed coverage (cf Lewis, 1964). The rocks in the Car Rocks area characteristically had very low coverage of short-fronded Fucacae seaweeds, particularly in comparison with the rocks in the Scoughall/Field Space area which were frequently covered with very dense long-fronded Fucacea seaweeds. On all but the calmest days the swell was greater at Car Rocks than at Scoughall or Field Space (Table 3.4). Greater exposure to wave action probably lowers the number of suitable prey itmes which can settle as well as making it more likely that prey items are swept away during storms (cf Evans, 1981), resulting in lower stability of prey numbers.

Increasing itinerancy seems to be associated with greater mortality, whether estimated by searching for corpses or by ´disappearances´ of colour-ringed individuals (see Chapter 2) (Table 4.12). The differences in mortality as estimated by the numbers of corpses found were probably greater as corpses of itinerant

TABLE 3.4

Mean values of sea swell at Car Rocks and Field Space/Scoughall during the 1982-83 winter. Swell was scored as an integer on a 0-5 scale. Observations of the two areas were paired, swell being scored in one area within an hour of scoring the other. The differences between the two areas were therefore tested for significance using a Wilcoxon matched pairs test (T=8.5, N=25, P<0.01).

Car Rocks	Field Space/Scoughall	N
2.2	1.4	35

individuals were less likely to be discovered on the study site. The main mortality agent of turnstone on the study site was raptor predation, and at the Isle of May, a site which was probably used often by Car Rocks birds, turnstone were frequently kiled by raptors (S. Wanless, pers. comm.). Mortality differences may have been due to, for instance, residents exploiting food supplies more efficiently and/or avoiding predators more efficiently.

Although there was no relationship within intertidal ´flocks´ (i.e. groups of birds with the same home intertidal areas) between home range area (= degree of itinerancy) and status, there may have been an effect of status between flocks because, as I will argue later (Chapter 4), on average, Scoughall birds appeared to be of higher status than birds from other areas and these birds suffered the lowest mortality. Juveniles were subordinate to adults (Chapter 4) yet there was no difference in their itinerancy as measured by home range area within the study site, in contrast to sanderling in which juveniles are more itinerant than are adults (Myers, 1984). The lack of any age-related differences in turnstone itinerancy within the study site may be genuine, but it may be that age-related itinerancy differences are expressed over larger distances than those measured.

It was not possible to estimate directly individuals´ home range areas in each season but they appeared to be smaller in early winter, as evidenced by the clustering of individuals´ home range centres at this time. The results suggest that seasonal home range expansion was due to birds switching between a larger number of feeding sites. Such seasonal switches in feeding sites appeared to be partly related to seasonal changes in feeding site profitability (see also Connors et al, 1981; Townshend, 1981).

The spatiotemporal cohesiveness of turnstone flocks is greater than sanderling flocks: the mean Ekman's coherence index (no zeroes) observed for turnstone in the present study was 23% (mean random index 13%), whereas the mean index (no zeroes) observed for sanderling (Myers, 1983) was 10% (mean random index 8%). The difference between the two species was probably greater, as I believe Ekman's index underestimated the cohesiveness of turnstone flocks. The index assumes that all birds in a flock were recorded, but because of the topography of the rocky shore habitat I undoubtedly did not always see every bird in any particular flock. On several occasions I thought I had recorded every colour-ringed individual in a flock, only to find that as the tide rose, forcing the birds into the open more, I saw individuals which I had not recorded. This problem will not be so common in open sandy habitats, such as those inhabited by sanderling, where visibility is far better.

As pointed out by Myers (1983), amongst others, individuals within stable groups may derive benefits from associating with a relatively constant group of conspecifics. Several of these benefits, such as nepotism (Alexander, 1974) or reciprocal altruism (Trivers, 1971; Axelrod & Hamilton, 1981), depend on individual recognition, and turnstone appear to be capable of recognising individuals by plumage differences. Alarm calling and its associated benefits to flockmates through early warning of predator approach is frequently cited as a possible function of kin selection or reciprocal altruism (for waders see Owens & Goss-Custard, 1976) yet I very rarely heard turnstone alarm calling in winter. This is in marked contrast to breeding turnstone, which frequently alarm call, and members of breeding pairs can recognise their mate´s alarm call (Whitfield, unpubl. data).

Several lines of indirect evidence suggested that sometimes turnstone may have actively associated with particular individuals (e.g. Fig. 3.11). For instance, Tyninghame birds frequently flew up to the Coastguard to join other birds in a flock feeding on beaches around high tide, but as the tide ebbed, several birds, which had previously been scattered throughout the strandline flock, usually suddenly flew off south as one body. Subsequent checking of the identity of the remaining birds confirmed that the individuals which had flown off were Tyninghame birds. Quite how this response was achieved is unknown, but visual and vocal individual recognition may have been involved. Turnstone frequently utter a ´flight intention call´ immediately before or after taking flight and individuals may be able to recognise the calls of birds from the same area as themselves. Nowicki, (1983) has shown that black-capped chickadees Parus atricapillus can recognise the calls of flockmates.

Between birds from different intertidal areas status is site-dependent (Chapter 4), and moving to feeding sites away from ´home´ as part of a flock may benefit individuals in swamping the aggressive response of birds which are feeding at home (see Barash, 1974; for a similar argument). The possible advantages of reduced aggression betwen individuals who are familiar with each other is discussed in the next chapter. Associating with individuals who employ similar feeding techniques (Fig. 3.11) may provide individuals with knowledge of good feeding sites.

CHAPTER 4

DOMINANCE AND AGGRESSION

4.1 INTRODUCTION

Within groups of animals, individuals often compete with each other over resources, such as food or resting places. These competitive interactions often do not involve blatant aggression; one individual may give an aggressive display and the other merely withdraws from the site of the resource. The outcome of such interactions between any given pair of individuals are frequently predictable; one of the pair wins, the other usually loses. If the outcome of these interactions between several pairs, or dyads, are compared by, for example, placing the results in a matrix, it is often possible to rank the individuals of the group in an order reflecting their success.

To describe these features of behaviour and attempt to explain why some individuals win more interactions than others, the concept of dominanance was invoked (for a historical perspective see Gauthreaux, 1978). In each dyad, one individual who usually won was referred to as the dominant, the loser was called the subordinate. The sum of the dyadic interactions meant individuals could be ranked in a dominance hierarchy, the one dominant to most others at the top, the one subordinate to most others at the bottom. Since individuals differ in the numbers of others to whom they are dominant or subordinate, it becomes convenient to refer to an individual's position in the hierarchy as its rank, or status. It is in this sense that the words dominant, subordinate, hierarchy, rank and status are used in this thesis (see Deag, 1977)

Dominance is one of the most controversial and most debated concepts in social behaviour, although the general consensus of opinion is that it is useful in describing relationships in group living animals, albeit iin a modified form (e.g. Deag, 1977; Chalmers, 1979; Bernstein, 1981; Wade, 1978). Much of the controversy and debate surrounding dominance has been concerned with primates, although the concept has been applied to a vast range of animal species, including many birds (Gauthreaux, 1978). The study of dominance in waders is largely in its infancy, and to date most workers have investigated the possible ecological basis and competitive consequences of aggression and agonistic interactions rather than the applicability of dominance in describing relationships. Aggression in turnstone has been studied by several workers (e.g. Groves, 1978; Marshall, 1981; Fleischer, 1983) but the work of Marshall is most relevant to the present study. Working at Scoughall, Marshall examined rates of aggression in relation to season and flock size, and in captivity he observed the influence of status on feeding behaviour. Marshall suggested that turnstone may form stable dominant/subordinate relationships in the wild and a prime objective of this study was to examine the validity of this suggestion using data collected from a colour-ringed population which (unlike most other field studies of avian dominance and aggression e.g Patterson, 1977; Rohwer & Ewald, 1981) was not supplied with an artificial food supply. I then examined the possible consequences of aggression and dominance in terms of individuals' fitness components and attempted to examine the factors controlling the expression of aggression. In this chapter I am not concerned with adding to the already enormous body of literature and data used in deliberations over the concept of dominance. Rather, I am concerned with how wintering turnstone compete for resources, the predictability of competitive interactions and the effects of competition for individuals of different competitive ability. In directing my attention towards the nature of and role of competition in the social life of turnstone I concur with Seyfarth (1981) and Smuts (1981) in that the ultimate goal of studies of competition should be to determine how animals compete, why competition takes the form it does and the consequences of that competition, rather than agonising over the value of concepts in describing competition. Throughout this chapter terms such as dominance, aggression, etc. are as defined by Deag (1977).

4.1.1 DESCRIPTION OF AGONISTIC BEHAVIOUR IN WINTER

Previous descriptions of the aggresive displays of the turnstone include those of Bergman (1946), Marshall (1981) and Cramp & Simmons (1983). The main aggressive display of the turnstone, the tail-down hunch, involves the displayer depressing and slightly fanning its tail, raising its back feathers and crouching. The tail may also be vibrated, particularly if the displayer is also vocalising. At its lowest intensity the displayer crouches lower with its head raised slightly and utters an ´aggressive rattle´ vocalisation (inaccurately labelled ´chattering alarm call´ by Cramp & Simmons, 1983). There are considerable individual differences in the tail-down hunch display (Marshall, 1981; pers. obs.), such as the extent to which the tail is depressed and/or fanned, and in the ruffling of the back feathers. Moreover, some individuals raise their forehead feathers and a few droop their wings: each indidvidual seems to have a characteristic display. The tail-down hunch is usually used as a threat display.

In wintering turnstone the tail-down hunch is often performed when the aggressor supplants the aggressee from a resource such as a feeding site or roosting site. If the aggressee does not immediatly move away from the resource, the aggressor may peck its opponent. If the aggressee shows greater resistance, it performs the tail-down hunch at the aggressor. The aggressor may then attack the aggressee and chase the aggressee if it moves away from the resource as a result of the attack. If the aggressee reciprocates the attack a fight usually ensues. In a fight the two birds face each other, stretched upwards, and then may fly at each other, each bird trying to peck its opponent on any part of its body but particularly the head. Each bird appears to attempt to get on to the back of its opponent; if it achieves this objective it pecks the back of its opponent's head. In particularly intense fights feathers may be removed and very occasionally I have seen birds injured. If at any point one bird breaks off the fight, the victor may display chase after the loser.

A bird may perform a tail-down hunch display if it is feeding on a prey item or small feeding site or is roosting, and another bird moves towards it or near it. In such situations the displayer appears to be defending its position and I have termed the display given in this context as a display threat.

I have never seen a wintering turnstone perform a submissive display; a bird either avoided another bird or moved away from the site of the interaction. Neither have I seen a wintering turnstone perform a tail-up aggressive display (see Cramp & Simmons, 1983).

4.2 GENERAL METHODS

Most observations of agonistic interactions were collected from two hours before to two hours after high tide. However any additional interactions seen outside this time period were also noted. Records were made by scanning a flock repeatedly from one end to the other until an interaction was seen. When an interaction was seen, the following information was noted:

(a) the initiator of the interaction;

(b) the identity of the interacting birds; i) colour ring combination, ii) colour-ring combination unknown, iii) unringed, juvenile or adult and male or female (if birds were in breeding plumage);

(c) the winner and the loser;

(d) the form of the aggression, either i) display, ii) supplant, iii) display supplant, iv) display peck supplant, v) peck supplant, vi) display chase, vii) peck display chase, viii) fight, ix) display threat, x) peck threat, xi) display peck threat or xii) avoid;

(e) the object of the aggression, i) feeding site, ii) food, iii) roost site, iv) bathing site, v) individual distance, vi) no apparent reason (unprovoked attack), or vii) unknown;

(f) the degree of retaliation of the loser, i) no retaliation, ii) weak retaliation, iii) strong retaliation.

In addition, where possible, I noted the size of the flock where the interaction took place, and before each observation session started I recorded the date and time (also noted periodically within each session), and the nearest neighbour distance, measured in bird lengths, for at least half the birds in the flock. I also noted the proportion of unringed adults and juveniles in the flock, the sex ratio of the flock (only possible with birds still in summer plumage), the site where the flock was feeding or roosting, and, if the birds were feeding, the prey that they were feeding on and the microhabitat the birds were feeding in. For birds feeding around high tide on beaches I differentiated between 5 ´strandline´ microhabitats: sand (S), tide edge sand (TES), tide edge wrack and sand (TEWS, sand>30%, wrack<70%), tide edge wrack (TEW), wrack (TW).

Periodically I also made running commentaries on birds´ feeding behaviour and recorded them on tape. For the purposes of the present chapter, the following behaviours were recognised: walk, run, fly, preen, peck, swallow, supplant, supplanted, look up (head raised above the horizontal). Before recording the running commentary I noted the following: time, date, identity of focal bird, number of birds within 10m of the focal bird, flock size, nearest neighbour distance, prey being taken and microhabitat. Each commentary lasted a minimum of 30s. and maximum of 3min.

The commentaries were analysed with the aid of Keybehaviour (Deag, 1983a) and Keytime (Deag, 1983b), in which commentaries are transferred onto program discs and analysed to produce basic behavioural records consisting of composite behaviours´ frequency, latency, duration and rate per minute. A more detailed explanation of this process is given in section 6.5.2.2.

4.3 DOMINANCE

4.3.1 DYADIC RELATIONSHIPS AND AGONISTIC HIERARCHIES

4.3.1.1 INTRODUCTION AND METHODS

As I showed in chapter 3, turnstone at the study site were normally site-faithful to the same intertidal area over most of the study period, thereby confirming the suggestion of Marshall (1981) that the turnstone on the study site could be considered as a ´resident community´. Marshall further speculated that within this relatively stable group of individuals, stable dyadic agonistic relationships existed which when arranged into a matrix would reveal a basically linear agonistic hierarchy. Marshall´s speculation was based on observations of a captive turnstone flock, and it is well known that several species of animals can only be ordered into such hierarchies when forced into captivity (e.g. Kaufmann, 1983); indeed, it has been claimed that in primates hierarchies are an artifact of captivity and are tenuous or absent in the wild (Gartlan, 1968; Rowell, 1974; but for critiques see, e.g. Deag, 1977; Wade, 1978). Using observations of colour-ringed turnstone at the study site I tested Marshall´s prediction by examining dyadic agonistic relationships between birds known to regularly occur in the same intertidal area.

The methods used were as outlined earlier (section 4.2). Matrices were constructed of the distribution between any given individuals of all dyadic agonistic interactions. Unless otherwise stated, I have employed the results of dyadic interactions occurring at all stages of the tide and at all levels of the littoral zone.

4.3.1.2 RESULTS AND DISCUSSION

During the winters of 1982-83 and 1983-84 I recorded over 7000 agonistic interactions: a summary of the nature of these interactions is shown in Table 4.1. It can be seen that the majority of interactions involved one bird supplanting another bird from a resource, or one bird display threatening another as the threatener fed at a feeding site or stood at a roost site. It is worth noting that very few interactions occurred over personal space i.e. the individual distance: the object of aggression was usually a feeding site or a roost site.

Combining the results from all dyadic relationships into a matrix for the members of any given intertidal area ′flock′ showed that at least within one winter and in a given context, e.g. incorporating interactions occurring over food or feeding sites, birds could be organised into a basically linear hierarchy. For example, in the Scoughall flock (see Chapter 3) when interactions over food or feeding sites in the winter 1983-84 were ordered into a matrix, reversals were uncommon: this is shown by the small proportion of the total number of interactions which were below the diagonal on the matrix (fig. 4.1). This lack of reversals indicates that the direction of agonistic behaviour within dyads was stable. Dominance also tended to be transitive, so that if bird A beat bird B, and bird B beat bird C, then bird A beat bird C, and for future purposes where data were lacking I have assumed transitivity. Birds which used the same intertidal home area could therefore be ranked with respect to each other, based on the results of dyadic interactions. To further examine how resource-specific dominance relationships were I compared the results of interactions over feeding sites or food with those interactions over roost sites.

TABLE 4.1.

A summary of the agonistic interactions which were observed:

(a) the object of the interactions, S=site, F=food, R=roost, P=reening, B=bathing, ID=individual distance (personal space), U=unknown.

(b) the form of interactions, s=supplant, d-display, p-peck, t=threat. All values are percentages of N, where N=sample size of interactions

(a)	N	FS	F	RS	ID	PS	BS	U
	6777	70	3	18	7	0	0	2

(b)	N	s	ds	ps	dps	peck chase	fight	dt	pt	dpt	p
	6777	7	64	1	4	4	2	16	0	2	1

LOSE

WIN

		YOBN	YNLG	YWOB	YNNG	YLLB	YLGR	YWWL	YWNR	YLBG	YOWL	BWRY	YWWR	YWLR	YWGN	YGRW	YWWB	BWLW
M	YOBN		7	2	2	3	7	2	2			1	1	2		3	5	1
M	YNLG			6		7	6	2	2	1		2	2	1	2	5	4	
M	YWOB				11	2	8		1	1	1	2	1	2	6	1	2	
M	YNNG		10	1		8	7		1			3	1	4	7	11	4	1
M	YLLB						3		1	1	1	2	1	1	3	3		1
M	YLGR					1		2	3	2	1	4		3	3	9	3	1
M	YWWL								2	1	1	1			3		1	
M	YWNR									1		1		1	3		2	
M	YLBG										1							
M	YOWL											1	1					
M	BWRY												1		1	2	3	
F	YWWR														3		1	
F	YWLR														3	1	1	1
F	YWGN							1	1	1	2					1	4	3
M	YGRW							1				1		1	1		1	
F	YWWB																	1
F	BWLW																	

For each dyad, involving birds from the same intertidal area I examined whether a bird dominant over feeding sites or food was also the bird dominant over roosting sites within the same winter. Bird A was judged to be dominant over bird B if it beat bird B on more occasions than it was beaten by bird B. The direction of the relationship was judged to be the same if bird A was dominant over bird B both in encounters over food or feeding sites and over roost sites; if bird B was subordinate, for example, in food encounters but dominant in roost encounters then the direction was reversed. Within a given winter sufficient data existed for 159 dyads, and in 158 (99.4%) the direction of the relationship was the same, showing that dominance was not resource-specific: i.e. bird A was dominant over bird B regardless of the resource being contested.

I then compared the direction of relationships across winters, assuming dominance was not resource-specific. From the winters of 1982-83 and 1983-84 sufficient data existed for 189 dyads, and in 170 (89.9%) the direction of relationships was the same, indicating that if bird A was dominant over bird B in winter x, it was also dominant in winter x + 1. Results from the winters of 1981-82 and 1984-85 also confirmed the notion that relationships were stable in successive winters. I will discuss the nature of the few reversals later.

Finally, I examined whether dyadic dominance relationships involving birds from the same intertidal area were site-specific or not i.e. whether bird A was dominant over bird B regardless of whether the interaction took place on the home area of A and B (or on the beaches landward of the home area of A and B) or away from the home area of A and B. Data were available from 72 dyads and in every one (100%) the direction of the relationship was the same. To summarise, provided that birds were from the same intertidal area, dominance was neither resource- nor site-specific and tended to remain the same in successive winters.

I combined the results of dyadic agonistic interactions within two matrices, one for the Coastguard (CG) ´flock´ 1982-83 and 1983-84, the other for the Scoughall-Field Space (S-FS) ´flock´ 1982-83 and 1983-84 (Fig. 4.2, 4.3). These matrices show again that reversals were uncommon, that dominance tended to be transitive and that within a given intertidal ´flock´ (i.e. birds from the same intertidal home area) basically linear agonistic hierarchies could be described. The matrices allowed birds to be assigned a rank, and when certain dyadic relationships were absent I have ranked a bird as high as the data allowed whilst minimising the sum of interactions below the diagonal.

In the S-FS flock most of the interactions below the diagonal were the result of reversals in dominance occurring between winters. For example, YWGN was dominant over YWWL, YWNR, YWNL and YWLR in 1982-83 but was subordinate to them in 1983-84, and YNNG was dominant over BWWL in 1982-83 but subordinate in 1983-84. Most of the reversals involving YGRW winning were due to YGRW apparently becoming particularly aggressive in his third winter (1983-84): occasionally he won interactions against birds which were ranked higher. The matrix and ranking of birds for the S-FS flock as presented in Fig. 4.3 is therefore based on relationships as they stood at the end of the 1983-84 winter. For the CG flock, relationships remained the same in both winters, save that the rank of BGWL appeared to increase from when it was a juvenile in 1982-83 to when it became an adult in

lose

win		YRM	YLWM	YWMW	YMBG	YMWO	YLWL	YWBW	YRWR	YBOL	YLBG	YLOL	YLOM	YOWL	YWGB	YWMB	YMGB	BWWO	YORW	YMOB	YMWM	YOBL	YRLG	YLLG	YLGM	BWWB	BWYL	BWOG	BGWL
F	YRM		4	19	1	7	3	8	11	2	1	5	1	4	11	2	3	1	1	4	8	8		2	1	2			
M	YLWM			2	4	4	6	3		1	2	1	4		11	4	8	1	1	3	5	3		5	1	6	1	1	
M	YWMW				1	8	7	4	7	7	4	10	4	6	4	1	5	7	1	3	10	2	1	4	3	3		1	2
M	YMBG					9	10	11	1	4	2	9	9		8	4	8	2	9	3	3	3		3	1	8			1
M	YMWO						10	2	3	3		3	1	1	1	1	2		1	2	4	2		3	1	4		2	
M	YLWL							10	5	3	1	3	8	1	1	2	8	4	1	3	4		1	9	1	4	2	1	1
M	YWBW								5			4	2		5	4	2	2	5	4							1	1	1
M	YRWR									2	5	3	3	2	2	4	2	2	1	3		1	2	2	1				
F	YBOL							2	1		2	1					2	1	3	5	1		1	5		2		3	2
M	YLBG							2				1	2	1	4	1	2	3	3	1	1	3		3	3	1			
M	YLOL					1	3	1					4		8	2	1	1	2	1	4	2	2			5			
M	YLOM														2	2		2	1	4	4			1		3			
M	YOWL														1		2	2				1				3			1
M	YWGB															2	2	2	8	3	2			2	2	8	1	2	8
M	YWMB									1				3				4	1	4						1	1	1	
M	YMGB								1									1	2	3				4		1		1	1
M	BWWO																		1	3	2			1	4	3	1		3
F	YORW																2			4	5			1	2	3	1	1	1
F	YMOB																				1			1		3	1		
F	YMWM																							2		3			1
?	YOBL																						3	1	1				
F	YRLG																							1					
F	YLLG																								3	8	1	1	1
F	YLGM																									2	1		2
F	BWWB																										1		1
F	BWYL																											1	
F	BWOG																												1
M	BGWL																			(2)	(1)					(1)			

lose

win		YOBN	YNLG	YWOB	BWWL	YNNG	YWNL	YLLB	YBWL	YLGB	YWWL	YWNB	YLBG	YOWL	BWBY	YWWB	YWGN	YLNW	YWLB	YGBW	YONO	YLNO	YWWO	YWGW	YOWO	YOOW	BWYO	YNNW	YWLO	YBLG	YBOL	BGYW	BGYG	YWWG	YWWB	BWLW
M	YOBN		9	4	1	6	4	7	2	11	12	10	3	2	1	3	7	4	2	5	2	1	3			1		2							11	1
M	YNLG			9	3		1	9		6	4	6	2		2	3	3	4	1	5			3	1	1			3			1	2	4		5	
M	YWOB				8	15	3	3	3	8	2	1	1	1	2	2	7	11	4	2	3	1	5	2	5	2	1	4	3			8	1	1	3	
M	BWWL					5	3		8	9	2		2		4		3	1		5		6	10	6	2	3	3	5	2	2		4	2	2	2	
M	YNNG		13	2	5		5	9	2	10	2	3	2		5	1	15	9	7	14	5	4	20	3	4	2	4	10	7		1	8	3	3	5	1
M	YWNL							1	2	3	3				6		3		3	2	2		6	1			1	3	1			1	4	1		
M	YLLB					1			1	4	8	2	2	1	2	2	7		1	3			2	1				3				1				1
M	YBWL									2					1			2	3	1		1		2		1						3	6	1		
M	YLGB				1			1			2	4	2	2	4	1	4		4	11	1	1	2	2	1	1	1	2	1		1	5	3	1	5	1
M	YWWL							1		2		5	1	1	1		4	2	5	1		1	6		1					1		2	1	1	1	
M	YWNL			1				3					2		1	1	4	1	3			5	1									1	1		2	
M	YLBG													1				1				2											2			
M	YOWL														1	1							1									2				
M	BWBY															1	1	1		2			4		1		1	3							3	
F	YWWB																3	1	3				1												1	
F	YWGN						2	1			3	3	2	3				13	6	3	9		20	2	11		1	7	2			1	3	1	5	3
F	YLNW			1						6	1								3		1		11	2	2		1	2	1			6		2	3	
F	YWLB																3			2				1				1							2	1
M	YGBW										1				1	1	1	1	2				2	2	2			2				5	2		1	
F	YONO			1																		1	1				4					6				
F	YLNO																						1	2	1	1	1	2	1			1	2	1		
F	YWWO																							1	6			3	1			6	4	3	4	2
F	YWGW																								1									1		
F	YOWO																									1	1					2			3	
F	YOOW																										2					2	8	1	2	
F	BWYO																											1			1	2		2		
F	YNNW																							1					1		1	2		1	2	
M	YWLO																													1					1	
M	YBLG																														1					
F	YBOL																															2	1			
F	BGYW																		1														7	1		1
M	BGYG																																	1		
F	YWWG																																		2	
F	YWWB																			1								1								1
F	BWLW																																			

1983-84. Such apparent increases in the rank of juveniles (i.e. first winter birds) on becoming adults (i.e. second winter birds) represented four of nineteen between-year reversals in dominance relationships; three of these four reversals involved males becoming dominant. Ten of the other reversals involved males in their third winter becoming dominant over adult females. Although the data are scanty, birds in their first winter appeared to be subordinate to all older birds. In their second winter at least some individuals, particularly males, appeared to ´leap frog´ in rank over some low ranking females, and in their third winter males took ranks higher than the majority of females, but the rank of third winter females did not appear to change. After their third winter the rank of males did not appear to increase at the expense of higher ranking males, unless higher ranking males died. When a bird died its rank was assumed by the bird below it in the rank order, and so on, so that the rank of all lower birds increased by one i.e. the relative rank of birds remained the same but the absolute rank of birds increased. For example, when YRM was killed by a sparrowhawk the relative rank of CG birds remained the same but their absolute rank increased by one.

As can be seen from both matrices, adult males were usually higher ranking than adult females, and the sex of an adult was clearly an important determinant of its status. Other possible determinants of status will be examined later (section 4.3.3).

The small number of reversals suggests that each bird could recognise the status or identity of other birds from the same intertidal area. Moreover, out of 6777 interactions the initiator won in 6626 (97.8%) of instances, and of 6787 interactions the loser showed resistance to the loss of the interaction on only 170 (2.5%) occasions (1.0% weak resistance, 1.5% strong resistance). Marshall (1981) also found that initiators usually won interactions. These observations lend support to the notion that individuals could recognise the status of their opponents. As I will show in Chapter 5 there is evidence that birds could probably recognise other individuals by plumage differences.

I could only produce matrices for the CG and S-FS flocks because it was only from these flocks that I had sufficient observations of dyadic interactions. In an attempt to assess the ranking of birds in other intertidal flocks, I explored the possibility that birds could be ranked according to the proportion of interactions which they won.

The CG birds were ranked according to how many interations they won at home (i.e. on their home intertidal area or on the beaches landward of this area) between August and October 1982. When this rank order (A) was compared to the rank order derived from the matrix of dyadic agonistic interactions (B) there was a strong agreement between the two rank orders (Table 4.2: $r_s=0.82$, df=25, $p<0.001$), showing that provided the observations of interactions which were used to rank a bird were collected on its home area, the proportional success rank order provided a reasonably good measure of a bird's rank as derived from an agonistic hierarchy. The data suggest that the larger the sample size then the closer is the agreement between the two methods.

Based on interactions observed on their home area or home beaches, the rank order (A) of birds of the Car Rocks (CR) flock is shown in Table 4.3. The results confirm previous results in showing

TABLE 4.2.

Rank orders of the Coastguard flock as determined from % interactions won at home (A) and the results of dyadic interactions (B) Spearman´s rank correlation, $r_s=0.82$, df=25, $p<0.001$.

		Rank order (A) % interactions won at home			Rank order (B) from dyadic interactions
		% won	N		
F	YRM	100	174	F	YRM
M	YLWN	94	108	M	YLWN
M	YNBG	90	133	M	YWNW
F	YBOL	88	42	M	YNBG
M	YWNW	88	190	M	YNWO
M	YNWO	74	84	M	YLWL
M	YLWL	70	87	M	YWBW
M	YLOL	70	120	M	YRWR
M	YRWR	69	94	F	YBOL
M	YLBG	69	64	M	YLBG
M	YOWL	68	38	M	YLOL
M	YWNB	64	55	M	YLON
M	BGWL	63	8	M	YOWL
F	YNOR	58	73	M	YWGB
M	YWBW	52	67	M	YWNB
M	YLON	49	53	M	YNGB
F	YLWO	42	24	M	BWWO
F	YORW	37	41	F	YORW
F	YLGN	36	22	F	YNOR
M	BWWO	36	45	F	YNWN
F	YLLG	35	60	F	YLWO
F	YNWN	32	56	F	YOBL
F	YWGB	28	74	F	YRLG
M	YNGB	28	46	F	YLLG
F	YRLG	27	15	F	YLGN
F	YOBL	26	38	F	BWWR
F	BWWR	8	60	M	BGWL

TABLE 4.3.

The rank order (A) for birds of the Car Rocks (CR) flock based on the % of interactions won observed in the CR home area 1982-83, 1983-84.

Rank	Sex	Bird	% interactions won	(N)
1	?	YNBR	100	(19)
2	M	YBOR	100	(12)
3	M	YNOL	98	(41)
4	M	YLOW	92	(112)
5	M	YWNG	92	(112)
6	M	YBGO	89	(47)
7	M	YOGN	81	(21)
8	F	YNGR	81	(47)
9	M	YNLW	80	(30)
10	M	YRGN	75	(20)
11	M	YRRW	74	(19)
12	M	YBNR	65	(23)
13	M	YWRG	65	(37)
14	M	YLRN	64	(56)
15	M	BWYN	63	(30)
16	M	YLBR	62	(26)
17	M	YRNW	61	(23)
18	M	YBWB	60	(25)
19	M	YLLW	60	(15)
20	M	YLNR	59	(37)
21	M	YRGL	57	(21)
22	M	YGOW	57	(21)
23	F	YWOL	48	(21)
24	F	YOBR	46	(13)
25	M	YOGW	45	(33)
26	M	YRLW	44	(9)
27	M	YRNG	44	(17)
28	F	YRON	43	(7)
29	F	YRWL	42	(12)
30	F	YWOR	39	(23)
31	M	YRBN	36	(20)
32	F	YLOG	34	(32)
33	F	YNRG	33	(9)
34	F	YNLR	31	(13)
35	F	YLBW	27	(18)
36	F	YNRW	22	(11)
37	F	YBLR	20	(10)
38	F	YRNL	14	(7)
39	F	YOWG	11	(19)
40	JUV	BGWN	3	(31)

that males won more interactions than females, and although in this case there is only an inference that adult males were consequently dominant over adult females, data from dyadic relationships involving CR birds showed that adult males were dominant over adult females in 92% of relationships (N=362).

For the CG flock, inclusion of interactions observed away from the CG home area affected the CG proportional success rank order (Table 4.4). These data demonstrated that the proportion of interactions won by birds was lower as they moved away from their home area, which suggests that their status was probably reduced also. Since I have shown that for birds from the same home intertidal area the direction of dyadic agonistic relationships remains the same regardless of the site of interaction, site-dependent changes in the status (as measured by the % of interactions won) of birds must be a result of interactions between birds from different home intertidal areas. Such site-dependent changes in status is the subject of the following section.

4.3.2 SITE-DEPENDENT RANK

All data used in this section were collected from flocks feeding or roosting on beaches landward of the intertidal zone, and throughout I have referred to birds as being home or away. Birds were considered to be at home if they were feeding or roosting in a flock which was situated on a beach landward of their home intertidal area, and birds were considered to be away if they were feeding or roosting in a flock which was situated on a beach not landward of their home intertidal area. As I showed in Chapter 3, birds could be

TABLE 4.4.

Rank order (A) of Coastguard birds determined from % interactions won home and away. Correlation with dyadic rank order, $r_s=0.63$, df=25, $p<0.001$.

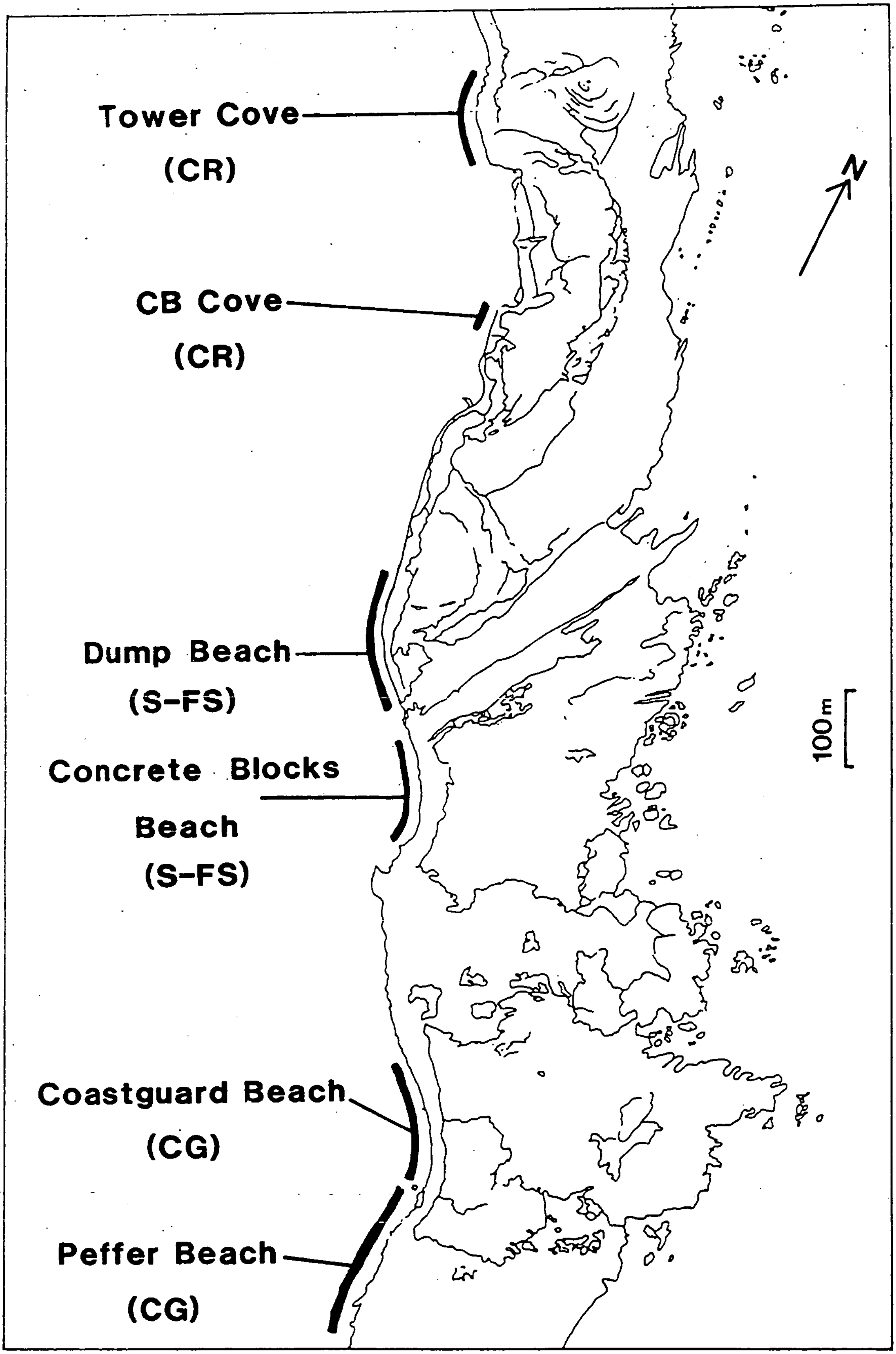
Rank order (A)
% interactions won
(HOME AND AWAY)
Nov 82-Jan 83

	% won	N
YLWN	100	36
YNBG	96	48
YLOL	91	22
YLON	85	13
YWNW	79	34
YBOL	75	20
YLBG	71	21
YNOR	68	38
YLWL	67	30
BWWO	50	28
YORW	46	24
YRM	40	15
YNWN	32	19
YNWO	31	13
YRWR	30	10
YWNB	29	7
YOWL	27	22
BGWL	25	12
YWBW	23	30
YLGN	21	24
BWWR	20	15
YNGB	19	16
YRLG	18	11
YOBL	17	6
YLWO	13	15
YLLG	11	9
YWGB	0	12

considered as members of reasonably stable groups which occupied relatively discrete intertidal areas. This allowed individuals to be classified as, for example, members of the Coastguard ′flock′ or members of the Car Rocks ′flock′, based on their home range on the study site. The home beaches of the various intertidal flocks as used in this section are shown in Fig.4.4. An example of a home bird would be a Coastguard bird feeding or roosting in a strandline flock on Coastguard or Peffer Beach; an example of an away bird would be a Coastguard bird feeding or roosting in a strandline flock on Dump Beach.

I have dealt with site-dependent rank by examining the subject at three levels: (1) possible differences between the observed and expected number of interactions initiated by home and away birds in strandline flocks; (2) the distribution of agonistic interactions between birds from three intertidal areas when gathered into strandline flocks observed at several points on the study site; (3) agonistic hierarchies involving birds from three intertidal areas and based on interactions collected from strandline flocks at different points on the study site.

(1) Number of interactions initiated by home and away birds. From the identity of individuals present in strandline flocks I could determine the composition, in terms of the numbers of home and away birds, of most strandline flocks. By noting the identity of individuals inititating aggressive interactions I could also determine the number of interactions initiated by home and away birds. The expected frequencies of aggressive interactions initiated by home and away birds were calculated from the number of home and away birds in each strandline flock, so that if:-


Tower Cove
(CR)
CB Cove
(CR)
Dump Beach
(S-FS)
Concrete Blocks
Beach
(S-FS)
Coastguard Beach
(CG)
Peffer Beach
(CG)
N
100m

c = number of home birds/(number of home + away birds)

f = number of away birds/(number of home + away birds)

then c + f = 1.

I used data collected from 27 flocks in each of three different home beaches and for each flock in each of the three areas the differences between the observed and the expected number of interactions initiated by home and away birds were summed and tested for significance using the Wilcoxon matched pairs signed ranks test (Table 4.5a). Home birds were more aggressive than away birds because home birds initiate more interactions than expected from their numbers, but away birds initiated fewer than expected: both these deviations from expectations were highly significant (Table 4.5b). Demonstrating that home birds initiated more interactions than away birds does not, of course, necessarily mean that home birds were dominant over away birds, but since initiators of interactions also won 98% of all interactions (section 4.3.1.2), it does seem likely. It is possible, however, that home birds were selectively aggressive towards other home birds and that other birds were simply less aggressive when away from home. More convincing evidence is needed before it can be concluded that site-dependent dominance occurred between birds from different intertidal areas.

(2) The distribution of interactions between birds from different areas. In several strandline flocks I noted the number of birds which were present from each intertidal area, either Coastguard (CG), Scoughall-Field Space (S) or Car Rocks (CR), and I also noted the participants and outcome of any agonistic interactions, i.e. CR over CR, CR over S, CR over CG, S over S, S over CR, S over CG, CG over CG, CG over S, CG over CR. The expected frequency of each possible

TABLE 4.5.

(a) Summary of flock composition of strandline flocks in terms of the number of home and away birds and the observed and expected number of interactions initiated by home and away birds. (b) Statistics associated with Wilcoxon matched pairs sigend ranks tests of the significance of differences in the observed and expected number of interactions initiated by both home and away birds. ****<0.0001, z is the standard normal variable, N=sample size.

(a)

	Mean No. of birds in flock		Mean No. of interactions			
			Home initiated		Away initiated	
Site	Home	Away	O	E	O	E
Dump	14.6	9.0	47.2	34.0	5.8	18.6
Peffer & CG.	12.0	9.0	33.5	25.1	5.8	14.1
Tower Cove & CB.	23.9	18.4	35.1	26.6	7.9	16.3

(b)

	Home initiated			Away initiated		
Site	N	z	p	N	z	p
Dump	26	-4.32	****	26	-4.32	****
Peffer & CG.	26	-4.46	****	26	-4.46	****
Tower Cove & CB.	26	-4.15	****	26	-4.15	****

type of interaction was calculated on the basis of the number of birds from three intertidal areas present in the strandline flocks.

For a mixed strandline flock of any specified combination of birds from the three intertidal areas,

c = number of CR birds/(number of CR + S + CG birds)

d = number of S birds/(number of CR + S + CG birds)

e = number of CG birds/(number of CR + S + CG birds)

so that $c + d + e = 1$.

Assuming random distribution of all types of aggressive interactions, $c^2 + 2cd + d^2 + 2de + e^2 + 2ce = 1$ predicted the expected frequencies of interactions where c^2 represented all CR over CR interactions; d^2 represented all S over S interactions; e^2 represented all CG over CG interactions; 2cd represented all CR over S interactions and all S over CR interactions; 2de represented all S over CG interactions and all CG over S interactions, and 2ce represented all CR over CG interactions and all Cg over CR interactions.

A summary of the composition of the strandline flocks observed on three home beaches (one home beach for each intertidal flock), and the observed and expected frequencies of types of agonistic interactions is shown in Table 4.6. For each flock and each type of interaction the magnitude and direction of differences between observed and expected frequencies were summed and tested for significance using the Wilcoxon matched pairs signed ranks test (Table 4.6). Regardless of where a strandline flock was situated on the study site, significantly fewer away over home interactions were seen, which strongly suggests that home birds were usually dominant over away birds: dominance between birds from different intertidal

TABLE 4.6.

Mean observed and expectd numbers of interactions between birds from three intertidal areas when feeding at (i) Dump Beach (S birds at home), (ii) Peffer and Coastguard Beach (CG birds at home), (iii) Tower Cove and CB Cove (CR birds at home).
*p<0.05,**<0.01; O>E=observed number of interactions greater than expected, O<E=observed number of interactions less than expected, NS not significant. Mean number of birds in flock: (i) 8.3 (CR), 17.1 (S), 6.7 (CG); (ii) 4.5 (CR), 8.5 (S), 15.2 (CG); (iii) 18.8 (CR), 7.6 (S), 5.3 (CG).

Direction and type of interaction

	CR>CR		CR>S		CR>CG		S>S		S>CR		S>CG	
	O	E	O	E	O	E	O	E	O	E	O	E
(i)	3.9	4.6	0.2	7.4	1.5	2.6	30.6	18.6	11.0	7.4	10.4	6.6
	NS		**O<E		*O<E		**O>E		**O>E		**O>E	
(ii)	0.6	0.9	0.1	1.8	0.1	4.1	3.6	3.6	1.6	1.6	3.1	6.9
	NS		*O<E		**O<E		NS		NS		**O<E	
(iii)	35.2	25.7	13.7	10.4	11.4	7.2	3.9	4.2	3.8	10.4	2.5	2.9
	**O>E		*O>E		**O>E		NS		**O<E		NS	

	CG>CG		CG>S		CG>CR	
	O	E	O	E	O	E
(i)	1.4	3.0	0.1	6.6	0.1	2.6
	NS		**O<E		**O<E	
(ii)	25.1	21.1	9.2	6.9	7.4	4.1
	NS		*O>E		**O>E	
(iii)	1.8	2.0	0.8	2.9	0.1	7.2
	NS		**O<E		**O<E	

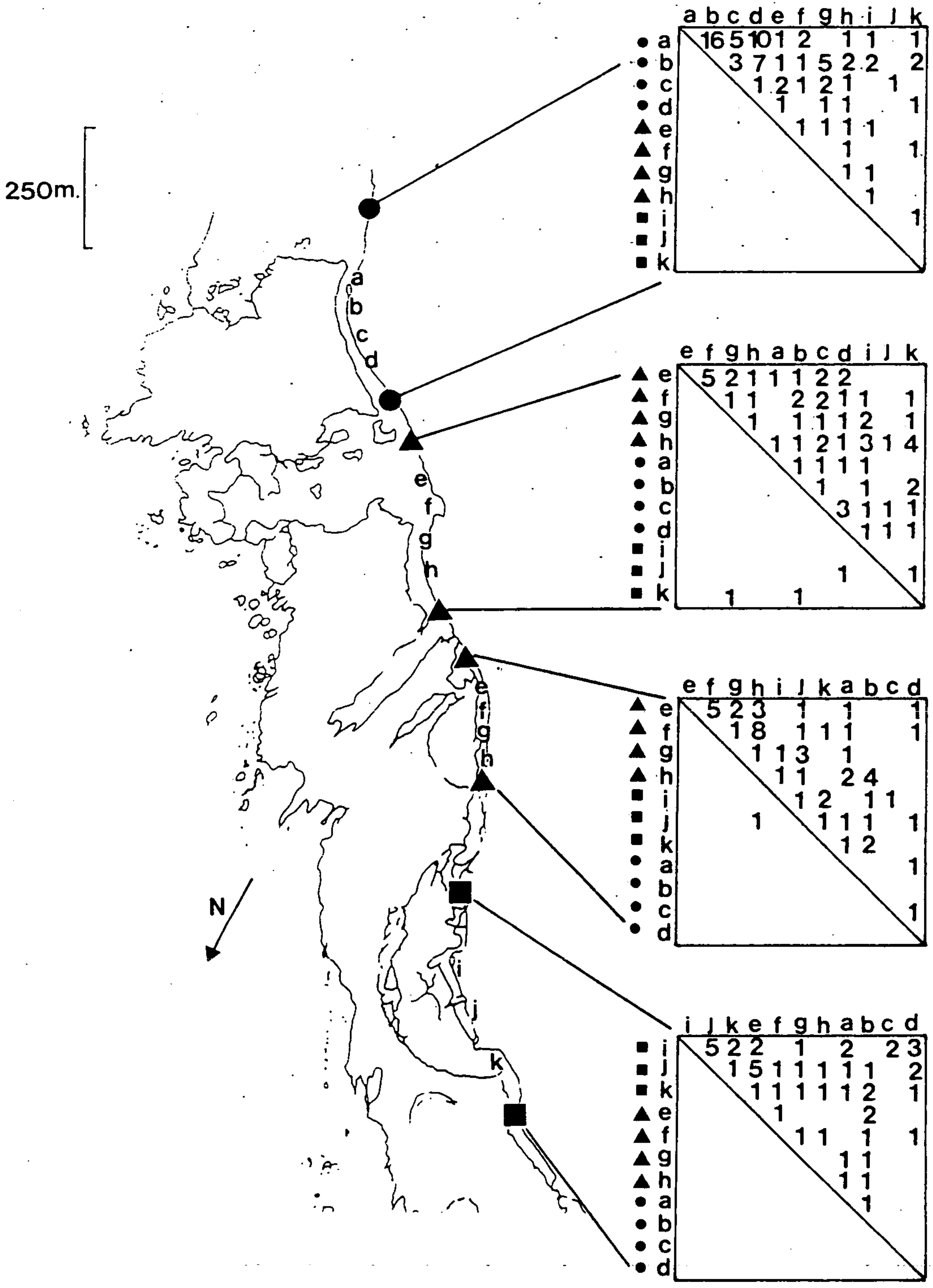
areas appeared to be site-dependent.

There was no significant difference, however, between the number of observed and expected interactions between ´familiar´ away birds i.e. CR over CR at Dump Beach). This result is to be expected if dominance in birds from the same intertidal area is absolute (sensu Kaufmann, 1983) and site-independent (section 4.3.1.2).

Although away birds appeared to be involved in fewer interactions with ´unfamiliar´ away birds than expected i.e. away birds not from the same intertidal area (e.g. CR over CG or CG over CR at Dump Beach), the behaviour of away birds towards unfamiliar away birds seemed to depend on how far away birds were from their home area. That is, when away birds were closer to their home area they appeared to win more interactions against unfamiliar away birds. For example, at Dump Beach (nearer to CR area than CG area) there were fewer CG over CR interactions than there were CR over CG interactions, and at Peffer and Coastguard beaches (nearer to S than CR) there were fewer CR over S interactions than there were S over Cr interactions (Table 4.6). This suggests an apparent waning of a bird´s status with increasing distance from their home intertidal area and is illustrated more clearly in the following section.

(3) Agonistic hierarchies. When the outcomes of dyadic agonistic interactions between birds from diferent intertidal areas were sorted into matrices according to the site of the interactions, it was clear that home birds were dominant over away birds and that an individual´s status waned with increasing distance from its home area (Fig. 4.5). Since lowered status away from home seemed to lower a bird´s feeding success in at least some strandline microhabitats (see later, section 4.3.4.1), this is perhaps one reason why turnstone

Fig. 4.5 Site-dependent agonistic hierarchies involving birds from three different areas. Individuals from the same intertidal area share a common symbol: corresponding symbols denote their home area. a=YRM, b=YWNW, c=YWBW, d=YRWR, e=YWOB, f=YNNG, g=YLGR, h=YWGN, i=YLOW, j=YLRN, k=YWNG.



	a	b	c	d	e	f	g	h	i	j	k
● a		16	5	10	1	2		1	1		1
● b			3	7	1	1	5	2	2		2
● c				1	2	1	2	1		1	
● d					1		1	1			1
▲ e						1	1	1	1		
▲ f								1			1
▲ g								1	1		
▲ h									1		
■ i											1
■ j											
■ k											

	e	f	g	h	a	b	c	d	i	j	k
▲ e		5	2	1	1	1	2	2			
▲ f			1	1		2	2	1	1		1
▲ g				1		1	1	1	2		1
▲ h					1	1	2	1	3	1	4
● a						1	1	1	1		
● b							1		1		2
● c								3	1	1	1
● d									1	1	1
■ i											
■ j								1			1
■ k			1			1					

	e	f	g	h	i	j	k	a	b	c	d
▲ e		5	2	3		1		1			1
▲ f			1	8		1	1	1			1
▲ g				1	1	3		1			
▲ h					1	1		2	4		
■ i						1	2		1	1	
■ j				1			1	1	1		1
■ k								1	2		
● a											1
● b											
● c											1
● d											

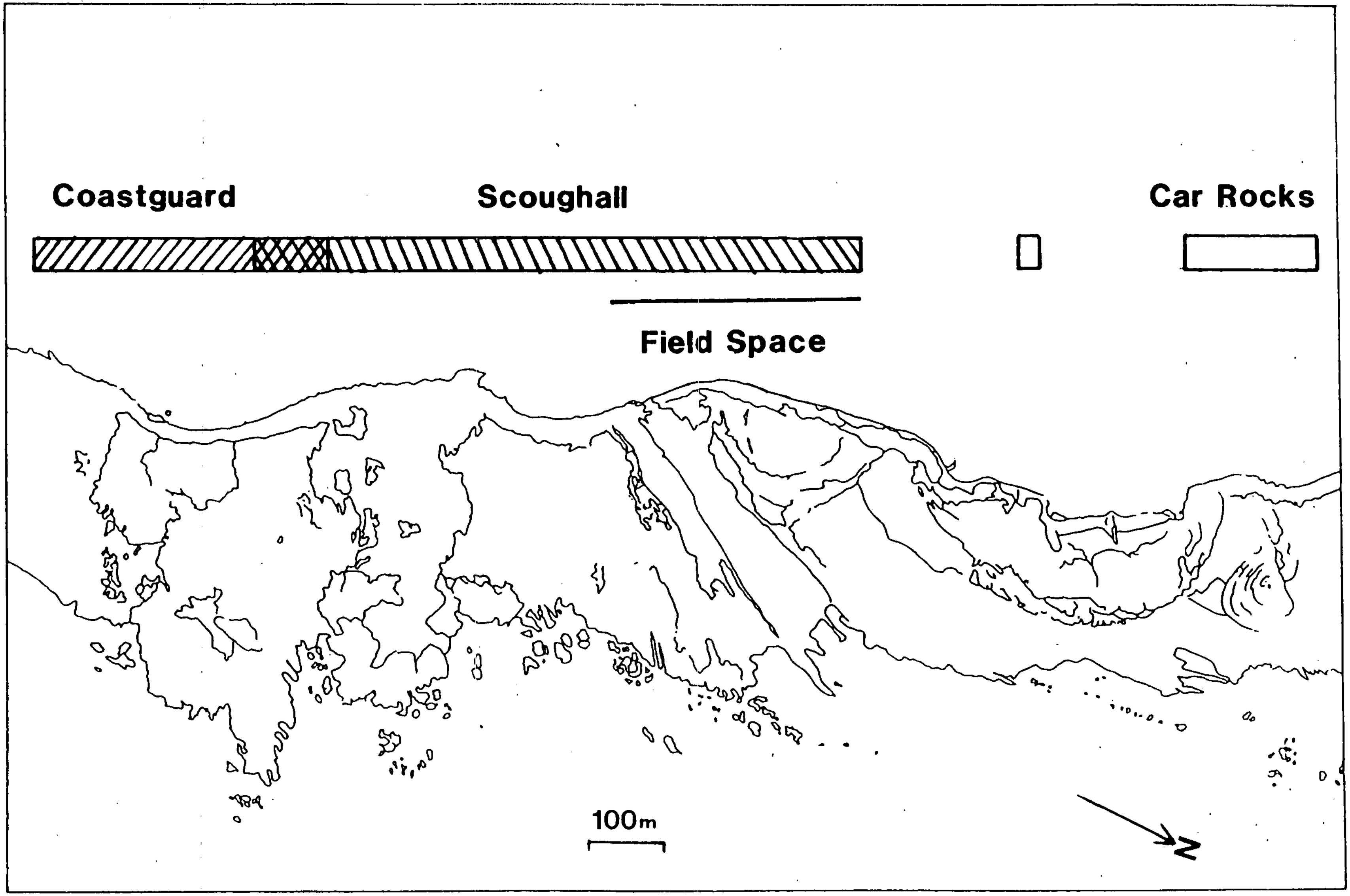
	i	j	k	e	f	g	h	a	b	c	d
■ i		5	2	2		1		2		2	3
■ j			1	5	1	1	1	1	1		2
■ k				1	1	1	1	1	2		1
▲ e					1				2		
▲ f						1	1		1		1
▲ g								1	1		
▲ h								1	1		
● a									1		
● b											
● c											
● d											

were more likely to be seen feeding on home beaches rather than on away beaches (Chapter 3).

The observation that status decreased with increasing distance from home immediately begs the question as to where on the study site did the switch in agomistic roles occur between birds from neighbouring intertidal areas? I attempted to answer this question by looking at the differences between the observed and the expected numbers of interactions initiated by birds from each intertidal area in 50m lengths of beach. In this analysis I differentiated between Car Rocks birds, Field Space birds, Scoughall birds and Coastguard birds (see Chapter 3). I assigned a stretch of beach to a group of birds if that group of birds alone initiated consistently more interactions than expected on that stretch of beach. If more than one group of birds initiated more interactions than expected, or if more than one group of birds each initiated approximately the expected number of interactions then I assigned that stretch of beach to those groups of birds. Whilst I have assumed that the number of interactions initiated is an indicator of dominance, this seems reasonable in the light of results described earlier. I was often interested in discerning trends in the number of interactions which were initiated so this made tests of significance unnecessary.

Considering the extensive intertidal home range of several Car Rocks individuals, the 'dominance domain' (the total length of beach where birds from one intertidal area were dominant over birds from other intertidal areas) of Car Rocks birds was noticeably small (Fig 4.6). This was probably because many of the home beaches of Car Rocks birds were poor or unsuitable as feeding sites, judging by the total absence of any sightings of turnstone feeding there (see

Fig. 4.6 The dominance domains´ of each intertidal ´flock´: areas where birds from a particular intertidal area alone initiated more aggressive interactions than expected. Field Space birds had no domain as such but on home beaches they usually initiated the expected number of interactions (denoted by a black line).


Coastguard
Scoughall
Car Rocks
Field Space
100m
N

Chapter 3). Although this effect probably also explained in part the size of the dominance domain of Coastguard birds (Peffer Beach usually provided few feeding opportunities), there also appeared to be an apparent ´encroachment´ of Scoughall birds onto the northerly sections of Coastguard home beaches. The dominance domain of Scoughall birds certainly extended further south than would have been expected given the limits of their home range, and consequently it was the largest domain, encompassing several good feeding sites (Fig. 4.6, and Chapter 3). THe Field Space birds did not have a dominance domain, but in an area opposite their home intertidal area they tended to initiate the expected number of interactions. This result may have been because most of the Field Space birds were lower ranking than Scoughall birds and their home intertidal areas overlapped. Interestingly, both Field Space birds and Scoughall birds appeared to be more aggressive at Chapel Brae (within the dominance domain of Car Rocks birds) when Car Rocks birds were not present.

Due to site-related dominance it was impossible to rank directly birds which had different home intertidal areas. However, an indirect method of ranking such birds may be achieved by comparing the dominance domains of the different intertidal ´flocks´. The results tentatively suggest that the status of Scoughall birds was higher than birds from other intertidal areas. Not only did the Scoughall birds seem to dominate other birds on arguably the most suitable beaches for feeding but also both relative to the size of their own home intertidal area and relative to the size of dominance domains of other intertidal flocks, their dominance domains was the largest.

4.3.3 FACTORS AFFECTING RANK

In several animals which compete for resources and form dominance relationships, factors such as age, sex, size, familiarity with an area, health and family connections have been shown to be determinants of rank (Brown, 1975; Wilson, 1975; Gauthreaux, 1978; and references therein). Groves' (1978) work on turnstone suggests that adult turnstone are dominant over juveniles (also see section 4.3.1.2). The status of juvenile oystercatchers is also lower than that of adults (Goss-Custard et al, 1982b, 1984). On the other hand, juvenile semipalmated sandpipers Calidris pusilla dominated adults more than adults dominated juveniles, in interactions documented by Harrington & Groves (1977). Size may be an important determinant of success in interactions between juvenile grey plover Pluvialis squatarola: Townshend (1985) found that juveniles which did not establish territories at Teesmouth, N.E. England, and left the estuary, were on average smaller than juveniles which did establish territories. Puttick's (1981) study of non-breeding curlew sandpipers Calidris ferruginea in South Africa demonstrated more frequent intrasexual aggression in males. However, sex was not a useful predictor of success in interactions between captive dunlin (Bradley, 1982).

4.3.3.1 MORPHOLOGICAL CHARACTERISTICS

Due to strong influence of an adult's sex over its status I have tested for possible morphological correlates of status within sex classes. Three morphological characteristics were examined for their possible relationship with status: wing length, bill length and body weight. To control for annual and seasonal changes in body weight I considered only data collected from four relatively large catches (14 Nov. 1981, 27 Jan. 1982, 9 Feb. 1982, 27 Feb 1982) and each individual´s weight was treated as a deviation from the mean weight (to the nearest gram) of all individuals of the same sex for each catch. If a bird was weighed on more than one catch a mean deviation was used. Similarly, if a bird´s bill or wing was measured more than once, a mean length was used. I tested for possible morphological correlates of rank in two flocks, the Scoughall-Field Space flock (S-FS) and the Coastguard flock (CG). The rank orders for each flock were based on the results of dyadic agonistic interactions (Fig. 4.2, 4.3). Within sexes, there was no significant correlation between rank and bill length, wing length or body weight for either flock (Table 4.7). Therefore, there appears to be no effect of body size, i.e. wing length, body weight, or bill length on a bird´s status, at least when data from a mixture of age classes are analysed. High ranking birds were not necessarily the largest individuals.

4.3.3.2 AGE

In mixed flocks of adult and juveniles autumn migrant turnstone on the coast of Massachusetts, U.S.A. aggressive interactions occurred nonrandomly. Adult over juvenile interactions occurred more frequently than expected, juvenile over adult interactions were never seen, and interactions between birds of the same age class occurred less frequently than expected (Groves, 1978). Groves postulated that

TABLE 4.7

Spearman's rank correlation coefficients, r_s, resulting from tests of correlation between rank and biometrics of male and female turnstone. None of the correlations are significant.

SFS flock	Rank			
	Males	N	Females	N
Wing	-0.10	13	0.18	15
Bill	-0.14	13	0.17	15
Weight	0.38	15	0.38	14
CG flock				
Wing	0.33	11	0.05	8
Bill	-0.21	13	0.21	7
Weight	0.28	15	0.48	9

there were two possible explanations of these results: (a) adults were selectively aggressive towards juveniles or (b) due to their social inexperience juveniles misinterpreted or responded ambivalently to the behaviour of adults and thus became vulnerable to aggression from adults. Whilst Myers (1984) cited the results as evidence that adults were selectively aggressive towards juveniles, Groves herself favoured the ´socially inept´ hypothesis. In this section I describe how I extended the methods of Groves by examining interactions between adults and juveniles over a longer time period. From the ´socially inept´ hypothesis it follows that juveniles should learn, presumably reasonably rapidly, to respond correctly to the behaviour of adults so that the frequency of adult over juvenile interactions should decrease over the course of a winter. On the other hand, if adults are selectively aggressive towards juveniles then there should not necessarily be any reduction in the number of adult over juvenile interactions during a winter.

The numbers and ages of birds were used to provide information on the age composition of flocks in which interactions occurred. As in Groves´ study all interactions could be identified by type according to the ages of the participants and outcomes of interactions: adult over adult, adult over juvenile, juvenile over juvenile or juvenile over adult. Similarly, the model of Ridpath (1972) was used to calculate the expected frequencies of age-related interactions. Thus for a mixed adult and juvenile flock of any specified composition

p = number of adults/(number of adults + juveniles)
q = number of juveniles/(number of adults + juveniles)
and $p = q = 1$

Assuming random occurence of all types of agonistic interactions, $p^2 + 2pq + q^2 = 1$ predicted the expected frequencies of interactions where p^2 represented all adult over adult interactions, q^2 represented all juvenile over juvenile interactions, and 2pq represented all adult over juvenile and juvenile over adult interactions.

I analysed data from two winters, 1982-83 and 1983-84, and I divided each winter into three periods, August to October, November to January, and February to to April, to facilitate detection of any possible changes in the occurrence of types of interactions (Table 4.8). For each flock the observed frequencies of each type of interaction were compared to the expected frequencies, and the magnitude and direction of deviations were evaluated using the Wilcoxon matched pairs signed ranks test (Table 4.9). In all time periods significantly more adult over juvenile interactions were seen than expected and there were significantly fewer juvenile over adult interactions than expected. This confirms Groves´ finding that in mixed age flocks of turnstone aggressive interactions are nonrandom. However, the persistence of these differences over several months raises doubts about the validity of the ´socially inept´ hypothesis: juveniles may respond ambivalently to adults´ behaviour when they first arrive from the breeding grounds but I find it difficult to believe that they are still doing so some nine months later. Moreover there is some evidence that juveniles may actually try to avoid adults (Chapter 3). Implicit in Groves´ socially inept hypothesis is that her finding of lower than expected aggression within age classes is an indication, on one hand, that adults do not respond ambivalently to the postures of other adults and, on the

TABLE 4.8.

Mean numbers of adults and juveniles in flocks, and mean numbers of observed and expected interactions: adult over adult (A>A), adult over juvenile (A>J), juvenile over juvenile (J>J), juvenile over adult (J>A). N=number of flocks.

	Age composition of flock		Type of interaction								N
			A>A		A>J		J>J		J>A		
	A	J	O	E	O	E	O	E	O	E	
A	31.9	4.1	40.6	39.2	7.9	4.9	1.1	1.4	0.1	4.9	16
B	43.3	7.3	37.1	32.8	7.0	5.6	0.9	1.0	0.0	5.6	16
C	48.9	14.1	17.3	17.7	8.9	4.7	2.0	1.7	0.1	4.7	15
D	30.5	7.9	63.1	55.2	24.2	15.2	3.0	4.9	0.0	15.2	20
E	33.8	7.2	28.6	28.9	14.9	7.1	1.4	1.8	0.0	7.1	17
F	54.0	9.4	26.4	24.9	8.3	4.6	0.3	0.8	0.0	4.6	13

A=August-October 82
B=November 82-January 83
C=February-April 83

D=August-October 83
E=November 83-January 84
F=February-April 84

TABLE 4.9.

Summary of the results of Wilcoxon matched pairs signed ranks tests of the differences between the number of observed and expected interactions amongst adult and juvenile turnstone. Adult over adult (A>A), adult over juvenile (A>J), juvenile over juvenile (J>J), juvenile over adult (J>A). *p<0.05 **p<0.01; O>E=significantly more interactions observed than expected, O<E=significantly fewer interactions observed than expected; NS= no significant difference.

	Type of interaction			
	A>A	A>J	J>J	J>A
Aug-Oct 82	*O>E	**O>E	NS	**O<E
Nov 82-Jan 83	**O>E	*O>E	NS	**O<E
Feb-Apr 83	NS	**O>E	NS	**O<E
Aug-Oct 83	*O>E	**O>E	**O<E	**O<E
Nov 83-Jan 84	NS	**O>E	*O>E	**O<E
Feb-Apr 84	NS	**O>E	NS	**O<E

other hand, that juveniles have not learnt the social context in which aggression is relevant. Since, in contrast to Groves (1981), I found no evidence that juveniles were consistently less aggressive than expected towards other juveniles or that adults were less aggressive towards other adults, this is further evidence against the ´socially inept´ hypothesis. I believe that the differences between the findings of the two studies lie in differences between migrating and resident overwintering turnstone. It may be that on migration, being more likely to be surrounded by unfamiliar individuals, turnstone are less able to assess or remember the fighting ability of conspecifics of the same age class and so are less likely to risk possible fights (analogous to each bird being an away bird; see section 4.3.2).

My results appear to support the contention that adults are selectively aggressive towards juveniles, although, because I did not find a lower than expected number of adult over adult interactions, the evidence is less than convincing. Both the present study and Groves´ point to juveniles being subordinate to adults, so it is not surprising that adult over juvenile interactions were seen more frequently than expected.

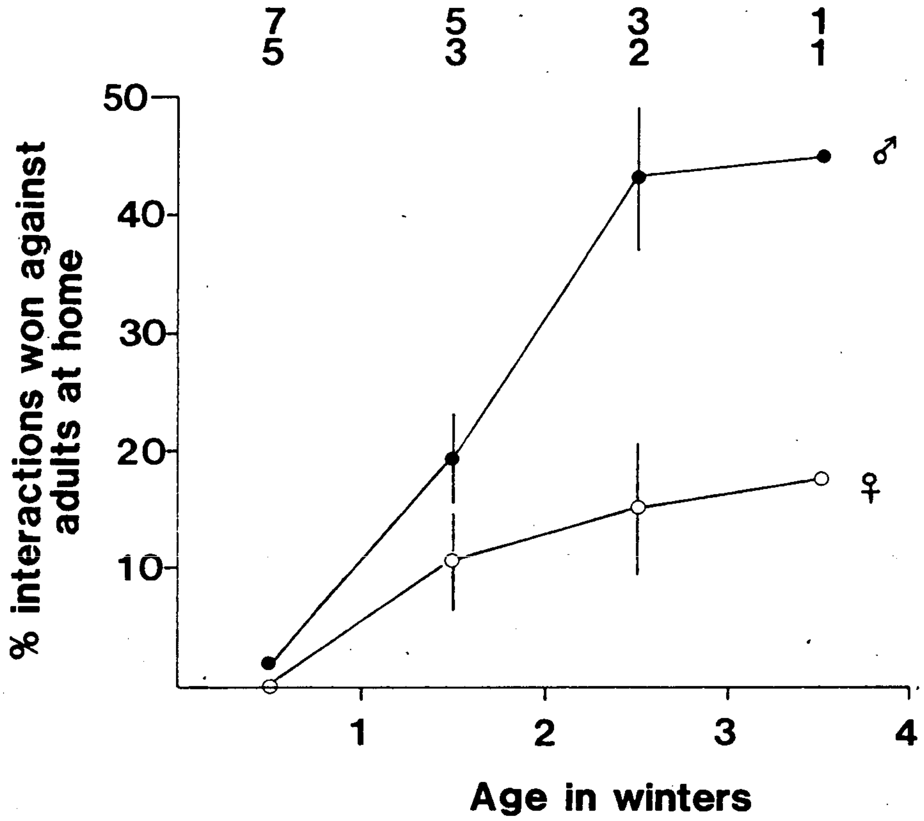
I very rarely saw any juveniles winning an interaction with an adult; even away adults beat home juveniles. Indeed, most of the interactions which away adults won were usually against familiar adults from the same intertidal area or against juveniles. Of 147 colour-ringed adult-juvenile dyads, in 145 (99%) the adult was dominant. Clearly, almost without exception, adults were dominant over juveniles.

I suggested earlier (section 4.3.1) that based on year-to-year changes in dyadic dominance, the rank of males increased in their second winter and further increased in their third winter, thereafter rising mainly as a result of higher ranking birds dying. The rank of females, in contrast to males, did not appear to increase to the same extent, unless higher ranking birds died. Due to small sample sizes the evidence was admittedly sketchy, although changes in birds' success in aggressive interactions over their first three winters did tend to confirm the postulated differences between the sexes and the increase in the rank of males within the first three winters of life (Fig. 4.7). It should be noted, however, that sample sizes were again small.

According to the proposed relationship between age and rank, it would be expected that the highest ranking birds were the oldest individuals, but without the benefit of a long-term study it was impossible to examine this directly. It was known, however, that the highest ranking CG bird (a female, YRM) was at least ten years old when she was killed by a sparrowhawk in January 1983: she was ringed on the study site as an adult in March 1974.

In sum, between birds from the same home intertidal area, the prime determinant of rank is whether a bird is an adult or juvenile: adults are dominant over juveniles. Within adults, males are usually dominant over females and, based on the available evidence, the within-sex rank and to a lesser extent, the between-sex rank, is possibly related to a bird's age: older birds are probably dominant over younger birds, particularly if they are of the same sex. However, this is not to say that age *per se* affects status: in long-lived birds such as the turnstone, past experiences of

Fig. 4.7 Mean (± S.D.) changes in the % of agonistic interactions won by individuals of known age. Each individual was treated as a datum. Figures above points show sample sizes.



7
5
5
3
3
2
1
1
50
40
30
20
10
% interactions won against adults at home
♂
♀
1
2
3
4
Age in winters

interactions with other individuals will contribute at least in part to the apparent effect of age on status. Site-related dominance and the increasing number of interactions won at home by young birds (Fig. 4.7) suggests that familiarity with an area also affects a turnstone´s status. Morphological characteristics, such as an individual´s size, do not appear to have significant effects on a bird´s rank, although the possibility that they are important can not be ruled out.

4.3.4 BENEFITS OF HIGH STATUS

In general most authors agree that high rank implies priority of access to resources (e.g. Brown, 1975; Kaufmann, 1983; Gauthreaux, 1978; Wilson, 1975). In wintering birds the resource which is most critical in affecting survival is probably food (Lack, 1966) although sites/positions reducing risk of predation (e.g. Moore, 1972) are probably important also. Priority of access to these resources probably increases the chances of winter survival and several authors have stressed the importance of rank-related access to resources in increasing the survival and factors assured to affect fitness (e.g. food intake) of high ranking birds (e.g. Baker & Fox, 1978; Ekman & Askenmo, 1984; Fretwell, 1969). Unfortunately most avian studies of the possible benefits of high rank have been conducted in the laboratory or on wild birds at feeders or bait. However, field studies of oystercatchers on the Exe estuary, S.W. England by Goss-Custard and his co-workers provide evidence that high rank probably increases intake rate and possibly survival (reviewed by Goss-Custard, 1985). One line of evidence is that intake rate of low ranking birds eating mussels Mytilus edulis is depressed at high bird densities whereas it is not in the highest ranking birds (Ens & Goss-Custard, 1984). A component of this interference which affectd low ranking birds appeared to be food theft: at high bird densities low rankers lost more mussels to high rankers. Goss-Custard *et al*, (1982b) found that the most aggressive oystercatchers increased their intake rate through stealing mussels and by suffering food theft least. Increased opportunities for high rankers to steal mussels from lower ranking birds at high bird densities may therefore have been a factor underlying observed individual differences in susceptibility to interference (Ens & Goss-Custard, 1984).

In this section I examine possible benefits of high rank in wintering turnstone. Using the data collected from strandline flocks I began by testing (a) whether interference was distributed unequally according to rank, (b) whether aggression, in the form of a supplant, increased the intake rate of the supplanter and decreased that of the supplantee.

4.3.4.1 INTERFERENCE AND FEEDING SUCCESS IN STRANDLINE FLOCKS

Interference is defined as the reversible and more-or-less immediate decrease in intake rate due to an increase in the density of conspecifics (Goss-Custard, 1980). Field studies of interference in waders have been reviewed by Goss-Custard (1980, 1984). In Chapter 6 I investigate the occurrence of interference in birds using different feeding techniques, but in this chapter I address the problem of whether interference was distributed unequally among turnstone surface pecking for Coelopa (seaweed fly) larvae in beds of strandline tide wrack.

To test whether the distribution of interference was associated with rank I monitored the intake rate of turnstone at different bird densities. In the 1982-83 winter observations were taken at or near high tide from flocks of turnstone feeding on <u>Coelopa</u> larvae in beds of rotting seaweed washed up on the strandline at three sites: Tower Cove, CB Cove and Dump Beach. Intake rate was calculated using one of two methods: (1) running commentaries of focal birds' feeding actions were recorded on tape and analysed later using the Keybehaviour and Keytime computer packages (Deag, 1983a, b). Intake rate was calculated from the Keytime analysis as the rate of swallows (number of swallows made by focal bird in a minute) (see section 4.2). (2) Noting the number of swallows a focal bird made in one minute, timed by a remote timer which emitted rapid bleeps at the end of the derived time period.

Prior to each recording session the colour-ring combination of the focal bird was noted. Bird density was measured by counting the number of turnstone within 15m of the focal bird. The frequency distribution of intake rate and turnstone density were both skewed towards low values so the data were transformed to natural logarithms in the analysis.

Low sample sizes make it difficult to test for interference, particularly if there is a high variance in intake rate at a given bird density, as in the present study (Ens & Goss-Custard, 1984). Therefore, rather than testing for possible differences between individuals, I have combined data for individuals and looked for differences between two sets of individuals of different rank. One set of individuals (YWNG, YLOW, YNOL, YBGO) were Car Rocks birds, whilst the other (YWOB, YNNG, YNLG, YWGN) were Scoughall birds. Due to site-dependent rank it was known (section 4.3.2) that at Tower Cove and CB Cove the Car Rocks birds were high ranking (at home) whilst at Dump Beach they were low ranking (away from home) and, conversely, the Scoughall birds were high ranking at Dump Beach (at home) but low ranking at Tower Cove and CB Cove (away from home).

At Tower Cove and CB cove the intake rates of the Scoughall birds were significantly reduced at high bird densities but the intake rate of the Car Rocks Birds were not (Fig. 4.8). In contrast, at Dump Beach the intake rates of the Car Rocks birds were significantly reduced at high bird densities, but the intake rates of the Scoughall birds were not (Fig. 4.9). The results demonstrate, therefore, that when each set of birds was at home, and therefore high ranking, they were not subject to interference but when away from home, and therefore low ranking, they were subject to interference. It is likely that controlling for the effects of prey densities would not radically alter the results since observations were very often taken when both sets of birds were feeding in the same flock.

Since dominance between sets of birds was site-dependent each set of birds could be both low and high ranking, and this suggests that the differences in susceptibility to interference was due to rank itself and not some intervening variable such as experience. Moreover, whilst it is feasible that familiarity with an area *per se* could contribute to differences in intake rates, tide wrack beds, and, therefore availability of *Coelopa* larvae, could change rapidly due to wave action, so it is unlikely that greater familiarity with an area afforded home birds with any significant advantage over away.

Fig. 4.8 Intake rate plotted as a function of turnstone density for Scoughall and Car Rocks birds feeding at Tower Cove or CB Cove. Scoughall birds away from home, Car Rocks birds at home. *$p<0.05$. Intake rate of Scoughall birds was significantly reduced at high flock densities. Scoughall: YWOB, YNNG, YNLG, YWGN. Car Rocks: YWNG, YLOW, YNOL, YBGO.

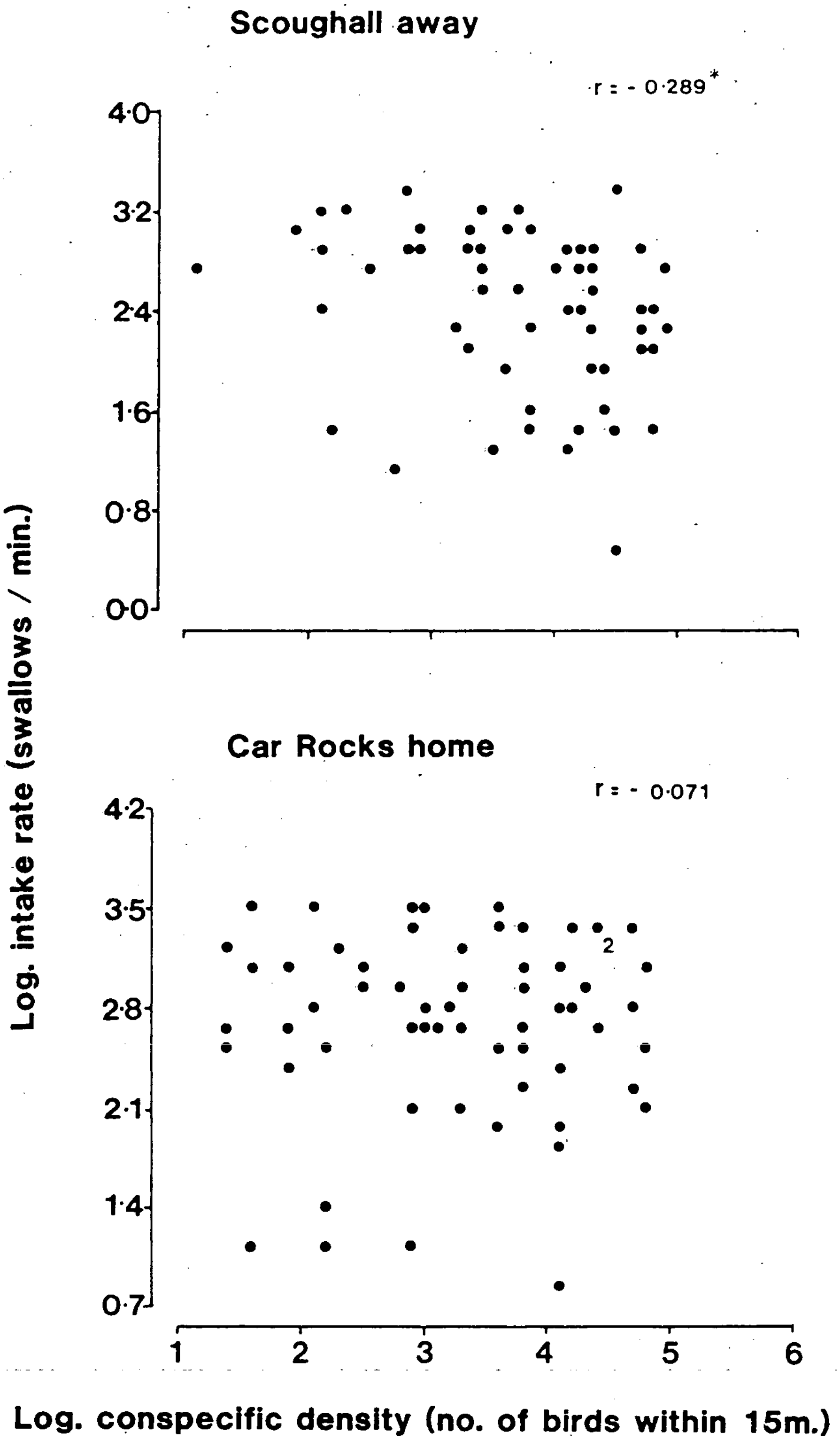
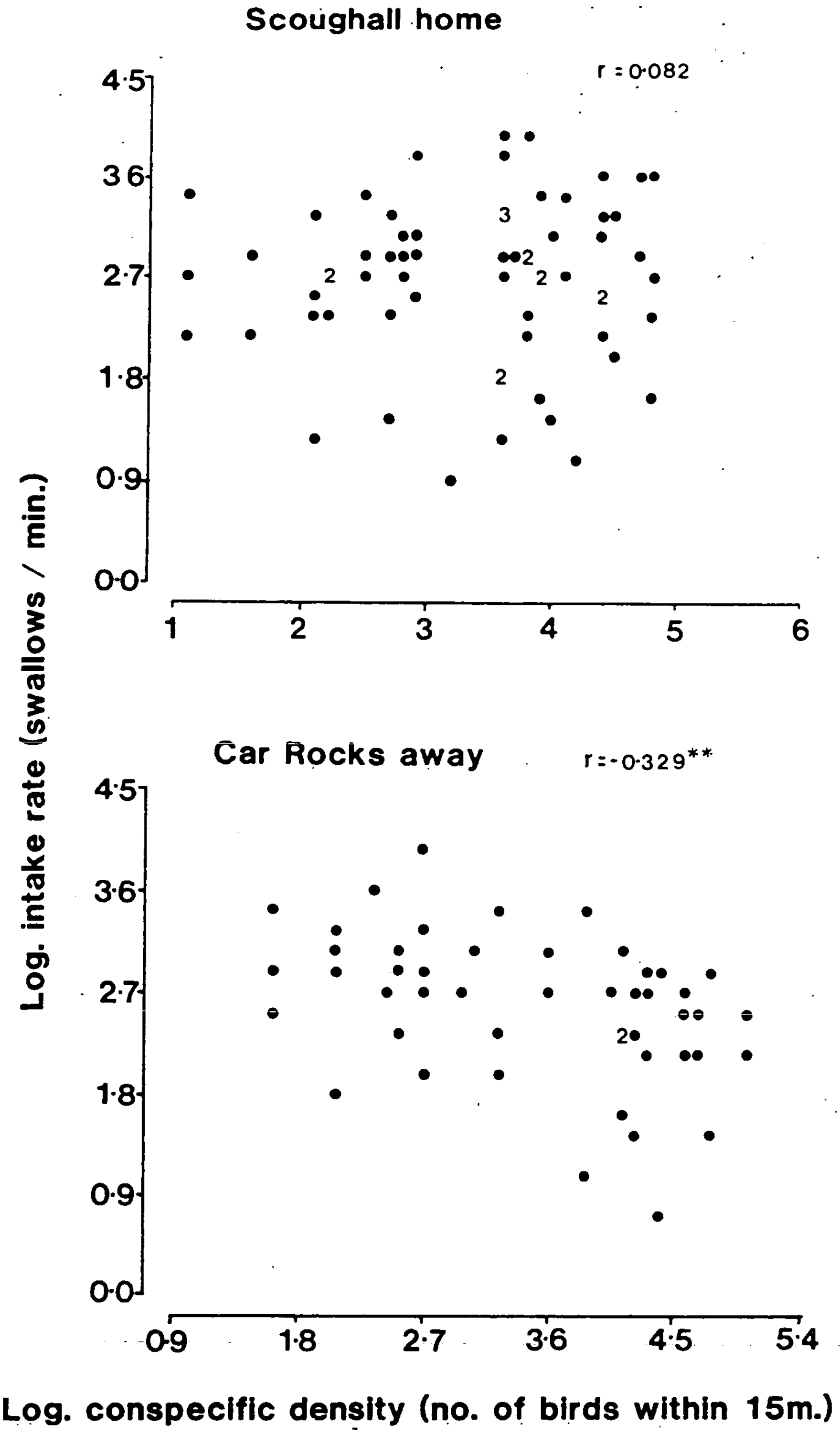

Scoughall away
r = - 0·289*
4·0
3·2
2·4
1·6
0·8
0·0
Car Rocks home
r = - 0·071
4·2
3·5
2·8
2·1
1·4
0·7
2
1
2
3
4
5
6
Log. intake rate (swallows / min.)
Log. conspecific density (no. of birds within 15m.)

Fig. 4.9 Intake rate plotted as a function of turnstone density for Scoughall and Car Rocks birds feeding at Dump Beach. Scoughall birds at home, Car Rocks birds away from home. $**p<0.01$. Intake rate of Car Rocks birds was significantly reduced at high flock densities.


Scoughall home

Car Rocks away

birds. Even if such an advantage did exist I can see no reason why it should only become apparent at high bird densities.

As I will show later (section 4.4.2) when turnstone were feeding on Coelopa in tide wrack, per capita aggression rates increased with increasing bird density, and since the vast majority of aggression involved supplants over feeding sites (section 4.3.1) this implicates an increased loss of feeding sites to high ranking birds at high bird densities as a major component of interference in low ranking birds. To test if supplants did affect birds' intake rates I employed the results of the Keytime analysis of running commentaries.

I selected commentaries which contained only one 'supplant' or 'supplanted' behaviour; 'supplant' meaning that the focal bird had supplanted another bird, 'supplanted' meaning that the focal bird had been supplanted by another bird. From the point in the commentary where the supplant occurred I counted the number of feeding actions (in this case 'pecks') and number of swallows which occurred in a time period (minimum length = 15s) before and after the supplant/supplanted. The exact length of the time period was determined by the position of the supplant in the commentary: if the supplant occurred nearer to the end of the commentary the time period was taken from the supplant to the end of the commentary, if it occurred nearer the start of the commentary the time period was taken from the start of the commentary to the supplant For example, consider a 3min. commentary where the focal bird was supplanted 30s before the end. In this case I would count the number of swallows and feeding actions made in the 30s before and after the focal bird was supplanted. The number of feeding behaviours occurring before and after a supplant were compared using the Wilcoxon matched pairs signed ranks test.

The results showed that supplanting another bird significantly increased the number of swallows (T=3.5, N=21, p<0.01), the number of pecks (T=45, N=20, p<0.05) and the frequency of successful pecks (swallows/pecks, T=24, N=19, p<0.01) of the focal bird. Conversely, being supplanted by another bird significantly reduced the number of swallows (T=0, N=19, p<0.01), the number of pecks (T=3, N=21, p<0.001) and the frequency of successful pecks (swallows/pecks, T=8, N=20, p<0.01) of the focal bird (Table 4.10).

These results suggest that interference occurred because birds lost feeding sites to higher ranking birds, as supplant rates increased at high bird densities (section 4.4.2). Another mechanism of interference was possibly low ranking birds avoiding high ranking birds: low ~~rankking~~ ranking birds tended to be found on the periphery of of flocks where prey denisty may have been lower and turnstone vigilance higher (section 4.3.4.3). I do not think that interference was caused by the presence of conspecifics reducing prey availability (Goss-Custard, 1970, 1980). If this mechanism occurred then all birds would probably have been affected equally and, moreover, the effect of turnstone activity on prey availability was probably negligible in comparison with the effects of wave action.

4.3.4.2 BREEDING SUCCESS

In brent geese Branta bernicla it seems that pairs which experience high feeding success during the spring pre-migratory period in Holland tend to have increased breeding success in the

TABLE 4.10.

Median values of number of swallows and number of pecks made by turnstone in a median time period (a) before and after being supplanted by another turnstone, (b) before and after supplanting another turnstone whilst feeding on <u>Coelopa</u> larvae.

(a) Supplanted by another bird

Time period used in comparison(s)	No. of swallows		No.of pecks	
	before	after	before	after
22	5	2	17	9

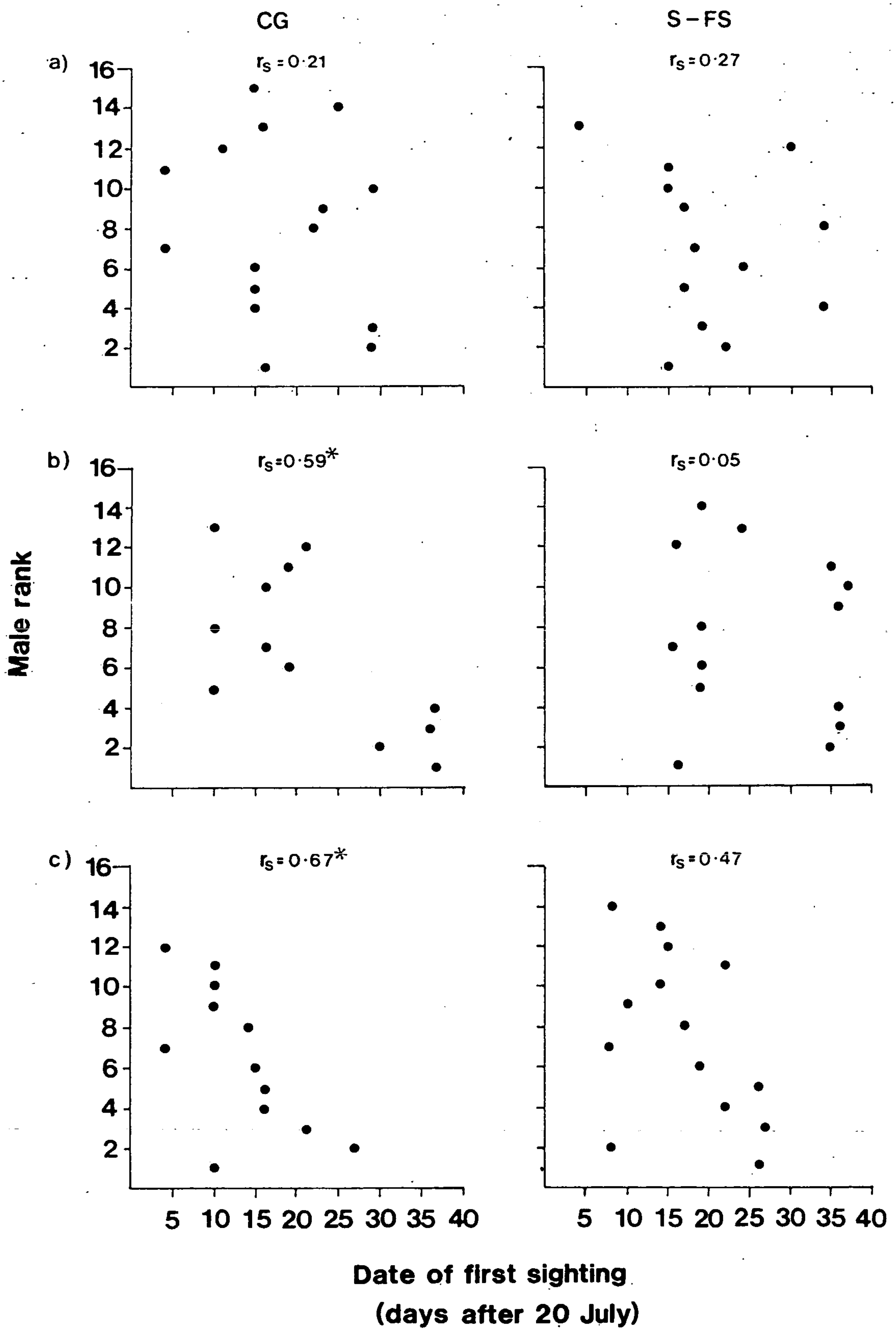
(b) Supplant another bird

Time period used in comparison(s)	No. of swallows		No. of pecks	
	before	after	before	after
27	3	6	13	19

following breeding season in the arctic, as measured by the number of young returning to Holland with the parents in the autumn (Ebbinge *et al*, 1982). It has been suggested that in non-breeding waders the fat reserves put on during the pre-migratory period may be devoted in part to reproduction, rather than being used solely as fuel for migration to the breeding grounds (e.g. Davidson, 1981). Increased feeding success in spring, reflected by greater fat reserves, may lead to increased breeding success. High rank in turnstone allows priority of access to food and feeding sites and leads to at least short-term benefits in feeding success (previous section and Chapter 6), so it is possible that high rank also has cross-seasonal reproductive benefits by enhancing the rate or extent of pre-migratory fat deposition. High non-breeding rank may also be indicative of high breeding rank, which may enable high ranking birds to procure the best breeding territories (Whitfield, in press: Appendix 2). Arctic breeding waders do not migrate or overwinter as family parties, and post-nuptial migration of parents and young is usually staggered making it less likely that pairs and/or siblings winter together (Chapter 2). It is not possible, therefore, directly to measure breeding success by counting the number of young associated with parents after breeding. In several waders, however, breeding success may be reflected by the timing of individuals' return to wintering or moulting grounds since failed breeders leave the breeding area before successful breeders (Chapter 2). If only one sex cares for the young, differences in the timing of return should be follows: if wintering status affects breeding success then all other things being equal, high ranking males should return from the breeding grounds later than low ranking males. I tested this prediction using sightings of males of known rank as they returned to the study site in late July and August 1982-84 (Chapter 2). I analysed data from two intertidal flocks, the Scoughall-Field Space flock (S-FS) and the Coastguard flock C(C) and if high ranking males returned later then there should have been a positive correlation between actual rank and rank predicted by the date of return (= date of first sighting in autumn).

The results are equivocal in their support for the prediction of the cross-seasonal hypothesis (Fig. 4.10). Of the six tests (2 flocks x 3 years) in only two was there a significant correlation between actual rank order and predicted rank order (assuming high ranking males returned later), although for the S-FS males in 1984 the correlation was almost significant. There are probably several factors apart from breeding success which influence the return date of males (Chapter 2) and these will act as confounding variables in the present analysis. Moreover, any correlation between actual and predicted rank may mean that high ranking males breed later, or at higher latitudes, rather than having higher breeding success. A long-term study tracking timing of return as the rank of males increased with age should be able to test this possibility. Nevertheless, the dominance domains of the two sets of males (section 4.3.2) suggested indirectly that S-FS males were possibly of higher status than CG males, so it is interesting to note that S-FS males tended to arrive slightly later than CG males in all three years (Fig. 4.10). Certainly the data do not contradict the cross-seasonal hypothesis, although to avoid difficulties in interpretation more detailed information, such as the timing of breeding of individual males, is needed before a more critical evaluation of the hypothesis

Fig. 4.10 Date of first sighting of a male´s return from the breeding grounds in (a) 1982, (b) 1983, (c) 1984, in relation to its rank, for Coastguard (CG) and Scoughall-Field Space (S-FS) birds. Spearman´s rank correlation coefficients, r_s, reflect the strength of association between the two rank orders, assuming early return confers high rank. $*p<0.05$


CG
S - FS
a)
rs = 0·21
rs = 0·27
b)
rs = 0·59*
rs = 0·05
c)
rs = 0·67*
rs = 0·47
Male rank
16
14
12
10
8
6
4
2
5 10 15 20 25 30 35 40
5 10 15 20 25 30 35 40
Date of first sighting
(days after 20 July)

can be made. Such information will obviously be difficult to obtain in any long-distance migratory wader.

4.3.4.3 SURVIVAL

Several authors have postulated that birds of higher status have higher survival (e.g. Baker & Fox, 1978; Kikkawa, 1980), although field studies demonstrating a relationship between status and survival are rare (but see Ekman & Askenmo, 1984). In this section I test whether high rank conferred any advantages or not.

The mortality of turnstone was monitored both directly, by searching for corpses, and indirectly, by noting disappearances of colour-ringed individuals (Chapter 2). Juvenile turnstone at the study site had lower wintering survival than adults (Chapter 2). Whilst this may have been a result of their being subordinate to adults (Whitfield, 1985: Appendix 1), it may also have been a result of their lower foraging experience which incurred reduced intake rates (Chapter 6). For the purposes of the present analysis, therefore, I have excluded juveniles.

Mortality of adults of known rank was examined in four groups of birds each delineated by common occupancy of intertidal areas (Chapter 3): Car Rocks (CR), Field Space (FS), Scoughall (S), and Coastguard (CG). Known mortality (i.e. corpses found) represented deaths in winter, whilst probable mortality (i.e. disappearances) represented year-round deaths, and all deaths between August 1982 and August 1984 were used in the analysis. The ranks of birds were derived from agonistic hierarchies (FS, S, CG) or from the % of interactions won (CR), calculated from interactions collected over the relevant period.

The results suggest that high ranking birds did not experience lower mortality than low ranking birds (Table 4.11). In CG turnstone more high ranking than low ranking birds appeared to die, but the opposite was true in S turnstone. In both CR and FS birds there was little difference in the mean rank of those birds which died and those birds which survived. It must be remembered that high ranking birds were probably the oldest individuals (section 4.3.3.2), and that the deaths of high ranking birds was possibly more a result of their age rather than their status; indeed it could even be argued that high status reduced the chances of older birds dying. It is difficult to disentangle the effects of status and age, but assuming that high ranking males were probably of similar age to high ranking females but were usually dominant over them, then high ranking females should experience higher mortality if high status increased survival independent of age. This did not appear to be the case, and females in general did not experience higher mortality than males (Chapter 2).

Site-dependent rank made it impossible directly to compare the status of birds from different intertidal areas. As I argued earlier, however, based on the length of shoreline on which birds from an intertidal area were dominant over birds from other areas i.e. each groups of birds' 'dominance domain', S birds appeared to have the highest status. It is worth noting, therefore, that S birds also experienced the lowest mortality (table 4.12). Great caution must be taken in interpreting this result beacuse S birds were also the least itinerant individuals and it is possible that this may have caused the observed mortality differences. Certainly the evidence

TABLE 4.11.

Mortality and survival of adult turnstone of known rank from four intertidal home range areas on the study site between August 1982 and August 1984, estimated by searching for corpses (D=direct) or by disappearance of birds (I=indirect).

Intertidal 'flock'	No. of ranked birds	Mean rank of birds which died D	(N)	I	(N)	Mean rank of birds which survived D	(N)	I	(N)
Coastguard	28	8.7	(3)	12.0	(7)	15.6	(25)	15.9	(21)
Scoughall	18	-	(0)	18.0	(1)	-	(0)	8.5	(17)
Field Space	15	7.5	(2)	9.0	(3)	8.2	(13)	7.8	(12)
Car Rocks	39	17.8	(4)	18.7	(6)	20.3	(35)	20.2	(33)

TABLE 4.12.

% Mortality of adult turnstone between August 1982 and August 1984 from four intertidal home range areas. Direct mortality estimated from discovery of corpses, indirect mortality estimated from disappearances of birds.

Intertidal 'flock'	N	% Mortality Direct (winter)	Indirect (winter)	Indirect (whole year)
Coastguard	28	11	18	25
Scoughall	18	0	6	6
Field Space	15	13	13	20
Car Rocks	51	14	18	25

for the itinerancy effect is greater than the status effect (Chapter 3). Perhaps the most plausible explanation of the results is that the high status of S birds allowed them to occupy the most favourable area on the study site in terms of food predictability (Chapter 3) and this increased their survival: the strong site fidelity being an indication of the high quality of feeding sites inside their home range. I will return to this possibility later.

To conclude, within birds from the same intertidal area there was no evidence that status affected survival. However, based on the dominance domains and mortality of birds from different intertidal areas it was possible that high status increased survival, although concomitant differences in itinerancy may have acted as an intervening variable.

4.4 FACTORS AFFECTING AGGRESSION

Myers (1984), in his excellent review of social behaviour of wintering waders, pointed out that although a relatively large body of literature has been published on aggression in waders there have been very few advances in our understanding of its ecological bases. Most agonistic interactions between turnstone are aggressive (sensu Deag, 1977, p.466) since they involve attack or threat of attack (section 4.3.1; Marshall, 1981) and in this part of the thesis I attempt to identify some of the factors influencing the expression of aggression.

4.4.1 SEASONAL EFFECTS

In a study of turnstone at Scoughall, Marshall (1981) found that per capita rates of aggressive interactions were highest in August and September but were low from October to January before rising again from February to April. Marshall postulated that the increased aggression rates were due to the presence of 'aggressive migrants'. Marshall's rationale was based on two assumptions: (1) that the population at Scoughall was composed of largely resident birds with mutually recognised status so rates of aggression were low in mid-winter. (2) Migrants passed through Scoughall in August and September and again in February to April: the presence of these aggressive individuals increased the rates of aggressive intractions during the autumn and spring migratory periods. The first assumption was derived from several studies (e.g. Summers _et al_, 1975) which indicated that turnstone showed remarkable site fidelity in comparison with several other waders, and also from Marshall's own observations of a captive flock of turnstone which formed stable dyadic agonistic relationships. The second assumption was presumably based on observations of the timing of migration at other sites, as no data from Scoughall were presented.

Unfortunately, Marshall did not control for confounding variables such as prey density, prey distribution or prey type, and so there are several possible explanations for seasonal changes in rates of aggression.

Using data collected from the same study site some nine or ten years after Marshall's study I re-examined the possible seasonal changes in rates of aggression in wintering turnstone. To conform to Marshall's methods I have only included observations recorded within two hours of high tide. I employed three 'aggression indices': (1) %

interactions involving physical contact, (2) % interactions involving unprovoked attacks, (3) per capita rates of aggression in roosting birds.

Seasonal changes in all three aggression indices were similar (Fig. 4.11, 4.12). Aggression was highest in August, then dropped until October, and thereafter it tended to remain at comparatively low levels for the rest of the winter (Fig. 4.13). Whereas each index revealed that rates of aggressive interactions were highest in August and September, there was no consistent evidence for any rise in the level of aggression in February through April. The most convincing data for the proposed seasonal changes were those collected from roosting birds (Fig. 4.12), because seasonal differences in the nature of the prey can obviously be excluded, and the changes in aggression were not reflected by changes in density of roosting birds (Fig. 4.14).

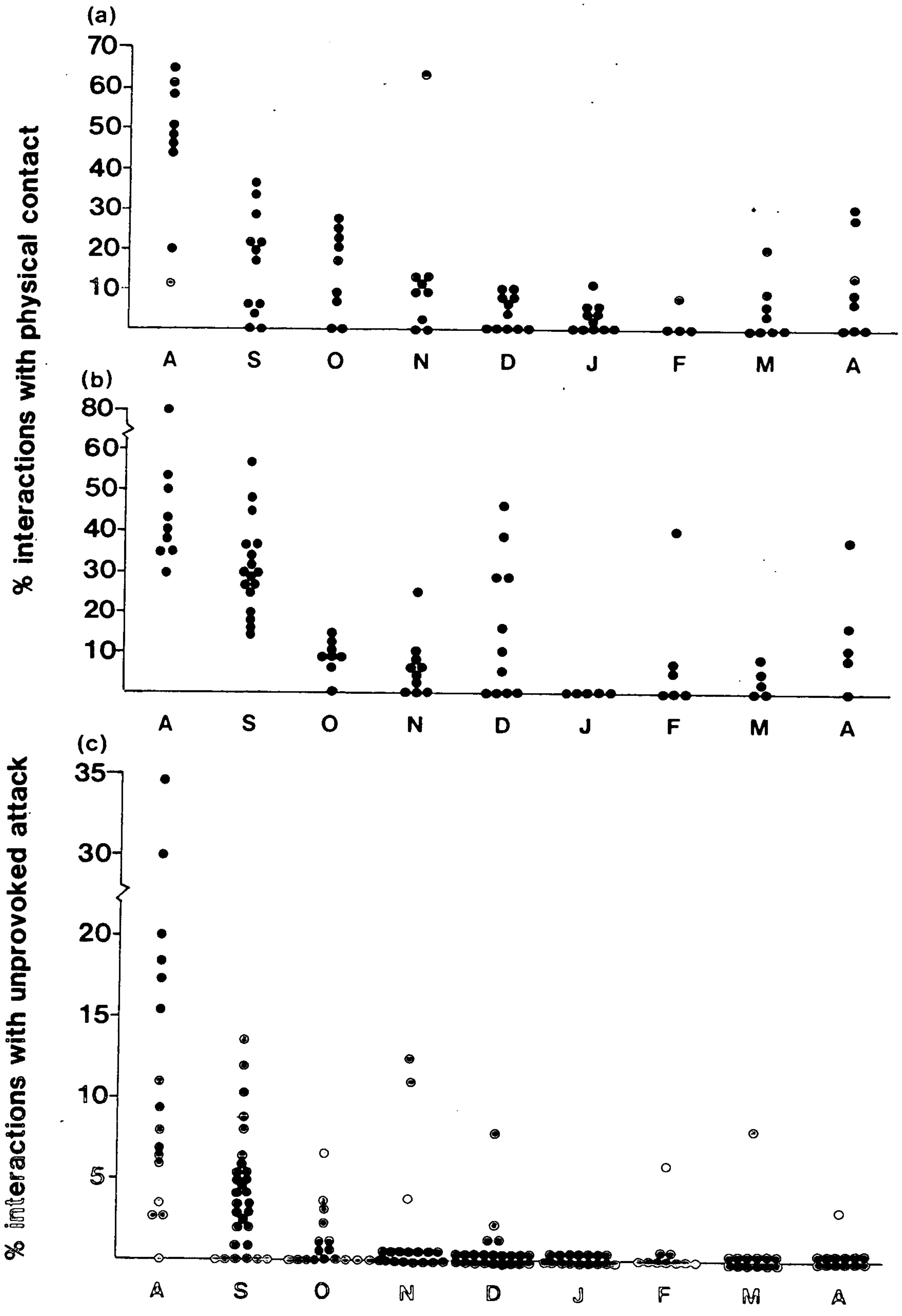
There remains several possible hypotheses for the observed seasonal differences in aggression.

(1) The high levels of aggression in August and September is due to the presence of ´aggressive migrants´; on departure of the migrants levels of aggression subsequently drop.

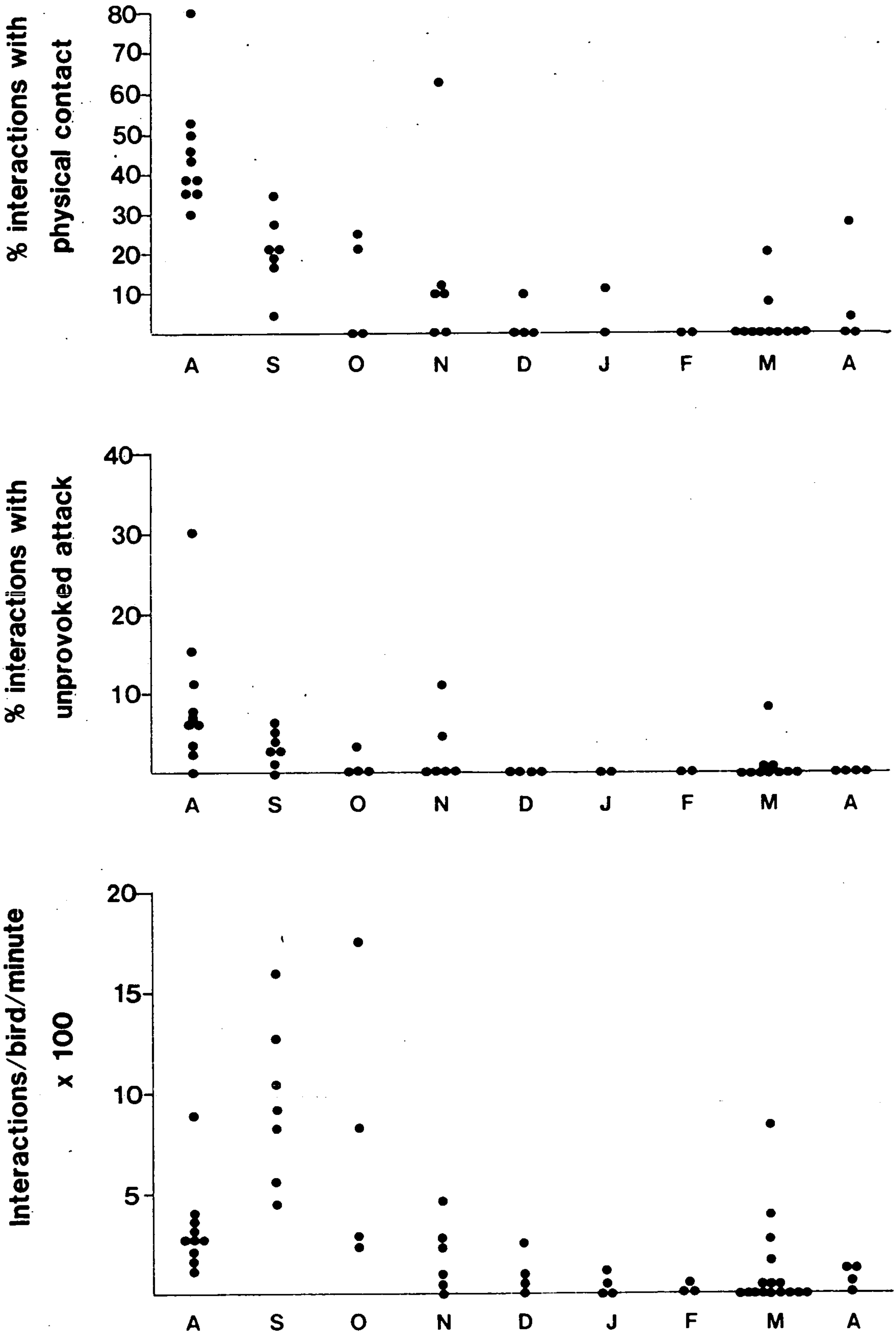
(2) Migrants represent a competitive threat to residents and are consequently attacked by residents during their stay on the study site (see also the ´xenophobia principle´ Wilson, 1975).

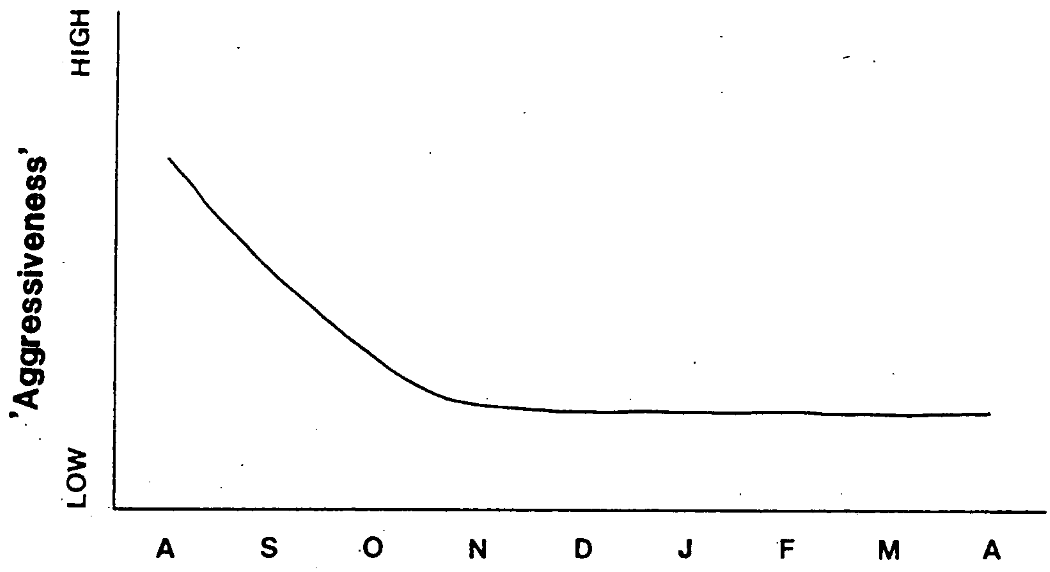
(3) The high autumn peak in aggression is due to residents attempting to (re-) assert their dominance, mainly over other resident individuals who they probably have not been in contact with for several months. When the rank of birds is more clearly recognised in later months, then the level of aggression drops. It is virtually

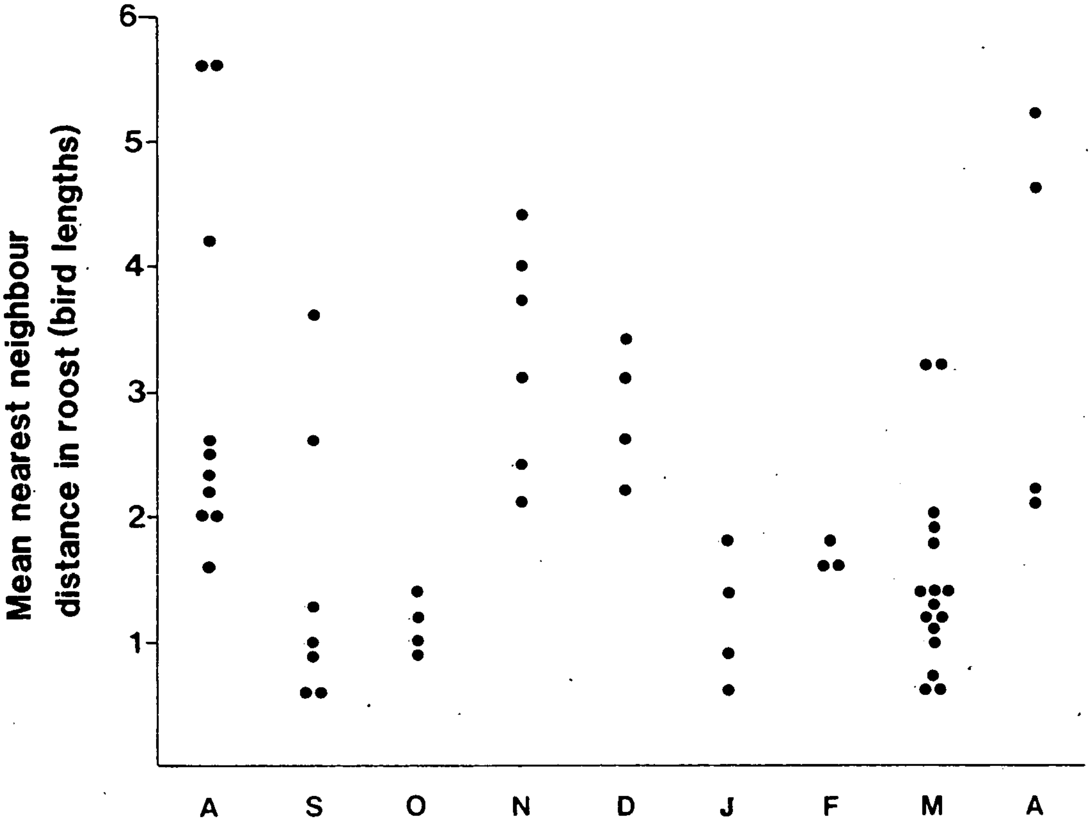
All microhabitats



Roosting birds only




'Aggressiveness'
HIGH
LOW
A
S
O
N
D
J
F
M
A


Mean nearest neighbour distance in roost (bird lengths)
6
5
4
3
2
1
A
S
O
N
D
J
F
M
A

axiomatic in captive studies of social behaviour that when individuals are first introduced to each other the resultant high levels of aggression are caused by individuals vying for or establishing rank (e.g. Bernstein & Mason, 1963; Gauthreaux, 1978). Hypothesis 3 is an extension of this ´rank ´assertion´ axiom into the field.

(4) As an after-effect of the preceding breeding season, individuals´ testosterone levels are highest in August and September, therefore non-breeding aggression is highest at this time.

(5) In autumn individuals need to spend less time feeding (Baker, 1978, 1981; Marshall, 1981) and so can devote more time to other activities such as aggression.

Hypotheses 1,2 and 3 each makes a testable prediction concerning the distribution of agonistic interactions in mixed flocks of resident and migrant individuals.

´Aggressive migrants´ hypothesis (hypothesis 1). Prediction: there should be a high frequency of migrant over resident interactions and of migrant over migrant interactions.

´Xenophobic residents´ hypothesis (hypothesis 2). Prediction: there should be a high frequency of resident over migrant interactions.

´Rank assertion´ hypothesis (hypothesis 3). Prediction: there should be a high frequency of resident over resident interactions. To test these predictions I examined the distribution of interactions in mixed migrant-resident flocks in August.

The proportion of colour-ringed individuals in the largely resident wintering study population was around 75-80% (Chapter 2). Thus although not perfectly accurate, the number of colour-ringed birds in a flock in August provided a rough measure of the number of residents in that flock. In flocks observed in August I identified all interactions both by type, according to whether the participants were colour-ringed (= resident, C) or unringed (=migrant, U), and by the outcomes of the interactions: C over C, C over U, U over U, U over C. The expected frequencies of all types of interactions were calculated from an adapted version of Ridpath's (1972) model (section 4.3.3.2). For a flock of any specified composition of C and U,

c = number of C/(number of C + U)
u = number of U%(number of U + C)
and c + u = 1.

Assuming random occurrence of all types of aggressive interactions, $c^2 + 2cu + u^2 = 1$ predicted the expected frequencies of interactions where c^2 represented all C over C interactions, u^2 represented all U over U interactions and 2cu represented all C over U and U over C interactions.

For each of the flocks the observed frequencies of each type of aggressive interactions were compared to the expected frequencies, and the significance of the magnitude and direction of deviations were evaluated by a Wilcoxon matched pairs signed ranks test (Table 4.13). In flocks containing migrants the observed frequency of U over U interactions was significantly higher than expected, but the number of U over C interactions was significantly less than expectd: these results do not confirm the prediction of the 'aggressive migrants' hypothesis (1), which can therefore be rejected. There was no difference between the observed and expected number of C over U interactions so the 'xenophobic residents' hypothesis (2) can be rejected. C over C interactions occurred significantly more often

TABLE 4.13.

Summary of the flock composition and the distribution of interactions within flocks and between colour-ringed (all resident birds) and unringed birds (mainly migrants) in August 1982, 1983. **p< 0.01, O>E=observed number of interactions greater than expected; O<E=observed number of interactions less than expected. NS=not significant. N=number of flocks.

Mean flock composition		Type of interaction								
		CR>CR		CR>U		U>U		U>CR		N
CR	U	O	E	O	E	O	E	O	E	
18.5	19.1	22.6	12.1	9.5	10.3	7.1	11.8	5.9	10.3	17
		**O>E		NS		**O<E		**O<E		

than expected, however, thereby conforming to the prediction of the 'rank assertion' hypothesis (3). This result was not due to my unwittingly paying more attention to colour-ringed birds, as data gathered from flocks later in the winter, when migrants were not present, revealed no differences between the observed and expected frequency of any type of interaction involving colour-ringed and unringed birds (Table 4.14).

The rank assertion hypothesis is also supported by the observation that a comparatively large proportion of interactions in August and September involved one bird attacking another for no apparent reason ('unprovoked attacks'). Unprovoked attacks frequently involved one bird persistently attacking and chasing another particular individual, who was often close in rank to the aggressor. In August 1982, for example, the highest ranked Coastguard bird, YRM, frequently initiated attacks against YWNW, who was ranked number 3, particularly if YWNW himself had recently initiated an interaction against another individual.

Interestingly, in another wader which seems to form stable dominance relationships, the oystercatcher, a so-called 'piping display' appears to be used to assert dominance (Ens & Goss-Custard, in press). At Scoughall and Tyninghame it was obvious that piping displays occurred most frequently when the oystercatchers returned from breeding in August (pers. obs.).

I do not believe that the high levels of turnstone aggression in August and September were due to a simple hormone effect (hypothesis 4). Johns (1964) has shown that the development of breeding or non-breeding plumage in red-necked phalaropes <u>Phalaropus lobatus</u> is dependent on testosterone levels: a high level leads to

TABLE 4.14.

Summary of the flock composition and the distribution of interactions within flocks between colour-ringed and unringed resident birds between September and April 1982-84. NS=not significant.

Mean flock composition		Type of interaction								
		CR>CR		CR>U		U>U		U>CR		N
		O	E	O	E	O	E	O	E	
CR	U									
37.2	9.2	28.2	27.6	6.8	7.3	3.2	2.3	7.3	7.3	18
		NS		NS		NS		NS		

the expression of breeding plumage, a low level leads to the expression of winter plumage. Turnstone moult both in August to October and March to May (e.g. Cramp & Simmons, 1983): in autumn, non-breeding plumage is acquired, in spring breeding plumage is acquired. This suggests that testosterone levels are higher in spring than in autumn, yet aggression was highest in autumn.

I also do not believe that turnstone were more aggressive in autumn simply because they devoted less time to feeding during this period. As in most other waders (e.g. Goss-Custard et al, 1977) turnstone at Scoughall spend less time feeding in both spring and autumn compared with mid-winter (Baker,1981; Marshall, 1981; Whitfield, unpubl. data) yet aggression levels would be expected to mirror these changes if hypothesis (5) was correct: the data suggests they did not.

My results confirm Marshall's observations of a high autumn peak in aggression, but I found little, if any, evidence for a second smaller peak in spring. Close scrutiny of Marshall's data reveals his own evidence for a second peak as being less than convincing, and may have been due to turnstone feeding on sandhoppers (Talitrus sp.) at this time of year. Digging in the sand for this prey was associated with high rates of agonistic interactions (section 4.4.3). Nevertheless, I would agree with Marshall's suggestion that the lower mid-winter rates of aggression are probably due to mutually-respected and stable dyadic dominance relationships.

4.4.2 DENSITY OF CONSPECIFICS

An increase in the rate of aggressive interactions with increasing density of conspecifics has been observed in several species of waders: oystercatchers (Vines, 1980), knot Calidris canutus (Goss-Custard, 1977a; Burger et al, 1979), pectoral sandpiper Calidris melanotos (Hamilton, 1959), sanderling Calidris alba (Silliman et al, 1977), semipalmated sandpiper Calidris pusilla (Recher & Recher, 1969a) and short-billed dowitcher Limnodromus griseus (Burger et al, 1979). On the other hand, Puttick (1981) found that increased curlew sanpiper Calidris ferruginea density was associated with decreased frequencies of aggressive interactions. The work of Burger et al (1979) also tends to suggest that the relationship between aggression and wader density is not as simple as it would first appear. They found that the same wader density did not always result in the same frequency of aggression in different habitats and at different times. Furthermore, a common assumption is that aggression controls spacing (e.g. Burger et al, 1979) but this assumption may not be true. On the whole the available evidence tends to favour avoidance as the major mechanism influencing spacing (e.g. Goss-Custard, 1980; Myers, 1984; Vines, 1980). In this section I investigate the possibility that conspecific density and rates of agonistic interactions in turnstone were correlated, with the aim of shedding some light on the function of aggression in this species.

From August 1982 to April 1984 interactions were recorded from feeding flocks on beaches within two hours of high tide. Flocks were judged to be feeding in one of the following habitats: sand (S), tide edge wrack and sand (TEWS), tide edge wrack (TEW), and wrack (TW) if over 75% of constituent members were so feeding. Flock density was measured as the mean nearest neighbour distance in bird-lengths, and measured before a timed session when I noted the number of interactions and flock size.

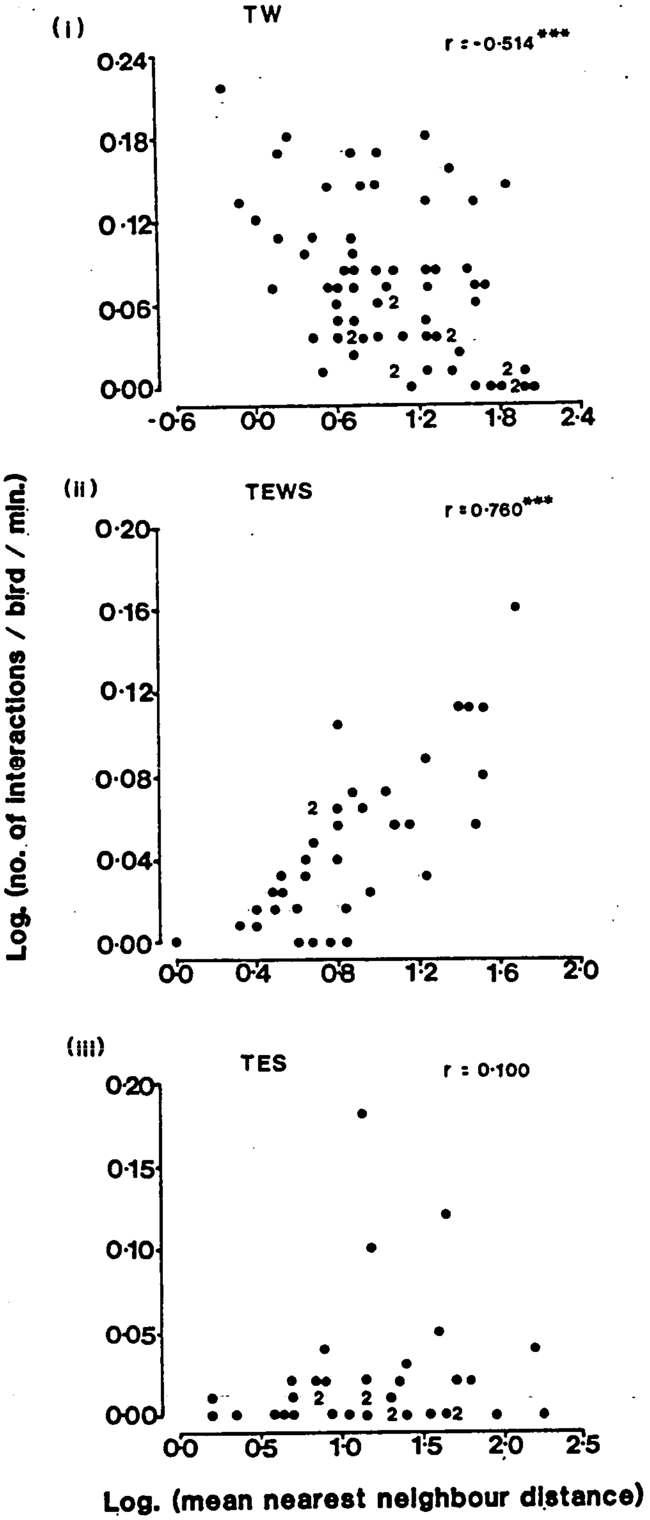
All data were log transformed as the frequencies of both flock density and per capita rates of aggressive interactions showed skewed distributions. Within flocks individuals often moved very rapidly, between TEW and TW, often making it difficult to decide which microhabitat the ´flock´ was feeding in, so I have combined the two data sets into one, labelled tide wrack (TW). Sufficient data were collected in two other microhabitats, TES and TEWS, so for all three microhabitats I reduced the data sets to include only those observation of birds feeding on <u>Coelopa</u> larvae and pupae.

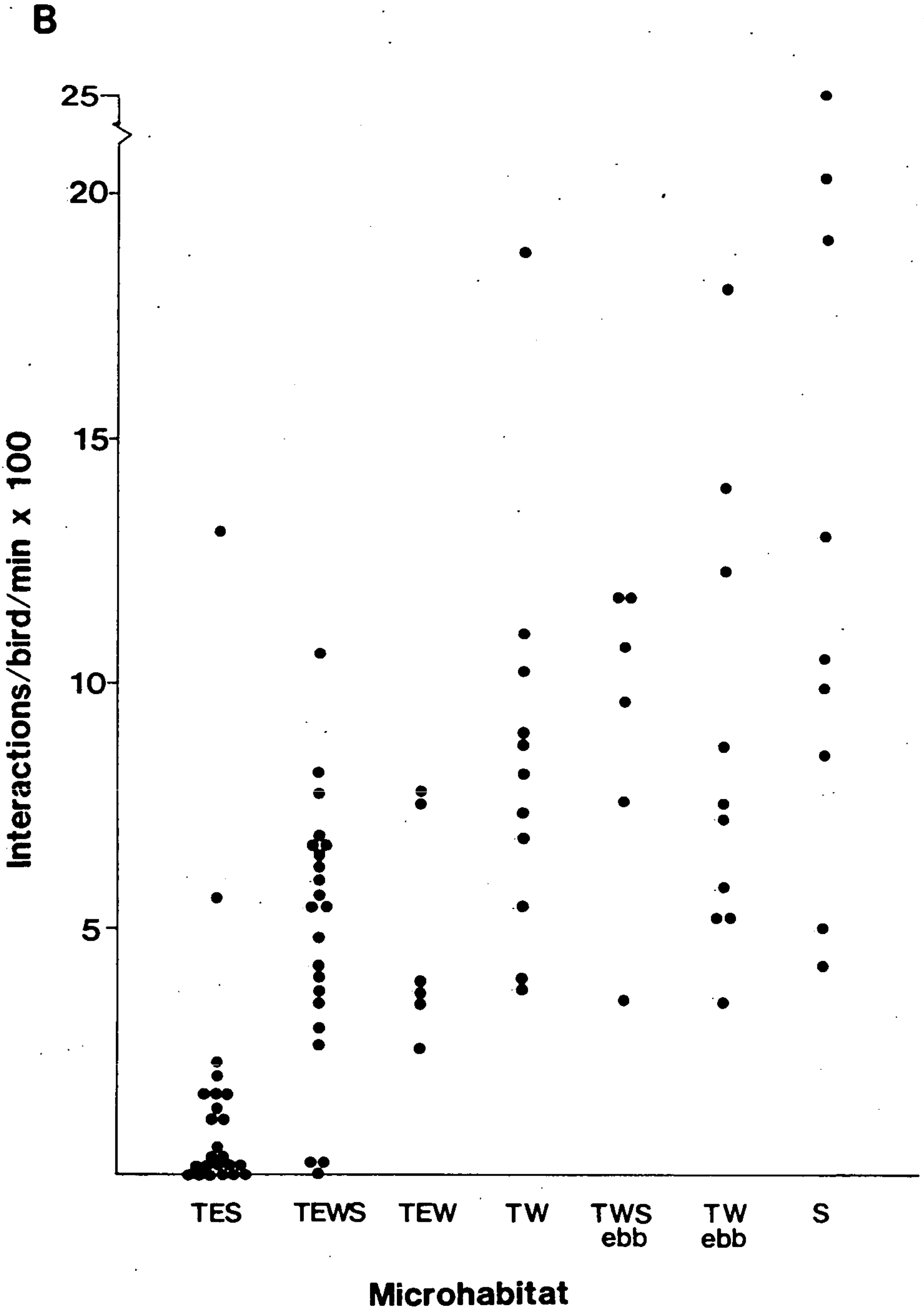
There was a significant negative correlation between mean nearest neighbour distance and per capita rate of aggression for turnstone feeding in TW. In contrast, there was a significant positive correlation between nearest neighbour distance and rates of aggression in flocks feeding in TWS. There was no significant correlation in flocks feeding in TES (Fig 4.15). Thus, in only one of the three microhabitats (TW) was there a positive relationship between density of conspecifics and rate of aggressive interactions. Instead, in one (TEWS) the opposite relationship was found.

The results do not appear to support the contention that an increased density of conspecifics should lead to an increased rate of aggression. In addition, they do not suggest that the primary function of aggression is to maintain individual distance. This interpretation is also tentatively confirmed by the low number of interactions between feeding birds, in all microhabitats, which were over individual distance: the large majority were over feeding sites

Fig. 4.15a Per capita rates of aggression as a function of conspecific density in birds feeding in (i) tide wrack, (ii) tide edge wrack and sand, and (iii) tide edge sand. r is the correlation coefficient, ***p<0.001.

A


(i)
TW
r = -0·514***
0·24
0·18
0·12
0·06
0·00
-0·6
0·0
0·6
1·2
1·8
2·4
2
(ii)
TEWS
r = 0·760***
0·20
0·16
0·12
0·08
0·04
0·00
0·0
0·4
0·8
1·2
1·6
2·0
(iii)
TES
r = 0·100
0·20
0·15
0·10
0·05
0·00
0·0
0·5
1·0
1·5
2·0
2·5
Log. (no. of interactions / bird / min.)
Log. (mean nearest neighbour distance)


B
25
20
15
10
5
Interactions/bird/min x 100
TES
TEWS
TEW
TW
TWS ebb
TW ebb
S
Microhabitat

(section 4.3.1). It is likely that another variable(s), other than flock density, was proximately responsible for the expression of aggression. The nature of prey is often cited as influencing rates of aggression (reviewed in Myers, 1984), and the differences in the aggressive response to conspecifics in different microhabitats may be due to concomitant differences in the nature of the prey (other than the prey type): this possibility is explored in the next section.

4.4.3 PREY DISTRIBUTION

According to Recher & Recher (1969a) rates of aggression in waders should increase with the patchiness of prey distribution. Mallory & Schneider (1979) found that when short-billed dowitchers were feeding on the patchily distributed egg masses of horseshoe crabs Limulus polyphemus, aggression rates were higher than when they were feeding on other, more evenly distributed prey, such as amphipod crustaceans or polychaete worms. As pointed out by Myers (1984), however, the authors did not control for other differences in prey characteristics, although their interpretation certainly appears to be the most likely explanation.

I have shown earlier that more aggressive interactions in feeding turnstone were of birds supplanting other individuals from feeding sites, or of birds preventing themselves being supplanted from feeding sites (section 4.3.1). This is perhaps an indication that most aggression occurred when the prey was distributed in such a manner which rendered supplants (=aggression) a profitable course of action. In this section, therefore, I investigate the notion that aggression between individual turnstone was related to the distribution of the prey they were feeding on. Specifically, I test the prediction that rates of aggression should increase with the patchiness of prey distribution.

I tested the prediction in two ways. First, by relating differences in prey density and distribution in three microhabitats, TEWS, TES, TW, to differences in aggression rates. Secondly, by performing an experiment using captive birds.

Characteristics of prey in TEWS, TES, and TW. I used the methods described in the previous section to assess rates of aggression in the three microhabitats. I sampled prey in the three microhabitats on several occasions throughout the 1982-83 winter; during each session I sampled from each microhabitat consecutively and, if possible, from neighbouring areas of the beach.

The sampling unit was a plastic ring cut from a household washing-up bowl with an area of $0.066m^2$, and within each microhabitat I took 10 samples at 1m intervals on a short transect along the tide edge. Within the area encompassed by the sampling unit I noted the number of Coelopa larvae and pupae; prey were counted rather than collected because I wished to carry out the sampling as quickly as possible and the action of incoming waves often made it difficult to collect the prey. Since I was interested only in Coelopa, I sampled TES in areas of sand seaward of tidewrack beds and/or in areas where I had seen turnstone feeding on Coelopa on the previous day. To quantify the patchiness of the Coelopa distribution during each sampling period I used Mallory & and Schneider´s (1979) coefficient of dispersion, s^2/x, where if x is the number of prey per sample and n is the number of samples, $x = \Sigma x/n$ and $s^2=(\Sigma x^2-(\Sigma x)^2/n)/(n-1)$. Unless stated otherwise, tests were Wilcoxon matched pairs signed ranks tests.

The coefficient of dispersion of Coelopa was significantly greater in TEWS and TW than in TES (TEWS v. TES $p<0.05$; TW v. TES $p<0.05$), but there was no difference in Coelopa dispersion in TW and TEWS ($p>0.05$). Coelopa density in TW was significantly greater than in both TEWS and TES (TW v. TEWS $p<0.05$, TW v. TES $p<0.05$), but there was no difference between TEWS and TES ($p>0.05$) (Table 4.15).

Rates of aggression were significantly higher in TEWS compared with TES (Mann Whitney U test, $p<0.0001$), and although flock density was higher in TEWS (Mann Whitney U test, $p=0.0012$) at a given flock density, rates of aggression were higher in TEWS than in TES ($N=17$, $z=3.527$, $p<0.0001$). Moreover, rates of aggression were higher at a given flock density in TW than in either TEWS (Wilcoxon test, $p<0.001$) or in TES (Wilcoxon test, $p<0.0001$).

The differences in the aggressiveness of birds feeding in TES compared with TEWS appears to be due to the greater clumping of the prey in TEWS, although the aggression differences associated with TW and TEWS appear to be due to the higher prey density in TW. Overall, however, the effect of prey distribution does appear to be most important.

Experiment using captive birds. In this experiment I assessed the effect of patchily distributed prey vs. evenly distributed prey on rates of aggression in a captive flock of 13 turnstone, held in the southern half of the Zoology Dept. roof aviary (see Chapter 1; Marshall, 1981).

The experiment consisted of 10 pairwise tests, each test consisting of an 'even' regime and a 'patchy' regime. In the even regime I sacttered evenly 45 prey items (half mealworms) within an

TABLE 4.15.

Median coefficients of dispersion (C.O.D.) and median density (D) of Coelopa larvae in the microhabitats TEWS, TES and TW. Number of sampling sessions=12; 10 $0.066m^2$ samples per microhabitat per session.

	C.O.D.	D
TEWS	3.03	1.7
TES	1.10	1.9
TW	3.85	8.7

area of 4x4m; in the patchy regime I placed 9 clusters of 5 prey items (half mealworms) at one metre intersections within the 4x4m area. In each test I changed the position of the clusters to avoid any effects of birds learning the future position of clusters. Two examples of cluster arrangements are depicted in Fig. 4.16. The experiment was conducted between 7-21 Jan 1984, and each regime was tested at about 10.00 (GMT) in the morning before the birds were given their standard daily food mix. In each test even and patchy regimes were conducted on consecutive mornings. After placing the prey items in position I retired from the aviary and in the following 10 min. I noted the number of aggressive interactions which occurred and kept a note of how many birds were feeding.

There were significantly higher per capita rates of aggression in the patchy regimes compared with the even regimes (sign test, $p<0.002$) (Table 4.16). This indicates that at a given prey density if the prey was patchily distributed, rates of aggression in turnstone were higher than if the prey were evenly distributed.

4.5 GENERAL DISCUSSION

It is now reasonably well established that flocking may reduce the risk of predation (for general reviews see Bertram, 1978; Pulliam & Millikan, 1982; for a review on wader flocks see Myers, 1984). Several lines of evidence, however, indicate there appears to be differential predation risk in different parts of a flock. Tinbergen (1951) and Wynne-Edwards (1962) both cite numerous examples where individuals on the edges of flocks were taken more often by predators. Yellow-eyed juncos Junco phaeonotus spent more time with

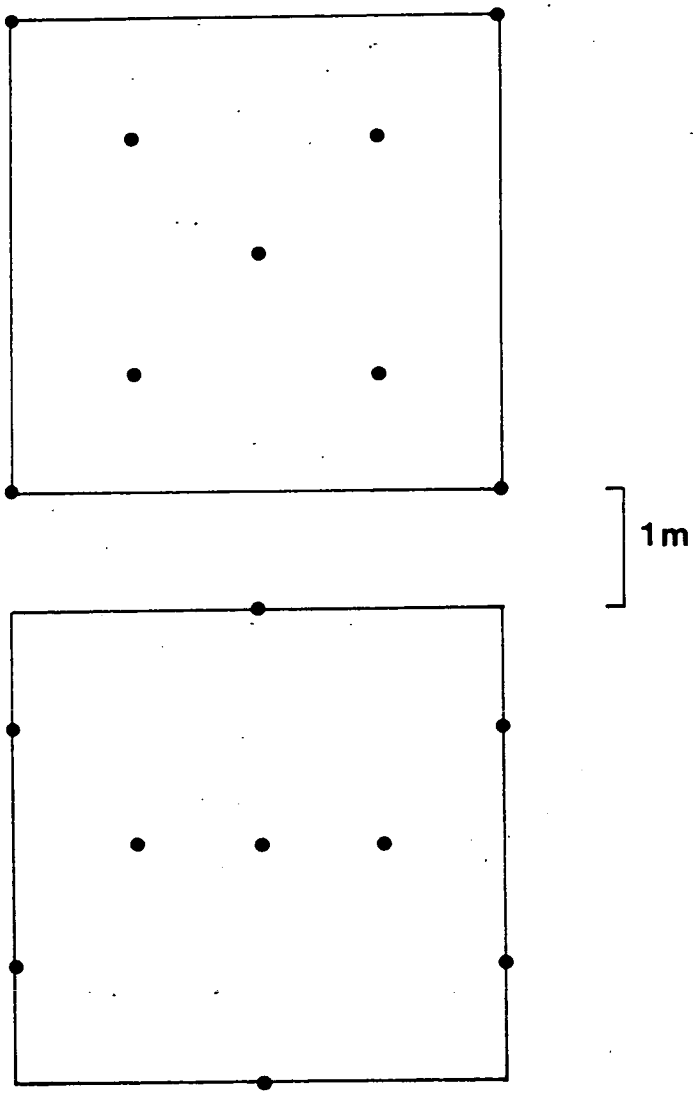

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TABLE 4.16

Mean number of aggressive interactions per turnstone in a 10 minute experimental period showing the effect of clumped and even prey distribution on aggression.

Mean number Aggressive interactions/bird	
Even	Clump
0.62	1.42

N=10; Sign test, $p<0.002$

their heads raised after a trained Harris' hawk Parabuteo unicinctus was flown overhead (Caraco et al, 1980) and other workers have noticed that in several species flock members increased vigilance after exposure to potential predators (e.g. Hegner, 1985). These observations demonstrate that birds increase their vigilance levels as the immediate risk of predation increases, so if peripheral flock members are more at risk it might be expected that they are more vigilant than central flock members: studies of starlings Sturnus vulgaris (Jennings & Evans, 1980) and brent geese (Inglis & Lazarus, 1981) suggest this is the case. Moreover, Hamilton (1971) has argued persuasively on theoretical grounds that peripheral flock members are more likely to be captured by a predator, since if a predator appears at a random point in space, peripheral individuals are more likely to be closest to it than are interior individuals. Hamilton predicted that in the presence of a predator individuals should attempt to move towards the interior of a flock, thereby causing the flock to contract in size but numerous workers have reported observations which are not consistent with this prediction (e.g. Pulliam & Millikan, 1982; Myers, 1984).

The position of a bird within a flock and therefore its likelihood of being eaten by a predator may in some cases be mediated by its status. For example, in both Mexican juncos Junco phaeonotus palliatus (Moore, 1972) and black-capped chickadees Parus atricapillus (Glase, 1974) peripheral flock members tended to be low ranking. Similarly, subordinate red-winged blackbirds Agelaius phoeniceus occupied the more peripheral positions in roosts, suggesting to Weatherhead & Hoysak (1984) that they were more prone to predation. The authors also postulated that the periphery of roosts were microclimatically inferior, so subordinates may have incurred higher metabolic costs. On this latter point, Swingland (1977) found that subordinate rooks Corvus frugilegus were apparently forced by dominants into microclimatically unfavourable roosting positions when environmental conditions became more severe (see also Yom-Tov, 1979).

When small passerines are attacked by avian predators their escape response is to fly into cover (e.g. Gaddis, 1980; Ficken & Wilkin, 1977; Morse, 1973): the importance of cover in avoiding predators is confirmed by observations showing that vigilance levels increase with increasing distance from cover (Barnard, 1980; Caraco et al, 1982; Grubb & Greenwald, 1982). By feeding nearer to cover (e.g. Grubb & Greenwald, 1982). By feeding nearer to cover (e.g. Schneider, 1984) high ranking individuals may reduce the risk of being captured by an avian predator.

Other possible examples of rank related habitat distribution have also been recorded (e.g. Fretwell, 1969; Monaghan, 1980) and implicated in the lower survival of low status birds (e.g. Baker & Fox, 1981; Ekman & Askenmo, 1984). Status may have important distributional effects at all geographical levels if, as suggested, social dominants tend to occupy more of the favourable habitats (e.g. Gauthreaux, 1978, 1982; Ketterson & Nolan, 1983; Sutherland & Parker, 1985).

Most studies of social status in winter flocks assume that high ranking birds have the highest food intake rates. Unfortunately, surprisingly little direct field evidence has been documented which actually demonstrates that this is the case. Although high status has been shown to increase intake rate or weight gain in captive birds (e.g. Baker et al, 1981; Kikkawa, 1980; Hegner, 1985), these observations may not be applicable in the field, and data may be confounded by researchers' artificially supplying food (e.g. Rowher & Ewald, 1981). Some of the best field evidence for the effect of status on intake rate has been reported for oystercatchers.

In oystercatchers on the Exe estuary low ranking birds had lower intake rates than high ranking birds when feeding on the most preferred mussel beds, where aggressive encounters occurred frequently (Ens & Goss-Custard, 1984; Goss-Custard et al, 1984). Low ranking birds, by avoiding (Vines, 1980) or being driven by high ranking birds (Goss-Custard et al, 1984), feed more in less preferred mussel beds and in other habitats, such as mudflats (Goss-Custard et al, 1981b, 1982c). Intake rate on mudflats is lower than on mussel beds (Goss-Custard & Durrell, 1983), but intake rate on a less preferred mussel bed was greater than on a more preferred bed for all but the most aggressive birds (Goss-Custard et al, 1984). At high bird densities aggression is frequent and the intake rate of low ranking birds is depressed, but that of high ranking birds is not (Goss-Custard & Durrell, 1984; Ens & Goss-Custard, 1984). It should be noted, however, that low ranking are also possibly less experienced or less skilled foragers which confounds the relationship between intake rate and social status (Goss-Custard et al, 1984). Similarly, young oystercatchers suffer heavier mortality than adults (Dare, 1977; Goss-Custard et al, 1982a) but the connection between mortality and status, rather than inexperience, has yet to be determined. Swennen (1984) has studied several oystercatcher roosts in the Wadden Sea, Holland, and found that birds in the larger roosts were larger and heavier than those in smaller roosts. These differences were reflected by differences in mortality, and Swennen suggested that a contributory factor to the higher mortality of birds in smaller roosts was the poorer feeding areas which were available to them. The roosts, and their associated feeding grounds, were close enough together to suggest that competition, rather than an inability to find better feeding areas, prevented birds from the smaller roosts using the best feeding areas. Therefore, as in the studies of Goss-Custard and his co-workers, the implication was that the birds in smaller roosts and therefore using poorer feeding areas were of low status. Interestingly, Swennen´s results suggest that females oystercatchers tend to be higher ranking than males as more females were found in the larger roosts. Unfortunately, other studies of the effects of status on intake rate and survival are virtually non-existant.

On a Californian estuary Kus <u>et al</u> (1984) found that a female Merlin ate more juvenile dunlin than was expected from the age-composition of the population. Kus´ study (cited by Myers, 1984) further suggested that within a flock, juveniles were located more peripherally than adults and that peripheral individuals were more susceptible to predation. Shanewise & Herman (1979) also discovered that in dunlin flocks juveniles were in positions of greater predation risk. On the basis of age-related differences in habitat distribution in the Dutch Wadden Sea, van der Have <u>et al</u> (1984) suggested that adult dunlin are socially dominant over juveniles, so it is possible that the position of individuals within flocks, and consequently their likelihood of dying, is determined by their status. The work of Bradley (1982), however, shows that captive dunlin do not form stable dominant/subordinate relationships. If such stability is lacking in the field (Rowell, 1974) Bradley´s study demonstrates that the results of past interactions may be of little use in predicting the direction of future interactions, at least between adults. It may be that juveniles do consistently lose interactions to adults: unfortunately no study has addressed this question.

Bradley´s work on dunlin and Myers´ (1983) on sanderling suggest that in at least two wintering waders predictable dominance relationships do not exist. I suspect this may be true in several other waders, particularly calidrine sandpipers. For example, wintering knot Calidris canutus are typically found in large flocks (up to several hundred individuals) and their dispersion when feeding is similar to dunlin (e.g. Goss-Custard, 1970; Cramp & Simmons, 1983) although knot appear to be more itinerant than dunlin (e.g. Evans, 1981). The work of Symonds et al (1984) on the Firth of Forth suggests that knot flocks are highly mobile and comparatively unstable and in such large flocks persistent individual associations may be difficult to maintain for long periods (although see Harrington & Leddy, 1982 for possible short-term associations). Individual associations do not persist within dunlin flocks (Shanewise & Herman, 1979) which also suggests they do not exist in knot, given the similarity in the two species´ flocking behaviour. Dominance is defined by the predictability in the direction of dyadic interactions (e.g. Bernstein, 1981) and implies underlying social stability, which most of the available evidence suggests does not exist in knot.

The possible lack of stable dominance relationships in some waders suggests great caution must be exercised when making assumptions regarding dominance and aggression. For example, when Myers (1981b) tested the hypothesis that dominance affects the latitudinal segregation of the sexes in several migratory waders he assumed that females were dominant over males in three calidrine sandpipers with reversed sexual dimorphism; the least sandpiper _Calidris minutilla_, the western sandpiper _C. mauri_ and the sanderling. This assumption was based on the observation that breeding female spotted sandpipers _Actitis macularisa_ and northern jacanas _Jacana spinosa_ are dominant over males, and both species show reversed sexual dimorphism. The mating system of these two species, resource polyandry, is radically different to those of the three _Calidris_ spp., and female spotted sandpipers and jacanas are probably far more aggressive because they defend territories whereas the _Calidris_ spp. do not (e.g. Oring, 1982; Pitelka _et al_, 1974). I have shown that female turnstone are not dominant over males, despite their larger size, and Bradley (1982) found that captive female dunlin, which show comparatively close affinities to Myers' _Calidris_ spp., do not consistently win interactions against males and aggressive rank could not be predicted on the basis of sex. Myers' assumption that in waders the larger sex is socially dominant does not appear to be true in every species, and this obviously has a major effect on his conclusion that the latitudinal distribution of the sexes was not consistent with a social dominance hypothesis. Bradley's results suggest that the concept of dominance may not even be relevant in some wintering waders.

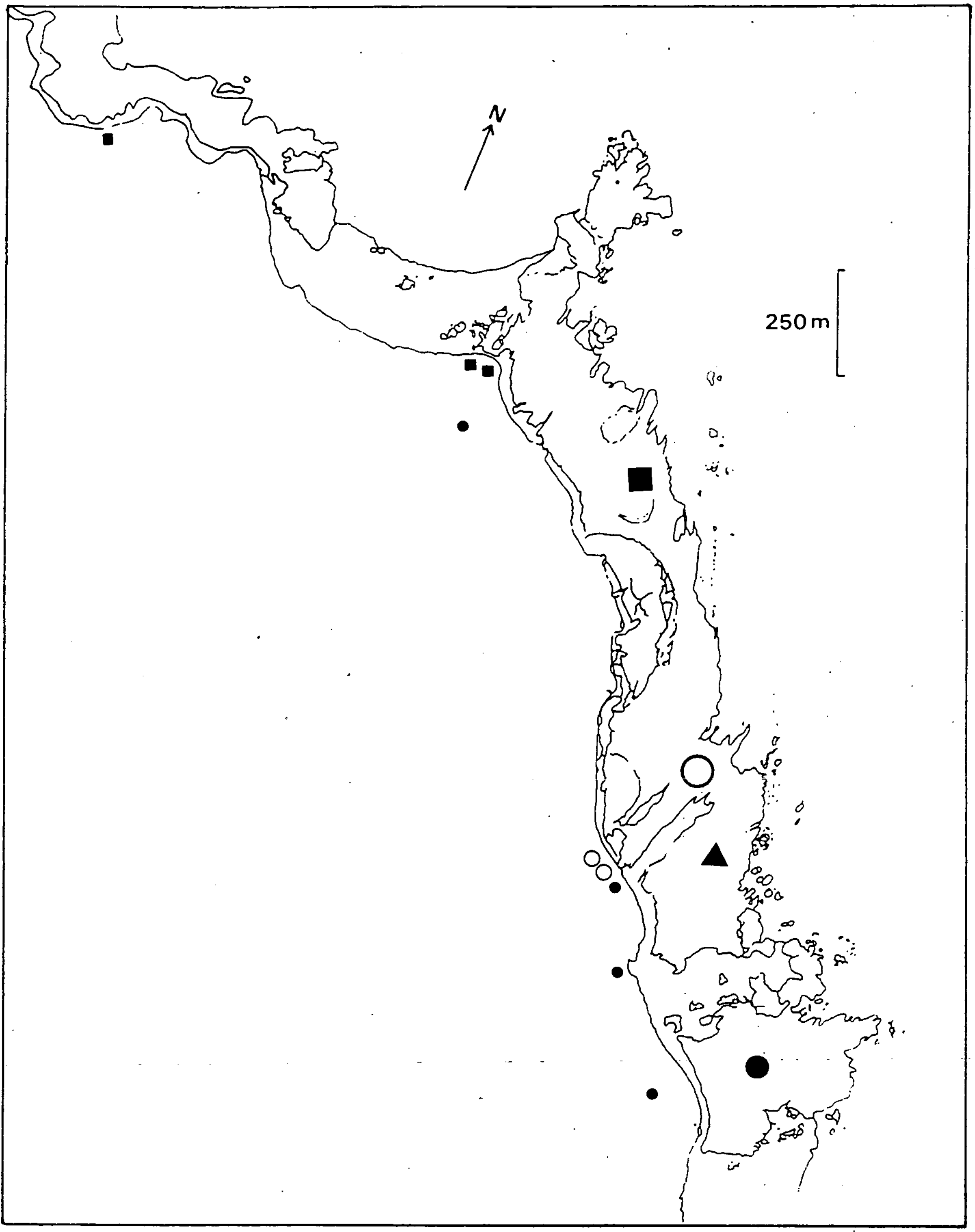
My results on dominance and aggression in turnstone indicate that within flocks access to resources is biased towards high ranking individuals. Why then do low ranking birds stay within these flocks?

One possibility is that the benefits of flocking (e.g. Bertram, 1978; Myers, 1984) outweigh the costs. Phenotypically inferior low rankers may therefore be ´making the most of a bad job´ (Krebs & Davies, 1981). However, if phenotypic differences are small then the behaviour associated with subordinancy would be expected to be eliminated by selection because such behaviour entails a loss in fitness. A possible solution to this quandary is to consider subordinates as ´hopeful dominants´ (West Eberhard, 1975): short-term fitness differs between birds but expected lifetime fitness does not. On the other hand, if high rankers suffer costs which compensate for benefits accrued from resource priority then the short-term fitness would be similar for both high rankers and low rankers. Frequency-dependent selecton would then maintain the balance between dominance and subordinancy which can be considered as a mixed behavioural strategy (Rohwer & Ewald, 1981; Barnard & Sibly, 1981; Maynard Smith, 1982).

High ranking turnstone appear to derive several benefits with their status. Around high tide they tend to be found in the interior of feeding flocks, where they may be less vulnerable to predation, and in the centre of roosting flocks where they may enjoy a more favourable microclimate through sheltering behind birds (Whitlock, 1979) as well as reduced predation risk. In some strandline microhabitats, apparently where prey distribution is patchy, supplanting confers significant short-term increase in intake rate, whilst being supplanted significantly reduces short-term intake rate. The benefits of supplanting will obviously accrue more to high ranking individuals: the differences between high rankers and low rankers in this respect is a factor likely to contribute to status differences in susceptibility to interference. Low rankers may also avoid high rankers and so move to the edge of flocks where prey density may be lower and vigilance demands are higher both of which will also lead to reduced intake rates. As I will show later (Chapter 6), status also has a significant impact on individuals' intertidal feeding behaviour.

Whitfield (1985: Appendix 1) found that due to raptor predation juvenile turnstone suffered higher mortality than adults (see also Chaper 2). Juveniles are subordinate to adults and are found more often in positions in feeding flocks and in sites where they are more vulnerable to predation. Whilst these age-related differences may have been due to the lower foraging experience of juveniles (Chapter 6), juveniles were also found on the periphery of roosting flocks and this is unlikely to be mediated by their foraging experience. Site-related changes in the position of adults in flocks reflected changes in site-related dominance, implicating status as the major factor determining birds' positions in flocks. Therefore , the higher mortality of juveniles was probably caused in part by their low status, although their inexperience was probably also a contributory factor (but see Discussion, Chapter 6).

The effect of status on the mortality of adults is less clear. Within groups of birds delineated by common occupancy of intertidal areas, mortality does not appear to be rank-related, but the mortality of birds from different areas suggests higher ranking birds have lower mortality. The data comparing birds from the same intertidal area is perhaps misleading in that it assumes that birds died when on their home area. Raptors seemed to be responsible for all deaths of wintering turnstone and most sparrowhawk attacks occurred when turnstone were closest to cover, which was usually as turnstone fed on beaches around high tide. Whilst turnstone were reasonably site faithful to 'home beaches' they were more mobile around high tide than at other times of the tidal cycle. Due to site-dependent dominance, moving to away beaches probably lowers the status of a home high ranking bird more than it lowers a home low ranking bird's status. For example, consider two birds, CG rank 1 and CG rank 21, when feeding on a CG home beach CG rank 1 defers to no other bird but CG 21 defers to more or less 20 birds, because probably most of the CG birds will be present on their home beach. However, when feeding away from home on a CR home beach (say, Tower Cove) both CG rank 1 and CG rank 21 will have to defer to more or less the same number of birds, because probably few other CG birds will be present. Consequently, when away from home the differences in rank will be reduced and all away birds from the same home area may be considered as low ranking, regardless of their home status. If turnstone were killed away from home then their home rank does not reflect their rank when killed, particularly birds high ranking when home. The position of the remains of turnstone certainly suggest that at least some them were killed when away from home (Fig. 4.17). Although this interpretation assumes that sparrowhawks ate their kills in the nearest suitable cover to where they captured their prey, my observations of successful attacks suggested that this was by and large true (Fig.4.18). On balance, therefore, I feel that the evidence comparing mortality of birds from different intertidal areas is probably a better indicator of the influence of status on mortality.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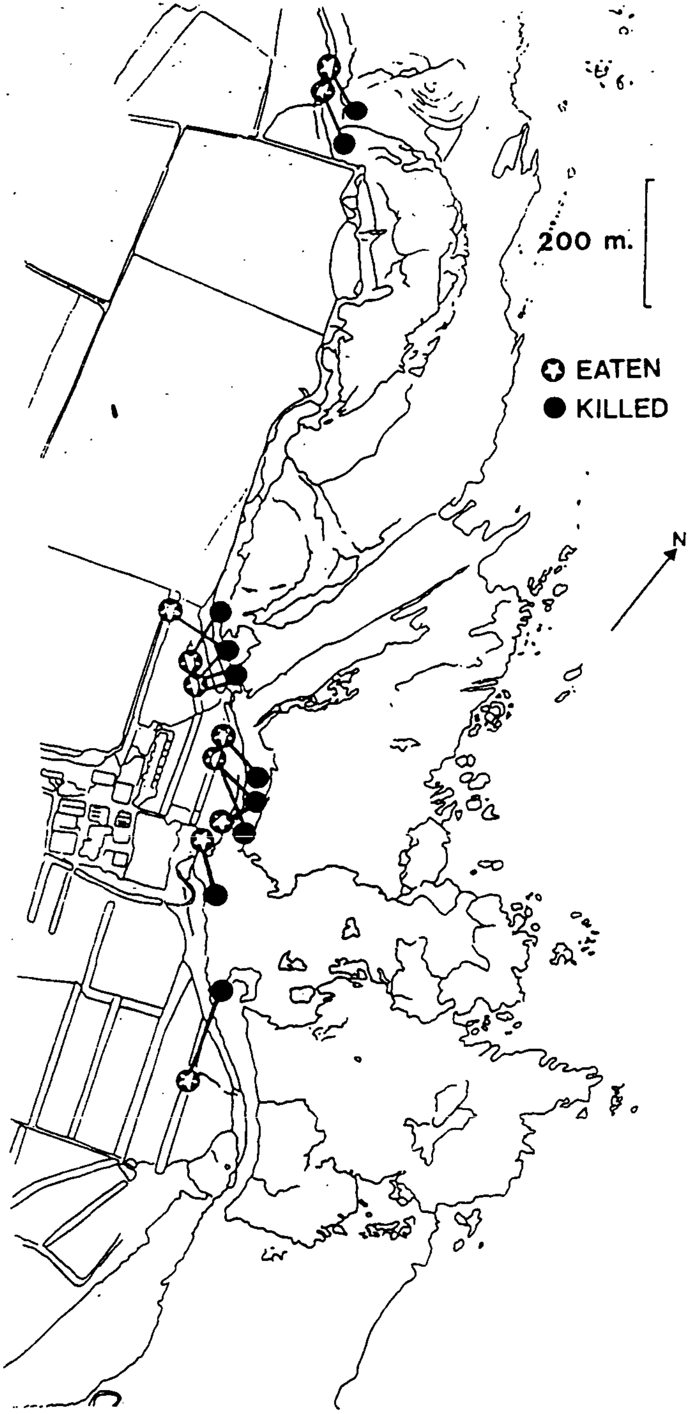
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In sum, although not conclusive the data suggests that low status probably did increase a turnstone´s likelihood of death, which argues against the view that dominance and subordinancy are strategies with equal fitness (Rohwer & Ewald, 1981), but is compatible with the hopeful dominants hypothesis (West Eberhard, 1975). My suggestion that as birds become older their status increases (section 4.3.3.2) is also consistent with the hopeful dominants hypothesis.

Baker (1978) proposed that subordinates may attempt to avoid dominants but are forced to stay in flocks with them because dominants follow subordinants, and effectively herd them. Although an attractive hypothesis, Baker´s suggestion has not received much support (e.g. Ekman & Askenmo, 1984; Rohwer, cited in Maynard Smith, 1982), and I do not believe that it explains the persitence of dominance and subordinancy in flocks of turnstone. Although subordinates do appear to avoid dominants, ample opportunities often appeared to exist for subordinates to leave flocks and feed elsewhere but these opportunities were not exploited, and subordinates frequently joined flocks of higher ranking birds. Kin selection is probably of little importance in the evolution of flocking in turnstone, as it appears unlikely that close relatives are flock mates (Chapter 2).

CHAPTER 5

WINTER PLUMAGE VARIABILITY

5.1 INTRODUCTION

In wintering birds of some species each individual's plumage is the same, while in other species there are large individual differences. Why such differences in intraspecific plumage variability should exist has recently been the subject of a considerable amount of research (Rohwer, 1975, 1977, 1978; Baker & Fox, 1978; Rohwer & Rohwer, 1978; Balph & Balph, 1979; Balph, Balph & Romesburg, 1979; Ketterson, 1979; Ewald & Rohwer, 1980; Parsons & Baptista, 1980; Rohwer & Ewald, 1981; Rohwer, Ewald & Rohwer, 1981; Fugle _et al_, 1984; Jarvi & Bakken, 1984; Watt, Ralph & Atkinson, 1984; Ens & Goss-Custard, in press).

The reason for this upsurge in the study of plumage variability was the development of a hypothesis (Rohwer, 1975), dubbed the Status Signalling Hypothesis (SSH), which attempted to explain inter-species differences in the extent of plumage variability. Rohwer suggested that in species where individuals compete for winter resources through dominance relationships, plumage phenotype signals social status, and because a bird's status is matched by its plumage other individuals can immediately assess its status. The number of costly fights a bird is involved in is thereby reduced because its fighting ability can be recognised. It follows that status signalling is of greatest advantage to individuals in species which characteristically form flocks with unstable membership, as it allows an individual to switch flocks without asserting its status in each flock it joins. Status signalling (and, implicitly, enhanced individual plumage differences) should therefore be found in species characterised by winter flocks with unstable membership, but not in species that form stable flocks.

A second hypothesis which also attempts to explain plumage variability is the Individual Recognition Hypothesis (IRH) (Collias, 1943). The IRH suggests that if a bird can be recognised individually by other flock members then they can remember its fighting ability, so the bird is involved in fewer costly fights. It follows, therefore, that the value of being recognised individually by other flock members will depend on the stability and size of flocks (van Rhijn 1980): if flocks are unstable or very large then the chance of repeated encounters with the same individuals is much reduced, so the value of being individually recognisable is also reduced. Among species with stable flocks, the IRH would probably predict that the degree of variability in plumage will be positively related to flock size up to a threshold beyond which it will be impossible for a bird to recognise all flock mates individually so that the benefits of plumage variability will again decline. Essentially, plumage variability is an inverted U-shaped function of flock size. In addition, plumage differences which function in individual recognition should be positively related to flock stability.

Although often viewed as potential competitors (e.g. Shields, 1977) the IRH and the SSH hypotheses are not mutually exclusive: individual recognition can be viewed as a more detailed version of status signalling (Barnard & Burk, 1979). As in the SSH, the IRH assumes that it is costly to maintain variability and such costs should only be met if they are outweighed by variability benefits. The IRH also assumes that associated with selection for plumage differences there is selection for the ability to discriminate between individuals.

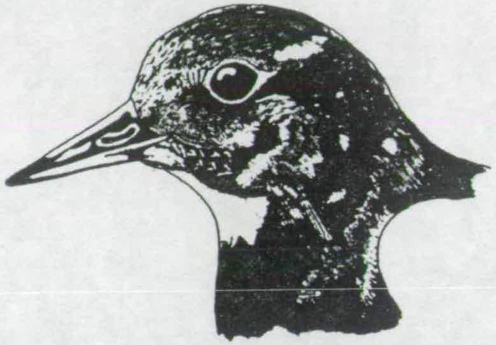
The possible origins of individual plumage differences in breeding turnstone has been discussed by Ferns (1978) and Whitfield (in press: Appendix 2). Following a post-nuptial moult turnstone lose their ginger, black and white breeding plumage and develop a more cryptic, basically brown non-breeding (= wintering) plumage (Cramp & Simmons, 1983). There are large individual plumage differences in wintering turnstone and in this chapter I investigate several aspects of this plumage variability. First, I describe differences between (and within) sex and age classes, then I test the main prediction of the SSH, that plumage signals status, and finally I test a prediction of the IRH, that individuals whose plumage is altered should not be recognised by flockmates.

5.2 PLUMAGE CHARACTERISTICS OF SEX AND AGE CLASSES

5.2.1 METHODS

Turnstone captured by cannon-netting were photographed onto slide film against a neutral grey background from two angles: lateral view and ventral view (Fig. 5.1, 5.2) (see Whitfield, in press: Appendix 2). A "standard outline" was constructed on a large sheet of paper for each of the two views and a slide of each bird was projected onto the appropriate standard outline. The projector was moved or the magnification altered until the image of the bird fitted into the standard outline. The boundaries of the various plumage markings were then drawn around in pencil within the standard

Fig. 5.1 Lateral views of four turnstone caught at Scoughall.



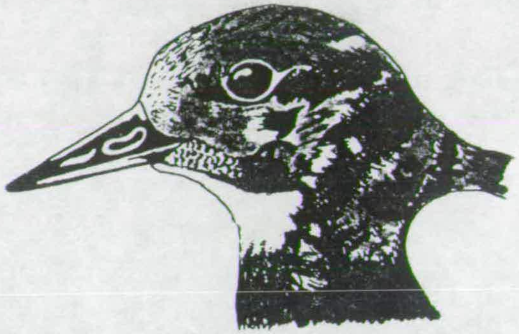
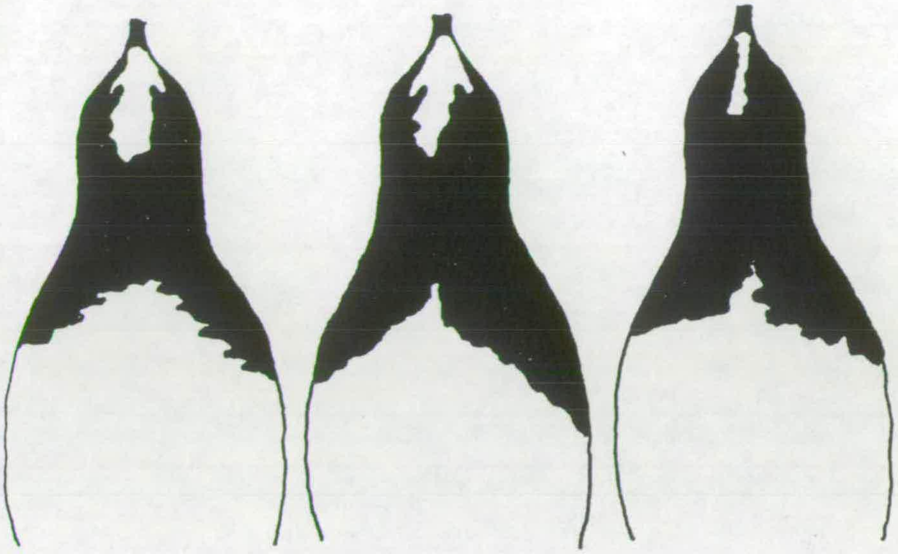
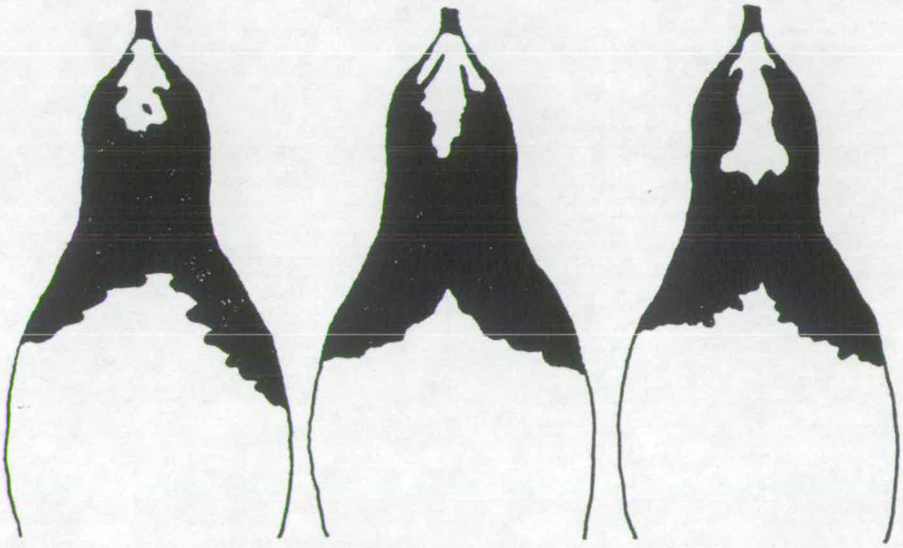


Fig. 5.2 Ventral views of wintering turnstone.





outline. Measuring the area encompassed by the pencil boundaries using a planimeter gave an index of each plumage variable, in cm^2. Indices were calculated for three plumage variables: (1) black breast; (2) white throat; (3) black neck stripe. These variables were chosen because they showed the greatest individual differences which could be readily quantified: other variables either showed less variation e.g. crown markings, or had individual differences of a more subtle nature e.g. white flecking on the head. The black breast index was calculated by measuring the amount of black below a line extrapolated from the position of the shoulder joint which, being relatively immoveable during handling, represented a fixed point, thereby minimising any effect of differences in the stretching of the neck whilst birds were being photographed. Two checks on measurement error were made: (1) repeat measurements for each plumage variable from the same slide were made on ten birds; (2) repeat measurements were taken for each plumage variable on ten birds whose feathers and neck were in different positions on different slides taken on the same day. Error was defined as the difference between measurements as a percentage of the highest measurement.

Birds were sexed and aged as described in Chapter 2.

5.2.2 RESULTS AND DISCUSSION

The technique used for measuring plumage variability has a measurement error of around 4% (Table 5.1), which suggests that it is a fairly consistent and reliable method. Eight adults were photographed twice on a separate day within one winter, and one adult

TABLE 5.1

Mean and ranges of measurement error for indices of the black breast, white throat and neck stripe plumage variables. (a) Repeat measurements from the same slide (N=10); (b) repeat paired measurements from the same bird with differing feather disorder (N=10).

	Percentage Error	
	Mean	Range
(a)		
Black breast	3.6	0.5-7.4
White throat	3.4	0.2-6.7
Cheek stripe	3.3	0.6-6.2
(b)		
Black breast	4.8	2.2-12.0
White throat	4.8	0.0-10.7
Cheek stripe	3.7	0.7-8.0

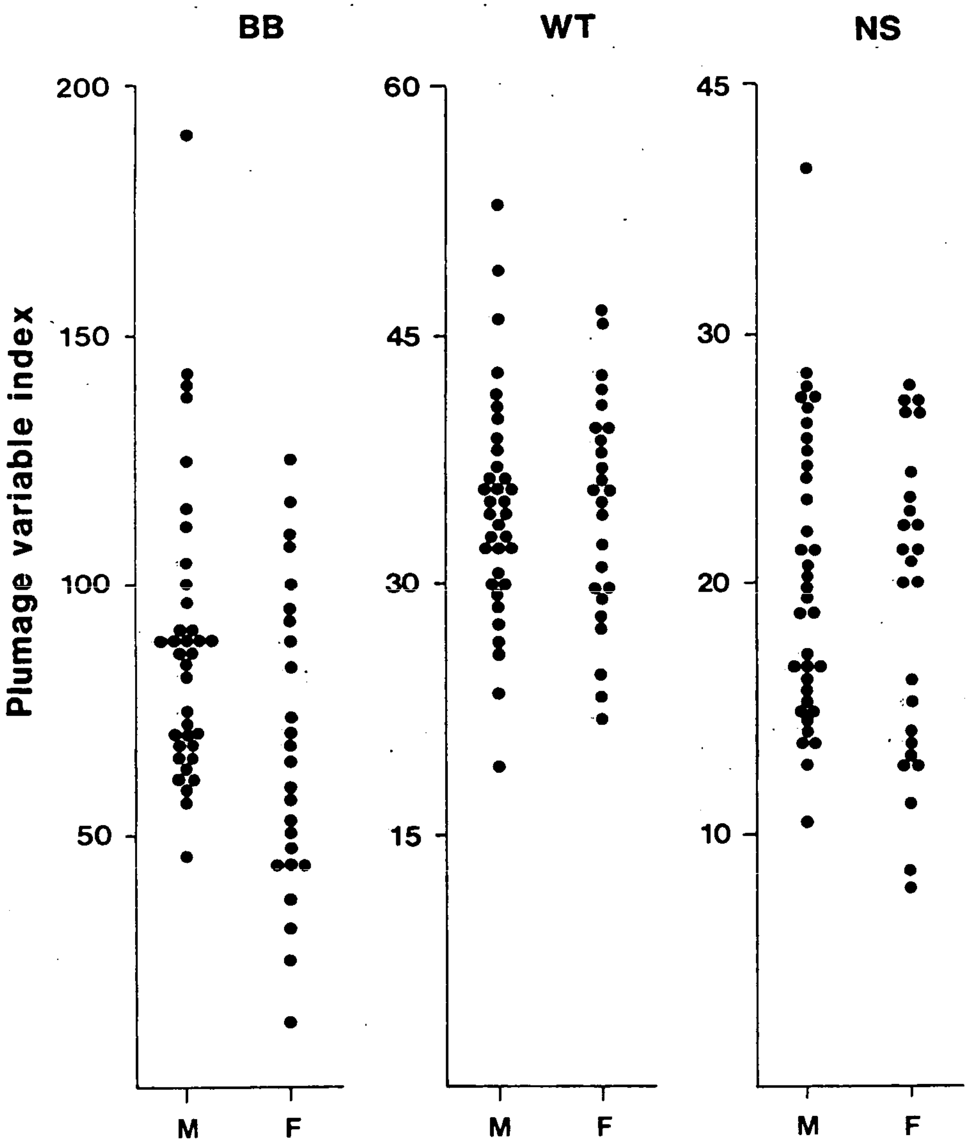
was photographed twice within three winters. I have assumed that only if differences in plumage indices taken from the same bird on different days exceed 10% can apparent changes not be attributed to measurement error: this seems reasonable given the range of measurement errors (Table 5.1). Repeat measurements of adults photographed on separate occasions within a winter show that adult plumage does not change within a winter as the slight differences in plumage indices for each bird are consistent with normal measurement error (Table 5.2). That the plumage of adults does not change within a winter is hardly surprising given the lack of any moult within a winter. Differences in the plumage indices of individual adults measured in different winters are almost always within the margin of measurement error (only a single measurement greater than 10%) (Table 5.2) which suggests that from winter to winter the plumage of adults remains the same, despite intervening pre- and post-nuptial moults. The slides show that the plumage generally is the same in different winters, even in the shape, colour and contrast of each marking: individuals are quite easily recognisable as the same bird to the human eye in different winters. This result suggests a strong genetic influence over plumage characteristics, or that each adult's physiological state remains more or less consistent during each post-nuptial moult.

Adult males tend to have more black on their breasts than females but this difference is not significant (Mann-Whitney U test $p>0.05$). There are no sexual differences in the size of white throat patch (Mann Whitney U test $p>0.05$) or in the size of the neck stripe (Mann Whitney U test $p>0.0.5$) (Fig. 5.3). These results are similar to the findings for breeding turnstone (Chapter 2). I could discern

TABLE 5.2

Percentage difference in repeat measurements for indices of black breast, white throat and neck stripe plumage variables of adult turnstone on different days (a) within a winter (N=11); (b) in different winters (N=15).

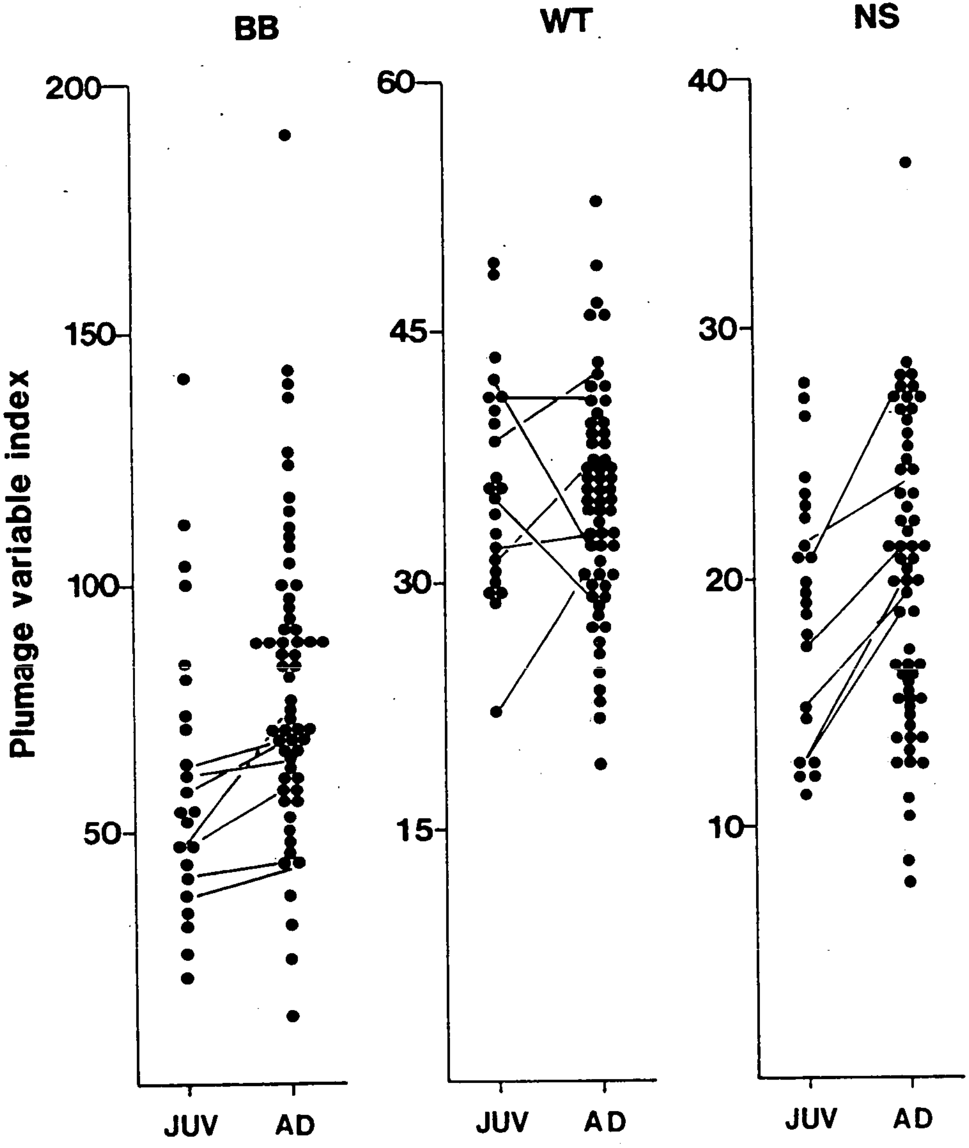
	Percentage Error	
	Mean	Range
(a)		
Black breast	3.2	0.8-7.3
White throat	4.0	0.9-8.3
Cheek stripe	4.7	1.1-10.3
(b)		
Black breast	4.7	0.6-13.0
White throat	3.8	0.3-10.6
Cheek stripe	4.0	0.6-8.9


BB
WT
NS
Plumage variable index
200
150
100
50
60
45
30
15
45
30
20
10
M
F
M
F
M
F

no sexual differences in other plumage characteristics.

Only one juvenile was photographed on separate days in the same winter: this individual showed no apparent changes in its index for black breast (6.6% difference), white throat (0.0% difference) or neck stripe (5.1% difference). There was no difference between the plumage indices of a sample of juveniles photographed in early winter (N=7) and the indices of a sample of juveniles photographed in late winter (N=9) (Mann Whitney U test; $p>0.05$ for all three variables). These results suggest that whilst juveniles can progressively lose their diagnostic wing coverts in the course of a winter (e.g. Prater et al, 1977) other features of their plumage may remain the same. Juveniles tended to have less black on their breasts and larger white throat patches than adults but these differences were slight and not significant (Mann Whitney U test: black breast $p>0.05$; white throat $p>0.05$). There were no differences in the size of the cheek stripe (Mann Whitney U test $p>0.05$) (Fig. 5.4). Seven individuals were photographed as juveniles and later as adults. Three individuals showed an increase in their black breast index as adults, four did not change. The size of the white throat patch increased in two individuals, decreased in two and showed no change in three on becoming adults. All seven showed an increase in the size of their neck stripe when they were adults, but in two the increase was not above the 10% margin of error (Fig. 5.4). Most of the increase in the amount of black on the breast and neck stripe was due to the replacement of white edged black feathers, typical of many juveniles, with totally black feathers. Although six of the seven juveniles showed some change in their head and breast plumage on becoming adults, the results presented earlier indicate that once they become

Fig. 5.4 Plumage variable indices of adult and juvenile turnstone caught at Scoughall in winter. Lines join indices of juveniles remeasured as adults. BB=Black breast, WT=white throat, NS=neck stripe.


BB
WT
NS
Plumage variable index
200
150
100
50
60
45
30
15
40
30
20
10
JUV
AD
JUV
AD
JUV
AD

adults their winter plumage remains the same as they become older. This long term stability of individual plumage differences provides a means by which year-to-year stability of dyadic agonistic relationships (Chapter 4) can be maintained through individual recognition (this chapter, section 5.4).

5.3 TESTING THE STATUS SIGNALLING HYPOTHESIS (SSH)

5.3.1 METHODS

According to the main prediction of the SSH there should be a positive correlation between status and plumage phenotype. Three plumage variables, black breast, white throat, neck stripe, were measured as described in the previous section. If a bird had been photographed on more than one occasion a mean index was used. In the aggressive displays of the turnstone the white throat and particularly the black breast are prominently displayed to opponents (see Chapter 4 and Appendix 2) and seem to be the most likely candidates for badges of status. Status was measured from the results of dyadic interactions between flock members and this has been fully discussed in Chapter 4. For the test of the SSH I used the results of the hierarchy formed from the Coastguard flock in the combined winters of 1982-83 and 1983-84, and from the hierarchy of the Scoughall-Field Space flock in the winter of 1983-84. For the SSH prediction to be confirmed there should be a significant correlation between the actual rank order of birds and the rank order predicted by plumage phenotype.

5.3.2 RESULTS AND DISCUSSION

The actual ranking of birds in the S-FS flock and CG flock and the predicted rankings based on the indices for black breast, white throat and neck stripe are presented in Tables 5.3,5.4.There was no correlation between the actual ranking and the ranking predicted by any of the three plumage variables (Spearman´s rank correlation test; p>0.05 for each plumage index). Even if the correlations are maximised by altering the rank orders for the plumage variables allowing for up to ± 10% error in plumage index, there were still no significant correlations between the predicted and actual rank orders in either flock. I also had no impression that any other plumage variable was correlated with status, and the status of overall ´light´ birds or overall ´dark´ birds appeared unconnected to their plumage. Clearly the prediction from the SSH, that status should be correlated with plumage phenotype is not upheld by these data. This result is perhaps not surprising considering that an adult bird´s status probably changes as it becomes older (Chapter 4), yet its plumage does not (this chapter, section 5.2). It would be interesting to test status signalling in other species of long-lived birds to examine whether changes in rank of mature adults are reflected by concomitant plumage changes. Even status signalling between age and sex classes does not appear to be operating in wintering turnstone, as although adults almost invariably dominate juveniles and males usually dominate females these differences are not reflected by plumage differences. It is possible that the buff tipped wing coverts of juveniles act as a signal of status as well as serving other functions, such as cryptic colouration (probably on the

TABLE 5.3

ACTUAL STATUS	BB	WT	NS
1 YOBN	(4) YNNG 180.4	(9) YOWL 51.9	(11) YWWR 27.1
2 YWOB	(20) YROL 125.3	(23) BWLW 42.5	(21) YWWG 26.8
3 BWWL	(7) YWWL 111.5	(15) YLNO 41.2	(2) YWOB 26.0
4 YNNG	(21) YWWG 108.2	(7) YWWL 41.0	(5) YLLB 25.4
5 YLLB	(6) YLGR 103.6	(20) YROL 40.0	(1) YOBN 24.6
6 YLGR	(11) YWWR 102.5	(21) YWWG 39.5	(22) YWWB 24.5
7 YWWL	(14) YWLR 93.1	(2) YWOB 38.0	(7) YWWL 24.3
8 YWNR	(8) YWNR 89.4	(11) YWWR 37.5	(15) YLNO 22.8
9 YOWL	(5) YLLB 89.2	(14) YWLR 36.3	(8) YWNR 22.0
10 BWRY	(9) YOWL 89.0	(3) BWWL 36.2	(19) BWYO 21.9
11 YWWR	(22) YWWB 88.9	(17) YWGW 35.3	(4) YNNG 21.3
12 YWGN	(18) YOWO 83.3	(10) BWRY 35.1	(3) BWWL 20.8
13 YLNW	(10) BWRY 77.2	(18) YOWO 34.7	(18) YOWO 19.9
14 YWLR	(17) YWGW 70.8	(8) YWNR 33.6	(12) YWGN 19.4
15 YLNO	(3) BWWL 69.4	(19) BWYO 31.1	(10) BWRY 17.3
16 YWWO	(13) YLNW 68.9	(5) YLLB 30.1	(16) YWWO 16.1
17 YWGW	(1) YOBN 68.7	(1) YOBN 29.8	(14) YWLR 15.5
18 YOWO	(12) YWGN 65.7	(16) YWWO 29.7	(17) YWGW 13.6
19 BWYO	(2) YWOB 62.2	(4) YNNG 28.9	(13) YLNW 13.4
20 YROL	(16) YWWO 51.2	(12) YWGN 27.6	(20) YROL 12.7
21 YWWG	(19) BWYO 48.9	(22) YWWB 24.7	(9) YOWL 12.6
22 YWWB	(23) BWLW 44.5	(13) YLNW 22.5	(6) YLGR 12.3
23 BWLW	(15) YLNO 25.3	(6) YLGR 19.1	(23) BWLW 11.2
Spearman´s	r=0.15	r=0.23	r=0.17

TABLE 5.4

ACTUAL STATUS	BB	WT	NS
1 YLWN	(9) YNGB 132.9	(7) YOWL 51.9	(1) YLWN 28.7
2 YNBG	(14) BWYL 122.3	(1) YLWN 49.1	(9) YNGB 27.4
3 YNWO	(2) YNBG 120.1	(11) YORW 46.3	(12) YLGN 23.4
4 YLWL	(5) YRWR 96.4	(3) YNWO 35.6	(15) BWOG 22.3
5 YRWR	(8) YWGB 90.8	(12) YLGN 35.5	(11) YORW 21.3
6 YBOL	(7) YOWL 89.0	(14) BWYL 35.4	(13) BWWR 21.1
7 YOWL	(3) YNWO 83.3	(5) YRWR 35.1	(8) YWGB 19.6
8 YWGB	(1) YLWN 70.6	(4) YLWL 34.2	(5) YRWR 17.1
9 YNGB	(10) BWWO 65.8	(8) YWGB 32.8	(3) YNWO 16.2
10 BWWO	(6) YBOL 52.2	(9) YNGB 31.0	(4) YLWL 16.0
11 YORW	(4) YLWL 46.0	(13) BWWR 29.4	(10) BWWO 15.7
12 YLGN	(15) BWOG 44.9	(15) BWOG 28.5	(7) YOWL 12.6
13 BWWR	(13) BWWR 44.4	(10) BWWO 27.6	(2) YNBG 10.5
14 BWWL	(12) YLGN 32.3	(6) YNBG 23.4	(6) YBOL 8.4
15 BWOG	(11) YORW 13.0	(2) YBOL 23.3	(14) BWYL 7.6
Spearmans	r=0.32	r=0.14	r=0.13

breeding grounds before juveniles´ first southward migration). However, juveniles progressively lose their buff-tipped coverts throughout a winter, and this is not reflected by changes in status, but it may be because buff-tips act as a signal of social class until birds have learnt to individually recognise juveniles.

5.4 TESTING THE INDIVIDUAL RECOGNITION HYPOTHESIS (IRH)

5.4.1 METHODS

According to the IRH, if a bird´s plumage is altered, flock mates should be less likely to recognise it and should treat the altered bird as a stranger. Such a change in plumage should therefore elicit a change in flock mates´ response to the altered bird, regardless of the form of the alteration (provided, of course, that the alteration is sufficient to obscure the identity of the altered bird). This was the IRH prediction which I aimed to test.

The experiment was carried out on a captive group of thirteen turnstone in the Zoology Department roof aviary between 4 March and 24 March 1984 under Home Office Licence No. 62531. All birds were kept in the southerly half of the aviary which measured 5 x 5.5m (see Marshall, 1981, p.180). The experiment involved ten birds each receiving a control and experimental treatment.

The experimental procedure was as follows: a bird was captured and its plumage was altered using a black magic marker pen and/or Tipp-ex correction fluid. All alterations involved head and breast plumage, and ranged from, for example, enlarging the black breast, reducing white throat, blacking in the tip of the brown and white nape/upper breast patch, to reducing the black breast, enlarging the white throat and enlarging the black neck stripe. A full list of alterations made to each bird is given in Appendix 3. When the ink and/or correction fluid had dried the bird was returned to the aviary.

The control procedure was as follows: on the day before its experimental test the bird which had to be altered was captured. I then ´marked´ the plumage which would be altered the next day with a dry magic marker pen and/or a dried Tipp-ex brush, and dabbed the appropriate feathers with a little water. Thus, although no alterations actually occurred, the feathers received similar treatment. I then held a normal marker pen nib and/or correction fluid near to the bird´s nostrils for a total of twenty seconds in an attempt to control for any effects the fumes may have had on the bird. The bird was then returned to the aviary.

All tests were carried out in the late morning and immediately before the start of each test I scattered thirty mealworms onto the floor of the aviary. In the twenty minutes following the return of the bird to the aviary I noted the following: number of aggressive acts iniatiated against the test bird by higher ranking birds; number of aggressive acts initiated against the test bird by lower ranking birds; number of aggressive acts won by the test bird but with some ´resistance´ from lower ranking birds (see Chapter 5); the amount of time the test bird spent preening, bathing, roosting and feeding.

5.4.2 RESULTS AND DISCUSSION

The results of the experiment are presented in Table 5.5. After a bird was altered it was involved in more aggressive interactions (Sign test, p=0.002), had more aggressive behaviour initiated against it by higher ranking birds (Sign test, p=0.008), had more aggressive behaviour initiated against it by lower ranking birds (Sign test, p=0.002) and lower ranking birds showed more resistance in aggressive interactions with the altered bird (Sign test, p=0.002). These differences in the response of flock mates to an altered bird did not appear to be due to it behaving differently as there was no difference between control and experimental treatments in the amount of time the test bird spent bathing (Sign test, p>0.05), preening (Sign test, p>0.05) roosting (Sign test, p>0.05) or feeding (Sign test, p>0.05).

These results conform to the prediction of the IRH, that if a bird´s plumage is altered then its flockmates should respond more aggressively to it because they can no longer recognise it. However, it is worth pointing out that the increased aggressive response to the altered bird waned after about 30 minutes to one hour after its return to the aviary. The response of other flockmates was also not as aggressive as their response to genuinely strange birds, perhaps because these behaved differently in, for example, the rapidity with which they moved towards the food supplies. These observations suggest that birds used cues other than anterior plumage markings in recognising other flock members. Such cues may be plumage characteristics of the rest of the body, posture and, probably, characteristic behaviour patterns of individuals (see also Shields, 1977, Pearson, 1979). The possibility that birds were using colour rings to recognise each other can be discounted because I ran an

TABLE 5.5

The responses of a flock of captive turnstone to a flock mate whose plumage was altered (experimental=E) or not altered (control=C). A = no. of interactions test bird involved in; B = no. of interactions initiated against test bird by higher ranking birds; C = no. of interactions initiated against test bird by lower ranking birds; D = no. of interactions won by test bird but loser showed some resistance to defeat.

Test	Measures of aggression							
	A		B		C		D	
	C	E	C	E	C	E	C	E
1	7	15	6	11	0	2	0	3
2	1	19	1	11	0	3	0	2
3	5	12	5	9	0	3	0	3
4	10	12	3	3	0	2	0	4
5	4	8	1	4	0	3	0	2
6	8	10	0	0	0	1	0	1
7	8	13	2	3	0	4	0	4
8	4	9	2	5	0	1	0	1
9	6	14	2	8	0	3	0	2
10	4	7	2	4	0	3	0	1
Mean	5.7	11.9	2.4	5.8	0	2.5	0	2.3

experiment with ten paired tests where I caught birds and changed their colour ring combination or, as a control, caught them and put on new colour rings of the original combination. There was no difference in the aggressive response of flockmates to experimentals and controls on the return of the birds to the aviary (Sign test, $p>0.05$). It is also possible to interpret the results by postulating that flock members assessed the altered bird as sick, but nonetheless the same individual, as I have seen ill turnstone persecuted by other individuals in the field. However, as Rohwer (1978) notes, by the IRH altered birds should initially be attacked more as strangers but should regain their former position: this is exactly what happened in this experiment with turnstone.

5.5 GENERAL DISCUSSION

The main prediction of the SSH, that plumage phenotype should signal status, is not supported by data from wintering turnstone. Furthermore, according to Rohwer (1975) strange birds joining a new flock should assume the rank reflected by their plumage. That this does not happen is suggested both by site related dominance (Chapter 4) and the fact that strange birds introduced to a resident captive flock were subordinate to home flocks even after a month together, contrary to expectations based on their plumage differences (Whitfield unpubl.data). Thus, the SSH does not appear to be an adequate explanation of plumage variability in wintering turnstone; this is also the case with breeding turnstone (Whitfield, in press, Appendix 2).

The problem of the evolutionary origin of dominance/subordinance within the context of status signalling has been dealt with by several authors (e.g. Maynard Smith, 1982; Rohwer & Ewald, 1981; Jarvi & Bakken, 1984; Fugle _et_ _al_, 1984). The possible mechanisms maintaining status differences in general have also been discussed in Chapter 4. As indicated by Rohwer (1975), plumage variability in wintering species may take two forms, dichromatic i.e. bimodal variation, and polychromatic i.e. continuous variation.

Dichromatic species

Marler (1955) and Whitfield (1981) presented experimental evidence that when female chaffinches _Fringilla_ _coelebs_ and cutthroat finches _Amadina_ _fasciata_ are altered to resemble socially dominant males they are treated as males by other individuals. Balph, _et_ _al_ (1979) strongly suspected that sexually dichromatic non-breeding evening grosbeaks _Hesperiphona_ _vespertina_ are also attentive to plumage cues of sexual social status. Variability in the colouration of dark-eyed juncos _Junco_ _hyemalis_ is correlated with sex but there is considerable overlap, and hood darkness appeared to be a poor indicator of status unless associated with sex (Balph _et_ _al_, 1979, Ketterson, 1979). The white throated sparrow _Zonotrichia_ _albicollis_ is dichromatic for crown colour but both morphs include males and females, and there is negligible evidence for status signalling (Watt et al, 1984). Gambel's white crowned sparrow _Zonotrichia_ _leucophrys_ _gambelii_ is also dichromatic for crown colour but dichromatism is between age-classes: adults have black and white crowns and juveniles have brown crowns (e.g. Parsons & Baptista, 1980). Crown colour signals status but variations within each morph do not: as in dark-eyed juncos, status signalling within age and sex classes is minimal or non-existent (Fugle *et al*, 1984).

Polychromatic species

Jarvi & Bakken (1984) found that variation in the width of the breast stripe in great tits (*Parus major*) signals status. Multiple regression analysis showed that social status is the only variable that explains the observed variation in breast stripe width when all other variables i.e. age, sex and body size were held constant, although Svensson (1975) regards females as having narrower stripes than males. Status signalling appears to occur in Harris´ sparrows *Zonotrichia querula*: the blackness on the throat and crown is positively associated with status (Rohwer, 1975, 1977; Rohwer & Rohwer, 1978). However, blackness only predicts dominance on diffuse and not on concentrated food supplies (Rohwer *et al*, 1981). The pine siskin *Carduelis pinus* exhibits considerable individual variability in the brightness and the extent of the yellowish wing-stripe, not linked to sexual or age differences. There is a negative relationship between the brightness and extent of the wing-stripe and status (Balph & Balph, 1979).

From this and other evidence several conclusions on the limits of the SSH can be drawn and adjustments to Rohwer´s original thesis can be suggested.

1. Species which live in stable flocks may exhibit marked plumage variability e.g. turnstone (contra Rohwer, 1975, p. 596), but the best evidence for the SSH is found in species with unstable flocks (i.e. pine siskin, Harris´ sparrow, great tit).

2. Plumage variability has probably not evol~~o~~ved to signal status in several species and several species exhibit plumage variability which does not appear to serve a status signalling function e.g. white throated sparrow, dark eyed junco, turnstone.

3. Rohwer's (1975, p. 598) prediction that in a status signalling system status should be positively related to e.g. brightness, size, contrast or blackness of the plumage variable may not always be true (see also Maynard Smith, 1982) e.g. pine siskin, Cassin's finch _Carpodacus cassinii_ (Balph _et al_, 1979, p.84).

4. Sexual dimorphism may be a confounding variable, particularly in those species such as the cutthroat, chaffinch and evening grosbeak which do not undergo both a pre- and a post-nuptial moult. In such species dimorphism may be a result of sexual selection acting in the breeding season and is only secondarily used to signal status in the non-breeding season.

5. In status signalling dimorphic species variability within morphs does not appear to signal status; signalling only occurs between morphs e.g. white-crowned sparrow (Fugle _et al_, 1984), cutthroat finch (Whitfield, unpubl. data).

6. Details of plumage variability and the underlying causal mechanisms appear to differ widely between species (e.g. Maynard Smith, 1982) and within a species the possible factors producing variability may often be complex (e.g. Balph _et al_, 1979). More research into these other factors is clearly required.

One such factor which has largely been ignored (although see Shields, 1977, Parsons & Baptista, 1980), but which may be important, is individual recognition. Unfortunately, the IRH has only rarely been tested formally, as most other authors normally conclude that a correlation between plumage phenotype and status precludes individual recognition (Rohwer, 1978; Jarvi & Bakken, 1984). Although confirmation of the SSH makes the IRH less likely to be correct the two hypotheses are not mutually exclusive (see 5.1 Introduction), and Parsons & Baptista (1980) found evidence for both the SSH and the IRH in Gambel's white- crowned sparrow. Wintering turnstone conform well to the IRH, as well as there being experimental evidence supporting a major prediction of the IRH; turnstone also form medium sized stable flocks whose members compete for access to resources through dominance-based relationships. Thus, by exhibiting marked individual plumage differences they conform to the IRH expectations. However, it should be noted that problems in testing the IRH are considerable (see Whitfield, in press: Appendix 2 for a discussion).

What can studies of wintering waders in general contribute to the problem of plumage variability? Unfortunately, as discussed in the previous chapter, very little is known about the persistence of associations between individuals in wintering waders, and consequently very little can be said about the predictions of the SSH and IRH. There is also very little information on the extent of plumage variability in species of waders although I am in the process of attempting to collect such data. Flocks of sanderlings consist of individuals which form transitory associations and competition for food does not seem to be based on dominance relationships (Myers, 1983). Both the IRH and SSH would therefore predict minimal plumage differences and this appears to be the case (Myers, 1983, pers. obs.). Dunlin typically form large flocks (Goss-Custard, 1970; Cramp & Simmons, 1983) in which aggression appears to be rare (Goss-Custard, 1970) and when it occurs it seldom seems to be related to food stealing (Worrall, in Cramp & Simmons, 1983). These observations suggest that dunlin do not form dominance/subordinance relationships as do the findings of Bradley (1982). Dunlin have few individual plumage differences (pers. obs.), as would be predicted by both the SSH and IRH. It is also possible that knot do not compete for food through social dominance (see Chapter 4) so, like dunlin and sanderling, both the IRH and SSH predict no individual plumage differences and, like dunlin and sanderling, this prediction is confirmed (pers. obs.). Oystercatchers form dominance hierarchies in winter (Ens & Goss-Custard 1984) and occur in loose flocks or are widely scattered over feeding areas (Goss-Custard, 1970). Oystercatchers do not defend territories, but feeding ranges overlap considerably and some birds regularly use the same feeding area (Goss-Custard et al, 1982b), which implies at least some form of stability in individual associations. The IRH would tentatively predict individual plumage differences and, as well as plumage differences associated with age (Prater et al, 1977) the width of the white collar is variable (Dare & Mercer, 1974). Vines (1980) suggested that white collar width may signal status but Ens & Goss-Custard (in press) found that this was not so, and postulated an individual recognition function. Non-territorial grey plover form loose flocks of up to 30 individuals (Cramp & Simmons, 1983), which apparently exhibit dominance hierarchies (Dugan, in Cramp & Simmons, 1983) although actual data were not presented. I can find no information concerning the stability of associations between individuals within grey plover flocks, but if Dugan's assertion is correct, then grey plover flocks would be expected to exhibit individual plumage differences, which seems to be the case (Evans, 1984).

In conclusion, I feel that a fruitful approach to the study of plumage variability in wintering birds would be to consider a model incorporating elements of both the SSH and IRH. Both hypotheses make clear predictions about relationships in different species between: (1) cohesiveness of flocks in time and space; (2) flock size; and (3) nature of intraspecific competition for food. Finally, it is worth pointing out that there may be several confounding variables which produce difficulties in testing hypotheses about plumage variability (Whitfield, in press: Appendix 2), and the origins of individual plumage differences may often be complex (e.g. Balph et al, 1979).

CHAPTER 6

FEEDING BEHAVIOUR

6.1 INTRODUCTION

The feeding behaviour of wintering waders is one of the best studied aspects of their biology (recent reviews by Burger, 1984; Goss-Custard, 1984, 1985; Puttick, 1984). In the past most research concentrated on species differences in feeding behaviour (e.g. Pienkowski, 1980), but it is becoming increasingly obvious that in many species large individual differences occur (e.g. Goss-Custard, 1985). For example, some oystercatchers feed on mussels by stabbing between gaping shells, severing the adductor muscle holding the two valves together. Others hammer open closed shells, some individuals attacking the prey's dorsal surface whilst others direct their blows to the ventral surface (Norton-Griffiths, 1968; Goss-Custard et al, 1982c; Goss-Custard & Sutherland, 1984). These different specialists can all feed in the same estuary, along with other birds who may use other techniques to obtain entirely different prey, such as ragworms Nereis diversicolor, clams Scrobicularia plana, or littorinids (Goss-Custard & Durell, 1983, 1984). Although individuals do not stick to one technique as rigidly as was once believed, there is a strong tendency to specialise in some techniques (Goss-Custard & Sutherland, 1984). Cultural inheritance appears to play some role in influencing an individual's feeding behaviour (Norton-Griffiths, 1968), but other factors, such as social status, are increasingly becoming implicated too (see Goss-Custard, 1985).

Marshall's (1981) work on unmarked turnstone at Scoughall showed that this species can use a wide variety of feeding techniques to obtain its prey, and Marshall suggested that individuals may specialise in their use of a particular technique. As mentioned earlier (Chapter 1), individual differences in feeding behaviour can have important consequences at several biological levels, and on the basis of Marshall's suggestion I instigated a study of individual feeding behaviour in turnstone: this chapter describes some of the results of the study, together with information on the diet of turnstone, and on age-related differences in feeding behaviour.

6.2 DESCRIPTION OF FEEDING TECHNIQUES AND MICROHABITATS

6.2.1 FEEDING TECHNIQUES

The following classification is based partly on Marshall (1981). I recognised six feeding techniques:

1. **Routing.** This is the manipulation of seaweed to locate prey concealed underneath it and consists of flicking small pieces of weed with an upward movement of the bill, bulldozing piles of seaweed by lunging forward and pushing with the bill and forehead, and pecking at potential prey items. Bouts of flicking and bulldozing expose prey items, and pecks are then employed to investigate and/or swallow prey items.
2. **Turning stones.** This technique is basically routing stones without the use of bulldozing. Stones are turned over by upward flicks of the bill and prey which was under the stone is then captured by pecks.
3. **Digging.** This technique is employed by birds feeding in sandy or muddy substrates. To expose prey which is below the surface of such substrates turnstone excavate holes using upward or sideways flicks of the bill and then capture the prey using pecks. Again this

technique may be regarded as a variation on routing. On the study site it is used in sand, mainly to capture sandhoppers _Talitrus saltator_ (Marshall, 1981; this chapter), on The Wash turnstone dig in mud to capture _Corophium_ (Jones, 1975) and in New Zealand turnstone have been seen digging for crabs (Robertson & Dennison, 1979).

4. **Probing.** This technique involves a turnstone inserting its bill into a substrate to a depth of greater than one quarter bill length. Maximum probing depth was a full bill length. Turnstone probe in seaweed, under stones but mainly in water when turnstone probe for littorinids or other gastropods. Inserting its upper mandible behind the gastropod operculum the turnstone then closes its mandibles, cutting the adductor muscle attaching the gastropod foot (and operculum) to the shell columella; the foot and operculum are then swallowed. Sometimes the gastropod is lifted out of the water by its foot, and placed on a firm substrate before the foot is severed. A firm substrate seems necessary to allow the bird to insert its bill as far inside the shell as possible, so more of the animal can be ´winkled´ out. Marshall (1981) claims that turnstone obtain about one third to nearly the whole animal by this technique, but I made many observations of probing turnstone in captivity and I found that they only obtained the foot of a healthy gastropod: the only occasions when they extracted the whole animal was if the gastropod was dead or dying. Using suitably sized forceps I could never insert them deep enough into a littorinids shell to reach the base of the adducter muscle,and the position of the adducter muscle´s attachment to the shell columella (Fretter & Graham, 1962) probably made it impossible for a turnstone to sever it at its base which would be necessary if the whole animal was to be extracted.

5. **Hammer-probing.** A description of this technique is given by Groves (1978). It is used mainly to extract large barnacles from within their lateral plates. A turnstone positions its head over a barnacle and rapidly hammers down at the barnacle´s tergal and scutal plates (upper plates); the bill mandibles are usually closed but may be held slightly apart. After a varying number of hammers (between one and five) the plates are smashed apart sufficiently to expose the underlying animal which is then extracted from its surrounding lateral plates by a series of probing and pecking actions. Bouts of probes and pecks are interspersed with swallows.

6. **Surface pecking.** This technique is employed by turnstone to capture prey on the surface or just below the surface (less than one quarter bill length) of a substrate, and its name is self-explanatory. Turnstone were regarded as surface pecking only if bouts were not interrupted by other feeding actions e.g. flicking.

6.2.2 MICROHABITATS

I differentiated between a maximum of eighteen microhabitats, twelve intertidal (1-12) and six strandline (13-18): one microhabitat (11) was usually intertidal but occasionally strandline.

1. **WR**. <50% bare rock, >50% seaweed, predominantly brown algae (Phaeophyceae- Fucus spp., Ascophyllum).
2. **SWR**. >50% bare rock, <50% brown seaweed.
3. **AR**. Rock covered with mixture of Chlorophyceae seaweed (Enteromorpha spp., Ulva).
4. **WAR**. Rock covered with mixture of Chlorophyceae and Phaeaphceae seaweed.

5. BR. Bare rock; may be encrusted with barnacles and/or limpets.

6-10. **WRE, SWRE, ARE, WARE, BRE.** Sea/substrate interface of microhabitats 1-5: ´tide edge´ microhabitats.

11. **Pebbles.**

12. **Pool.**

13. **S.** Sand.

14. **WS.** Sand with <50% coverage of tide wrack.

15. **TW.** Sand (or pebbles) with >50% coverage of tide wrack.

16-18. **TES, TEWS, TEW.** Sea/substrate interface of microhabitats 1315; ´tide edge´ microhabitats.

Judgements on microhabitat were based on an area within 2m of the focal bird.

6.3 DIET

6.3.1 INTRODUCTION

The turnstone is renowned for its catholic choice of foodstuffs; some of the most bizarre ´prey´ which turnstone have been seen to scavenge are human corpse (Mercer, 1966), sheep corpse (Selway & Kendall, 1965), coconut (Below, 1975) and gull excrement (King, 1982; pers. obs.). More serious winter dietary studies have been conducted on The Wash estuarine complex, east England (Jones, 1975), Morecambe Bay, northwest England (Davidson, 1971; Prater, 1972a) and on a rocky shore in North Wales (Harris, 1979). In Britain the most important foods appears to be amphipod crustaceans, barnacles and littorinids. Crabs <u>Carcinus</u> <u>maenas</u> are also a regular food, as are mussels <u>Mytilus</u> <u>edulis</u>, cockles <u>Cardium</u> <u>edule</u>, Baltic tellins Macoma balthica and spire shells Hydrobia spp. on estuaries (e.g. Jones, 1975) but not on rocky shores (Harris, 1979; Feare & Summers, 1985).

Marshall (1981) showed that turnstone swallow small littorinids whole but probe ('winkle') out larger individuals from their shells: intermediate size classes are not eaten. Marshall's observations at Scoughall demonstrate that different prey are taken by different feeding techniques. On the strandline birds dig for sandhoppers Talitrus saltator and surface peck for small oligochaetes, and in intertidal areas birds rout for small littorinids and amphipods but probe for large gastropod molluscs. Marshall did not directly analyse the diet by inspection of prey remains or gut contents, but arrived at his conclusions by observations of feeding birds combined with a knowledge of the available invertebrates. Other studies have examined gizzard contents of shot birds (Davidson, 1971; Harris, 1979). The major drawback of pellet analysis is that soft-bodied prey are likely to be underestimated, and a similar bias is true of gizzard analysis (Goss-Custard & Jones, 1976). If combined with direct observations of feeding birds, pellet analysis can provide as much information as gizzard analysis (Worrall, 1981, 1984) without resorting to killing birds. The technique can be further improved by knowledge of potential prey availability. Most of the potential prey of turnstone on the study site contained hard parts, and so to gain information on the diet of the study population I adopted an approach combining pellet analysis, feeding observations and 'spot' samples of invertebrates in places where birds were feeding. As well as describing what prey were taken, I was also interested in what size of prey were taken, which microhabitats they were taken from and which technique was used to capture them.

6.3.2 METHODS

6.3.2.1 OBSERVATIONS

When making running commentaries on individuals´ feeding behaviour and when taking instantaneous records of individuals´ feeding techniques (section 6.5) I recorded which prey items were taken, either identified or unidentified. If the identity of a prey item was unclear, I took samples of the invertebrates which were available in the area where the bird was feeding in an attempt to clarify the prey´s identity. For each prey item taken I noted which feeding technique was used to take it and the microhabitat it was taken from.

6.3.2.2 PELLETS

It was very difficult to find pellets on the feeding areas, particularly the intertidal areas. Fortunately pellets were comparatively easy to find at roost sites when they were produced around high tide. Pellets were produced by birds as soon as they left the intertidal areas, or later, after they had been feeding on the strandline. The vast majority of roost sites where pellets were collected were rocky, so footprints were of little use in identifying which species had produced the pellets (see Goss-Custard & Jones, 1976; Worrall, 1984). Therefore, I only collected pellets from where I had seen turnstone roosting, even though my disciminatory ability improved until it became possible to identify turnstone pellets comparatively easily.

Turnstone pellets were variable in size and, particularly, in shape, depending on what the pellets contained. Pellets consisting mainly of barnacle Balanus balanoides plates were loose in construction and easily broke when I picked them up. On the other hand, pellets were smooth, compact and well formed when they consisted mainly of amphipod crustaceans. The colour of pellets also varied according to the remains they contained. On average turnstone pellets were about 1.7x0.9x0.9cm.

I attempted to collect pellets in every month of the 1982-83 winter, but they were collected irregularly during the 1983-84 winter. Each pellet was placed in its own sealable tube and kept dry until its contents were examined.

After being left to soak in water for a few minutes each pellet was gently broken up in a petri dish containing about 5mm of water and examined under a binocular microscope. Parts of prey items which occurred only once or a few times in the intact animal were counted, and for main prey species, they were measured using a graticule in the eyepiece of the microscope (Table 6.1). Parts of the main prey species which were measured varied from the width of the opercular whorl (see Fretter & Graham, 1962) in Littorina littorea and L.obtusata, to the length of the terminal joint (the ´claw´) on the second thoracic limb of Hyale (Table 6.2, Fig. 6.1). It should be noted that I did not differentiate between the two Littorina species, L.mariae and L.obtusata (Sacchi & Rastelli, 1966) and both species were included under the collective title of L.obtusata. This was because L.mariae and L.obtusata can not be distinguished on opercular

TABLE 6.1.

Parts of prey items that were counted in each pellet.

Mollusca: Gastropoda:	Opercula	*Littorina* spp. *Gibbula cineraria* *Nucella lapillus*
	Intact animals and terminal whorls	*Littorina* spp. *Nucella lapillus* *Lacuna* *Rissoa* *Cingula*
Mollusca: Bivalves:	Hinges	*Mytilus edulis*
Crustacea: Amphipods:	Intact animals	*Hyale* sp. *Talitrus saltator*
	2nd thoracic claws	*Hyale* sp.
	Head parts	*Hyale* sp. *Gammarus* sp. *Talitrus* saltator
Crustacea: Isopoda:	Terminal abdominal plates and 2nd antennae	*Idotea granulosa*
Crustacea: Decapoda:	Chelae	*Carcinus maenus* *Eupagarus* sp.
Crustacea: Cirripedia:	Scutal plates	*Balanus balanoides*
Insecta; Coleoptera:	Elytra	Unknown species
Insecta: Diptera:	Tibial or	*Coelopa* spp. adults
	Head parts	Unknown species
	Intact or partially intact animals	*Coelopa* spp. pupae and larvae

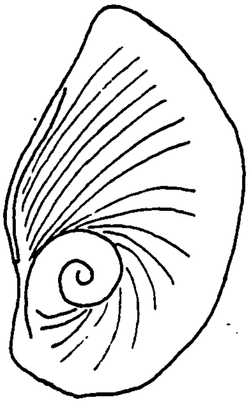
TABLE 6.2

Parts of prey items in pellets that were measured.

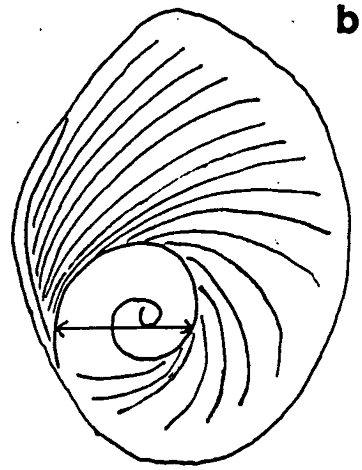
Width of operculum whorl	*Littorina littorea* *Littorina obtusata*
Diameter of central five ´rings´ of operculum	*Gibbula cineraria*
Right scutal plate	*Balanus balanoides*
Intact animal	*Littorina littorea* *Littorina* obtusata *Hyale* sp.
2nd antenna	*Idotea granulosa*
2nd thoracic claw	*Hyale* sp.

Fig. 6.1 Opercula of (a) Littorina obtusata, (b) L.littorea, (c) Nucella lapillus, (d) Gibbula cineraria (e) (i) Hyale (ii) Balanus balanoides. Arrowed lines indicate parts of prey species which were measured.

a



b



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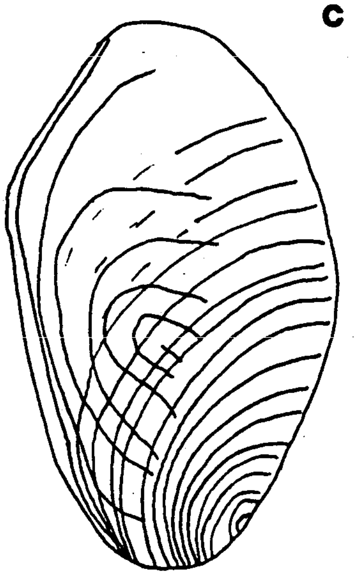
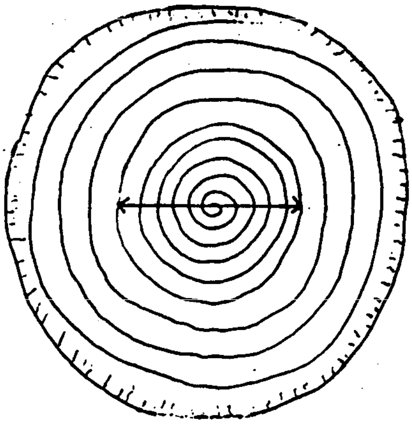
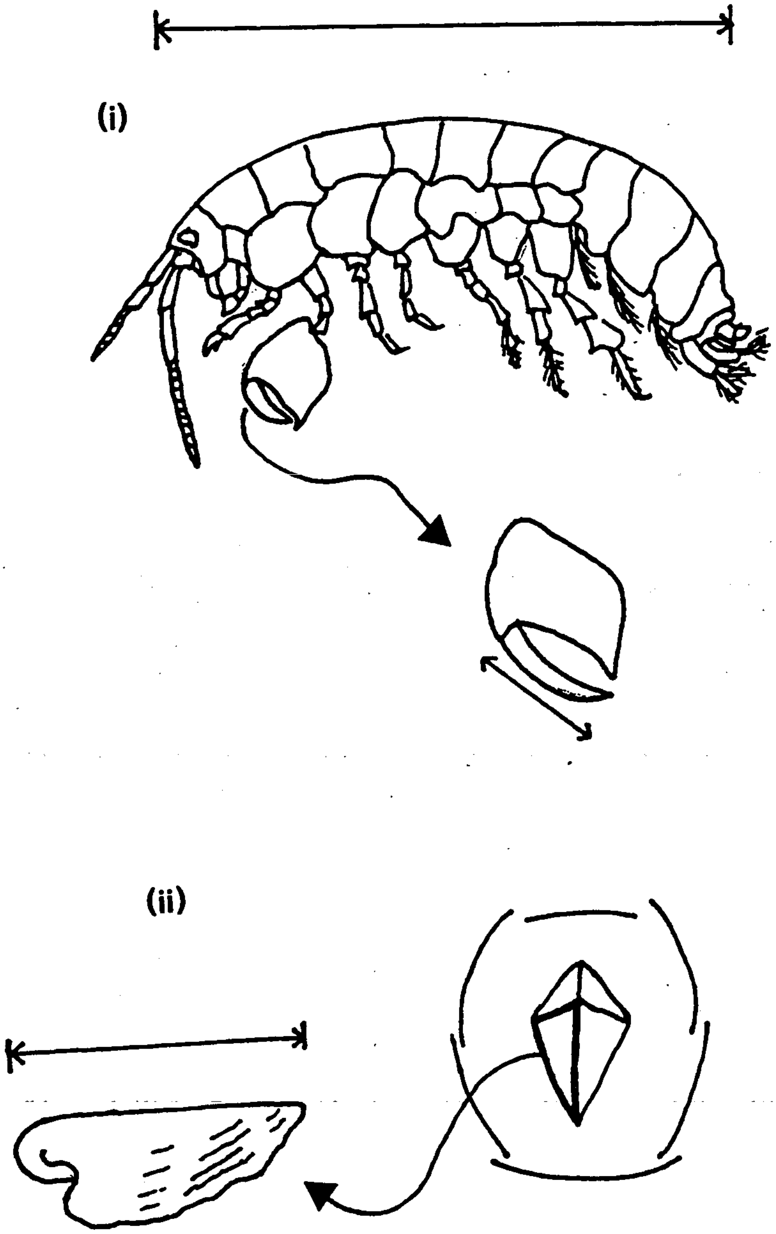


d



e



features (e.g. Goodwin & Fish, 1977). The opercula of L.littorea and L.obtusata could be separated on the basis of colour and shape (Fig. 6.1). To estimate the size of prey which were taken I measured whole animals collected on the study site then measured the part which was represented in pellets. For example, I measured maximum shell height of L.littorea and then the width of the operculum whorl. From regression analysis the equations describing the relationships between the size of prey parts and size of whole prey could be obtained. All measures of prey parts showed a high correlation with measures of whole prey, so the size of prey items could be estimated from measurements of prey parts (Table 6.3). The numbers of each prey species in a pellet were estimated by dividing the number of a particular part by the number of times it occurred in the intact animal. I also estimated, to the nearest 10%, the proportion of each pellet occupied by the parts of each prey species (cf Prater, 1972b).

Most observations and pellets were collected in the 1982-83 winter so I have restricted my analysis to that winter.

6.3.3 RESULTS

6.3.3.1 OBSERVATIONS

A summary of the prey taken as determined by direct observation is presented in Table 6.4. Routing birds feeding in WR/SWR (mainly Fucus spp. seaweeds) predominantly ate small yellow-orange crustaceans: these were undoubtedly an amphipod identified as Hyale as this animal was the predominant crustacean in samples of WR/SWR. Smaller numbers of small Littorina obtusata were swallowed whole and the isopod Idotea was also taken, as were crabs Carcinus maenas,

TABLE 6.3.

Regression equations relating measures of prey parts in pellets to measures of whole animals.

Prey species	x Measure of part	y Measure of whole animal	Equation	Correlation	
				r	N
_L_. _littorea_	Operculum whorl width	Maximum shell height	$y=1.35+7.06x$	0.973	69
_L_. _obtusata_			$y=-2.51+9.54x$	0.961	69
Gibbula	Central operculum rings	"	$y=4.82+3.49x$	0.729	26
Balanus	Right scutum length	Internal diameter	$y=0.14+0.94x$	0.962	66
Idotea	2nd antenna	Flattened body length	$y=2.12+2.86x$	0.981	33
Hyale	2nd thoracic claw	Curved body length	$y=1.79+4.38x$	0.938	33

TABLE 6.4

Summary of prey species eaten by turnstone as determined by direct observation and ´spot´ samples of site where birds were feeding. Season 1 = August to October; season 2 = November to January; season 3 = February to April. Hammer probing birds were seen feeding almost exclusively on large (> 5mm internal diameter) barnacles <u>Balanus</u>.

		--------probably-----------						
Technique	Season	Hyale	Idotea	small littorinid	Gammarus	large littorinid	crab	small prey
ROUT	1	285	49	22	-	-	12	73
	2	106	12	18	-	-	2	54
	3	199	21	39	-	-	4	38
PROBE	1	7	28	-	-	124	5	18
	2	3?	10	5	-	202	-	-
	3	2?	4	7	3	141	-	4
TURN STONE	1	-	-	15	2	-	1	4
	2	-	-	148	26	-	-	30
	3	3	1	177	38	1	1	43

particularly in August and September. A much larger proportion of Idotea were eaten in AR (mainly Enteromorpha seaweed), but this microhabitat had disappeared from the study site by December.

Probing birds mainly winkled the larger size classes of L.obtusata and L.littorea when feeding in or at the tide edge of intertidal seaweeds. The proportions of the two species which were taken seemed to vary from area to area, according to their relative abundance. In the Coastguard (CG) area, for example, L.obtusata predominated as prey, whilst at Car Rocks (CR) area L.littorea did. Idotea and Carcinus were also captured occasionally by probing birds, particularly in August and September, and Idotea was the main prey eaten by probing birds in AR. In pools the vast majority of probing prey were large L.littorea. There appeared to be a greater number of birds which were seen infrequently until late December when a number of birds appeared to switch from hammer-probing barnacles Balanus balanoides to turning stones (the 'Field Space' birds, see later and Chapter 3). In pools and pebbles, stone turners most frequently picked small littorinids off the bottom of an overturned stone and swallowed them whole: these littorinids were probably mainly L.littorea judging by the preponderance of this species in samples. Relatively large red-brown crustaceans were also taken but less frequently: sampling showed these to be an amphipod probably Gammarus spp.. On the pebble beach at Tower Cove birds turned stones on the strandline to expose Coelopa adults on their mass emergences on warm days in mid-winter.

Hammer-probing birds ate barnacles almost exclusively, but occasionally large crabs (c. 2cm carapace width) were broken open by birds hammer-probing on their ventral surface. After November the number of barnacles which were taken gradually decreased because the number of birds hammer-probing decreased (see later, and Chapter 2).

Surface pecking was a comparatively uncommon technique in intertidal feeding areas (see also Marshall, 1981). It occurred most often in birds in the Tantallon area where it appeared to be employed in taking some small L.littorea but mainly barnacles which were swallowed whole. In contrast, on the strandline surface pecking was by far the most common technique employed by birds feeding on small oligochaetes, all stages of Coelopa (particularly larval) and sandhoppers Talitrus saltator. Talitrus were also taken by birds digging and were eaten only in August, September and late February to April.

6.3.3.2 PELLETS

The vast majority of prey contained hard parts and therefore should be represented in pellets. The main intertidal prey species were Littorina littorea, Hyale, Balanus, L.obtusata and Gibbula (Table 6.5). Strandline prey species were Coelopa, particularly adults, Talitrus saltator and a small unidentified coleopteran. Perhaps due to comparatively small sample sizes, small monthly changes in diet composition were occasionally erratic (Table 6.6, 6.7; Fig. 6.2). Some broad trends, however, do emerge. Several species occurred in the diet mainly in August and September (Talitrus, Carcinus, Eupagarus, Rissoa, coleopteran), whilst the importance of others increased towards the end of the winter (whole L.Littorea and L.saxatilis, Gammarus). There is also a suggestion both that the proportion of Hyale dipped in mid-winter and that this

TABLE 6.5.

The proportional contribution of intertidal prey species to the diet of turnstone as revealed by pellet analysis.

	% contribution to diet in numbers	N
L.littorea opercula	30.7	4114
Hyale sp.	26.7	3583
Balanus balanoides	12.1	1621
L.obtusata opercula	10.3	1384
L.obtusata whole	7.1	956
Gibbula cineraria opercula	4.4	590
L.littorea whole	3.9	527
Gammarus sp.	1.4	192
Idotea granulosa	0.8	101
L.saxatilis whole	0.6	85
Carcinus maenas	0.6	76
Lacuna sp.	0.3	46
Nucella lapillus whole	0.3	34
Mytilus edulis	0.2	32
Rissoa sp.	0.2	26
Eupagarus bernhardus	0.2	22
Cingula sp.	0.2	8
Gibbula cineraria whole	0.1	8
Nucella lapillus opercula	0.0	1
Total:		13403

TABLE 6.6

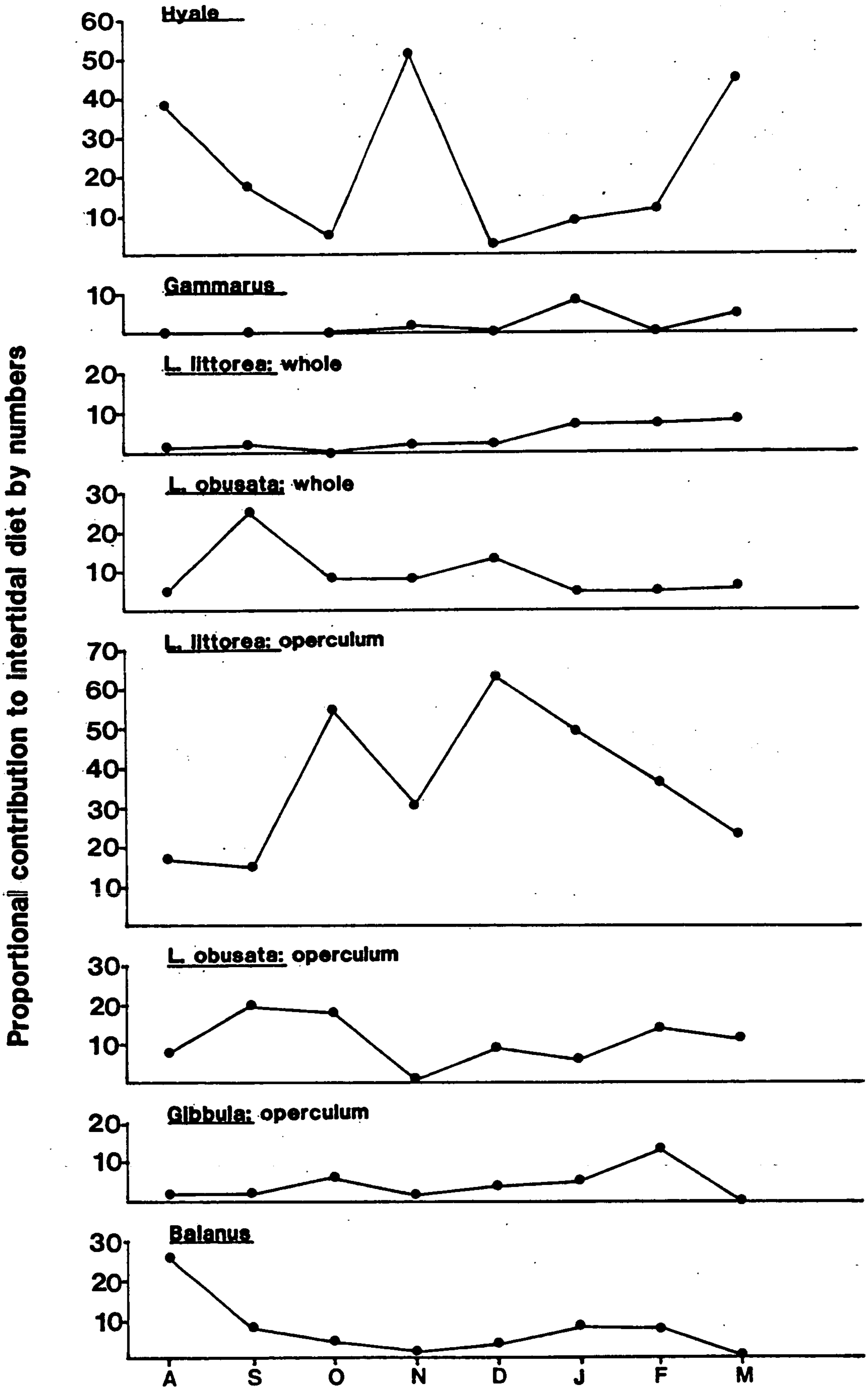
Mean % volume occupied by remains of prey species in pellets.

N pellets	81	50	23	15	36	23	55	33
Month	A	S	O	N	D	J	F	M
Idotea	1	0	0	0	1	1	0	0
Balanus	34	6	5	2	4	10	7	0
Eupagarus	0	0	0	0	0	0	3	0
Talitrus	2	2	0	0	0	0	1	0
L.littorea whole	0	0	0	2	2	12	11	11
L.littorea oper.	10	5	25	17	28	27	28	21
L.obtusata whole	4	11	7	18	22	7	11	12
L.obtusata oper.	4	4	7	0	3	3	10	12
Gibbula oper.	1	0	2	2	1	2	8	0
Coelopa	1	13	17	15	22	8	0	0
Coleoptera	1	15	0	0	0	0	0	0
Gammarus	0	0	0	1	0	5	0	5
L.saxatilis	0	0	0	1	0	0	4	3

TABLE 6.7

The percentage of pellets in which selected prey species occurred.

N pellets	81	50	23	15	36	23	55	33
Month	A	S	O	N	D	J	F	M
Hyale	33	18	13	27	17	4	13	42
Idotea	9	4	4	13	8	4	4	12
Balanus	58	10	9	7	31	43	20	0
Carcinus	46	26	13	7	6	4	11	6
Eupagarus	15	2	0	0	3	0	9	3
Talitrus	4	12	0	0	0	0	4	0
L.littorea whole	16	16	9	13	28	52	49	64
L.littorea operculum	19	14	43	27	64	57	55	33
L.obtusata whole	40	56	43	47	72	61	71	84
L.obtusata operculum	15	26	22	13	19	13	18	27
Gibbula operculum	11	2	22	7	19	17	33	0
Coelopa	5	38	48	33	36	13	2	0
Coleoptera	0	50	13	0	0	0	0	0
Gammarus	0	0	0	3	0	4	4	15
L.saxatilis	0	0	0	0	3	0	20	18


Proportional contribution to intertidal diet by numbers
Hyale
60
50
40
30
20
10
Gammarus
10
L. littorea: whole
20
10
L. obusata: whole
30
20
10
L. littorea: operculum
70
60
50
40
30
20
10
L. obusata: operculum
30
20
10
Gibbula: operculum
20
10
Balanus
30
20
10
A
S
O
N
D
J
F
M

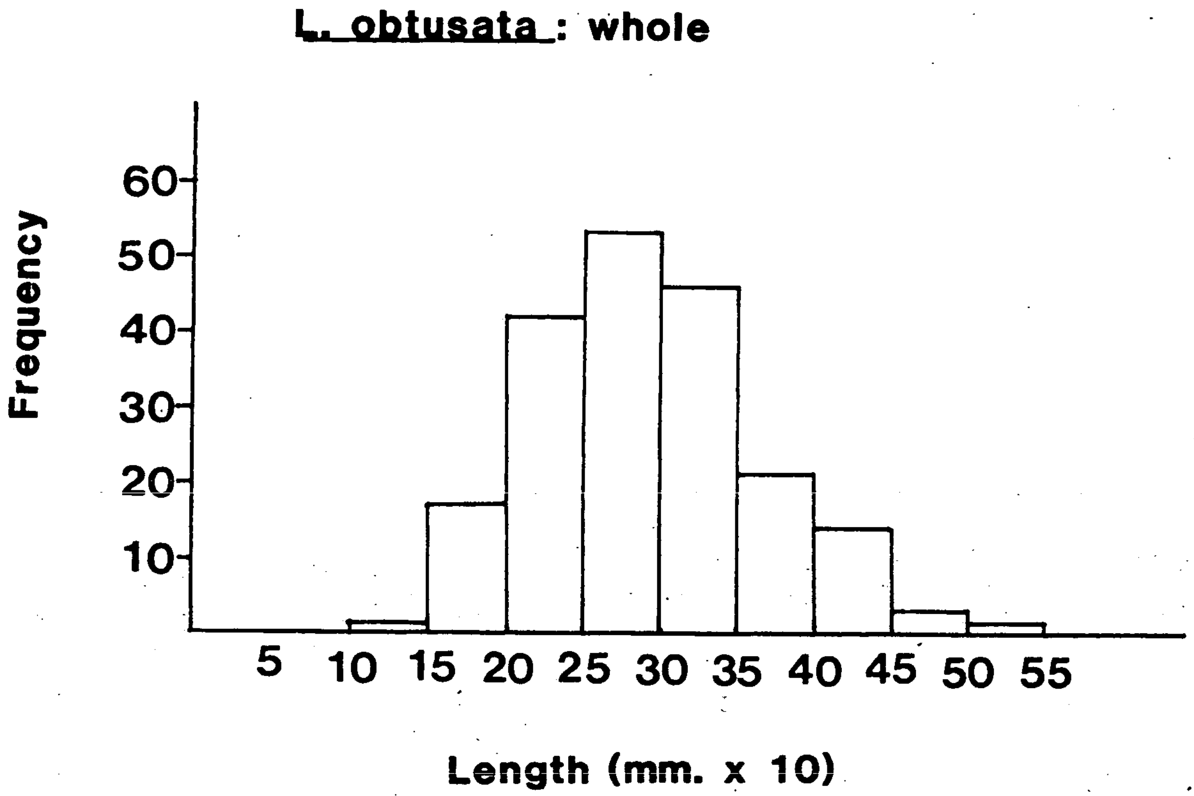
was reflected by a mid-winter increase in the proportion of L.littorea opercula.

The presence of gastropod opercula on their own is indicative that the prey were taken by probing, since then no shell is ingested (Marshall, 1981; previous section). Measurements of opercula in pellets showed that the larger size classes of L.littorea, L.obtusata and Gibbula cineraria were selected by probing birds, and that the smaller size classes of L.littorea and L.obtusata were swallowed whole: intermediate sized gastropods were usually not taken, thereby confirming the observations of Marshall (1981) (Figs.6.3-6.5).

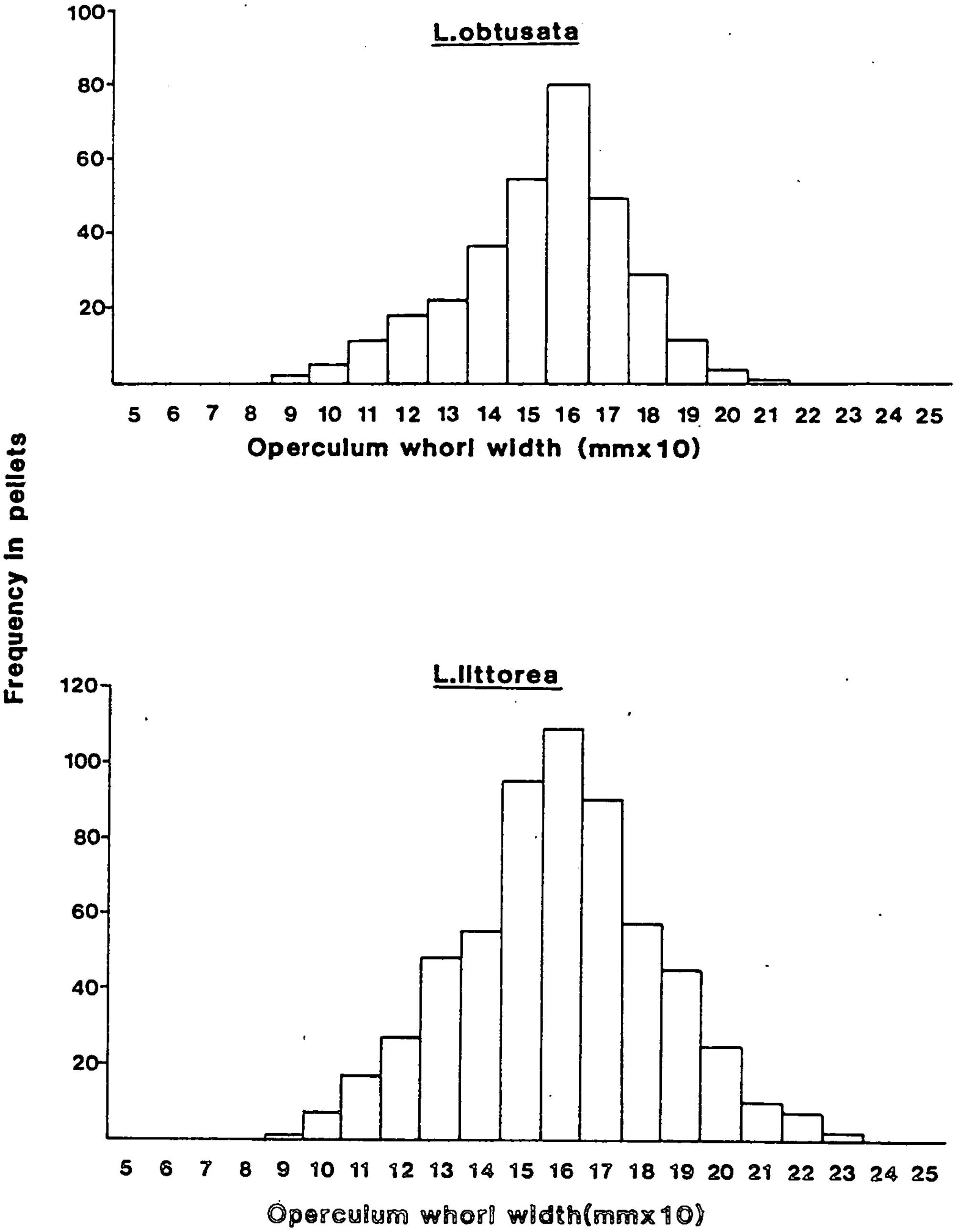
The mode shell height of L.obtusata which was taken by probing birds was 12.6mm (in size class 5, 12.6-15mm: see Chapter 3 and section 6.4). The smallest probed L.obtusata had shell heights of 6.1mm, in the middle of size class 2, but the vast majority of L.obtusata which were probed were of size classes 4 to 6 i.e. over 10mm shell height. This is in contrast to the size of L.obtusata which were swallowed whole, as these prey were always under 5mm shell height i.e. size class 1.

The mode shell height of L.littorea which was probed was 12.6mm (size class 3: see Chapter 3), the smallest which were probed were 7.7mm, the largest, 17.6mm (size class 2 and 4, repectively). Most L.littorea which were swallowed whole were of size class 1 i.e. less than 7mm shell height.

The size range of Hyale which were taken was large (Fig. 6.6) compared with the size distribution of Hyale which were available (section 6.4; Chapter 3) the data suggested that fewer small individuals were taken than would be expected. This may well have been due to passive selection (Hulscher, 1982; Ens, 1982): their

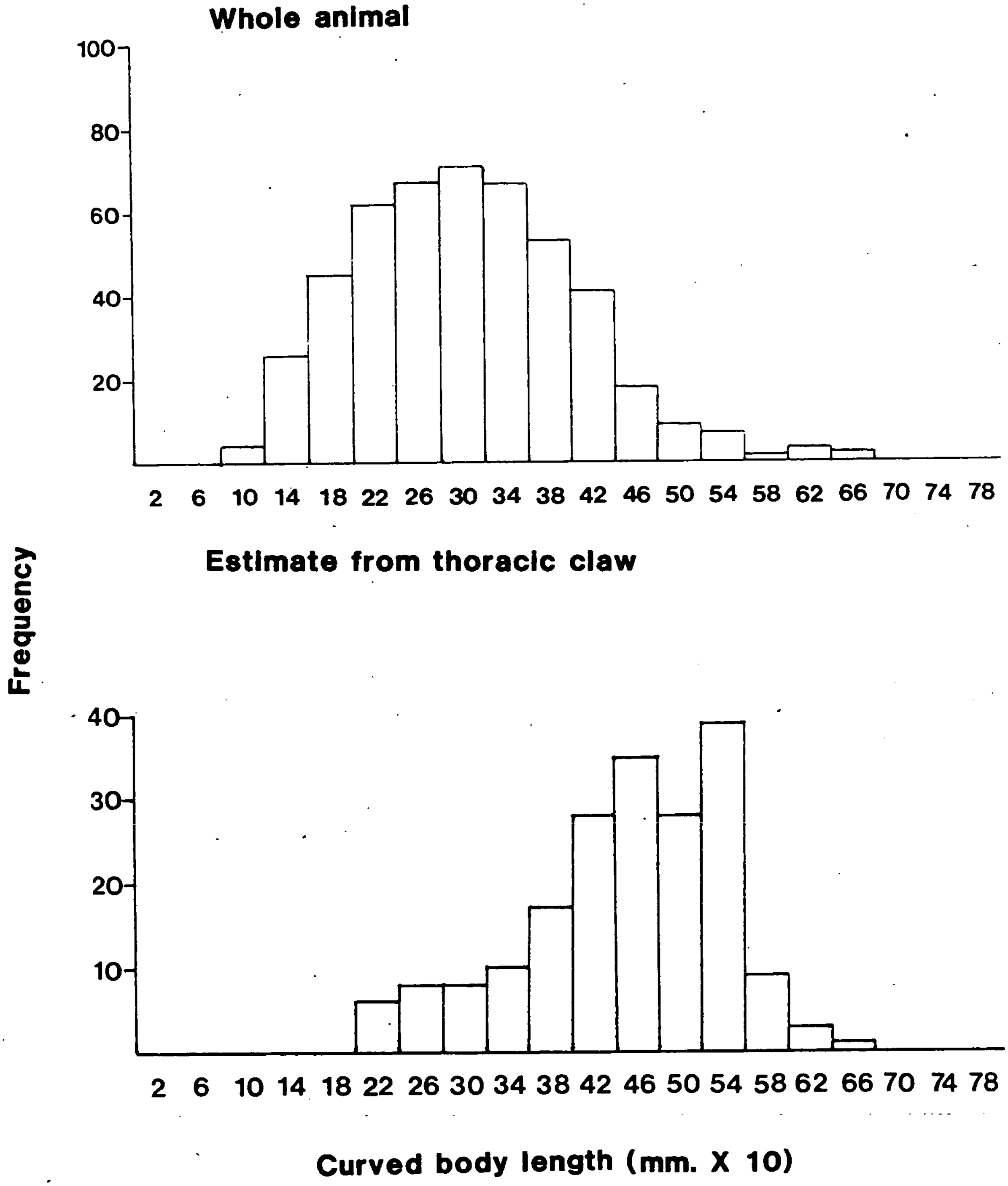


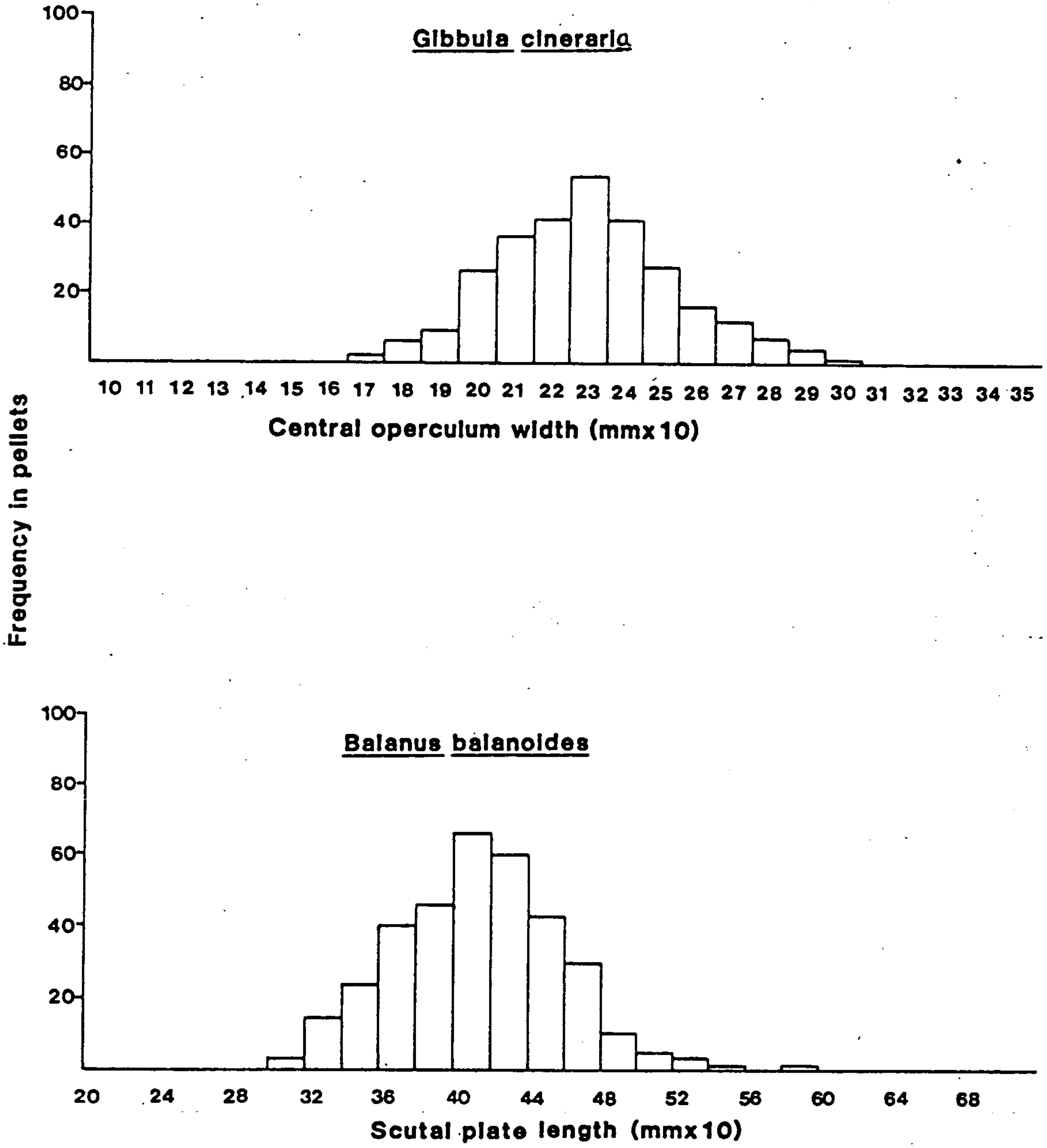
L. obtusata : whole
Frequency
60
50
40
30
20
10
5
10
15
20
25
30
35
40
45
50
55
Length (mm. x 10)



L.obtusata
100
80
60
40
20
5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Operculum whorl width (mmx10)
Frequency in pellets
L.littorea
120
100
80
60
40
20
5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Operculum whorl width(mmx10)

Hyale


Whole animal
100
80
60
40
20
2 6 10 14 18 22 26 30 34 38 42 46 50 54 58 62 66 70 74 78
Frequency
Estimate from thoracic claw
40
30
20
10
2 6 10 14 18 22 26 30 34 38 42 46 50 54 58 62 66 70 74 78
Curved body length (mm. X 10)


Frequency in pellets
Gibbula cineraria
100
80
60
40
20
10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35
Central operculum width (mmx10)
Balanus balanoides
100
80
60
40
20
20 24 28 32 36 40 44 48 52 56 60 64 68
Scutal plate length (mmx10)

small size made them less likely to be seen rather than their being actively ignored by feeding birds. The size distribution of Hyale as estimated by measuring the length of second thoracic claws perhaps indicated that measuring only intact Hyale in pellets produced a bias against larger individuals, although very small thoracic claws may have been missed in searching through pellet contents (Fig. 6.6). Their size probably made larger Hyale more likely to be broken up, although this possibility was not tested. Similarly, on the basis of broken fragments I suspect that large scutal plates of Balanus were less likely to remain intact in pellets, although this may have been more a result of birds hammering into the barnacle rather than the action of the gizzard. Notwithstanding this possible bias, turnstone did seem to select larger barnacles before attempting to hammer them open (Fig. 6.5; Chapter 3) and hammer-probers undoubtedly ignored smaller individuals. Moreover, as noted earlier, some small barnacles were probably swallowed whole which will produce a further bias in estimating the size classes which were hammer-probed. In pellets containing a large proportion of Balanus plates there were often relatively large amounts of shed fragments of gizzard lining, which was possibly due to the abrasive nature of Balanus plates. In addition, although not quantified in the sample which I analysed, there also appeared to be a greater number of intact left scutal plates compared with right scutal plates which may be indicative of some form of ´handedness´ in hammer-probing turnstone.

6.3.4 DISCUSSION

In terms of identifying the main prey species there was a reasonably good agreement between the observations and the pellet analysis. In addition, the late winter rise in the proportion of whole L.littorea, L.saxatilis and Gammarus in pellets coincided with an increase in the number of birds turning stones and confirmed observations of the prey species taken by some stone turners. Similarly the increased importance of some prey species (e.g. Carcinus, Talitrus) in autumn and, to a lesser extent, in spring as revealed by observations were confirmed by pellet analysis. However, several biases can be identified which caution against accepting the pellet analyses as they stand on their own. First, as noted by other workers (Goss-Custard & Jones, 1976; Worrall, 1984) pellets are biased against soft bodied prey. Whilst this did not appear to be a serious bias in the present study it can explain the absence of strandline oligochaetes and the low number of Coelopa larvae in pellets. A more serious problem is that different prey were probably digested at different rates (cf Goss-Custard, 1969). For example, Gibbula cineraria is characteristically a low shore gastropod species both on the study site (pers. obs.) and elsewhere (e.g. Fretter & Graham, 1962; Lewis,1964), yet remains of Gibbula opercula were surprisingly common in pellets given the time interval between probable ingestion and egestion. Their presence indicates that it probably took a comparatively long time to remove and break down the flesh of the foot attached to an operculum, as it is most unlikely that opercula were retained as grinding agents. In contrast, the very low numbers of Hyale and, particularly, Idotea in pellets in some months suggested that these crustaceans were digested relatively rapidly (see also Goss-Custard, 1969, for Corophium). Frequently the only sign of amphipods or isopods was a ´mush´ containing some fragments of limbs and thoracic and abdominal plates.

Some ´prey´ items may be ingested or retained in the gizzard as grinding agents, particularly small littorinids. It is impossible to say how frequently turnstone retained parts of prey items as grinding agents. It is worth noting, however, that many pellets contained several small stones as well as small litorinids. Barnacle plates would seem to be good grinding agents (very few stones or sand were found in barnacle pellets), yet they did not appear to be retained as such, which suggests that the disproportionate numbers of small littorinids in pellets was more due to a long digestion period rather than their grinding qualities.

A further bias in the pellet analysis is that the pellets will tend to contain the remains of prey eaten at higher tidal levels. There were also seasonal differences in the time of the tidal cycle that turnstone went to roost. In early and late winter (autumn and spring) turnstone frequently went to roost straight after leaving intertidal feeding areas, but in mid-winter they frequently fed on the strandline before roosting. The high proportion of Hyale remains in pellets collected in November was due to a large proportion of the pellets having been voided by birds straight after leaving their intertidal feeding areas, unlike the other samples of pellets collected in mid-winter months.

Many pellets contained remains solely or predominantly from one prey species, and this was an indication that many turnstone specialised on particular prey species (see section 6.5). The prey preferences of the birds which voided the pellets used in the analysis will therefore affect the results, particularly if sample sizes are small.

My results agree with those of Harris (1979) in showing that the main prey of rocky shore turnstone are amphipod crustaceans, barnacles and littorinids. They also suggest that the importance of Carcinus crabs in the diet of turnstone on The Wash (Jones, 1975) may have been lower than suggested because few pellets were collected in mid-winter when Carcinus are probably infrequently taken (cf Goss-Custard & Jones, 1976, for redshank diet on The Wash). Mussels were relatively common on the study site but were rarely eaten, in contrast to the results from studies of the diet of estuarine turnstone.

Although the pellet-observation method of assessing the diet of waders is perhaps a little too qualitative, I would agree with Goss-Custard & Jones (1976) and Worrall (1984) in concluding that under the circumstances it is as good or better than other methods, particularly if the biases associated with pellet analysis are borne in mind.

6.4 INVERTEBRATE SAMPLING

6.4.1 INTRODUCTION

Marshall(1981) undertook a thorough sampling programme of the prey available to turnstone within a representative section of the study site at Scoughall. He discovered that prey biomass was lowest in mid winter, in comparison to early winter, but rose a little in late winter. High autumnal prey densities followed by low mid winter densities and moderate spring levels have been discovered by most workers sampling the invertebrates eaten by non-breeding waders (references in Pienkowski et al, 1984; Johnson, 1985; Goss-Custard et al, 1977). The object of the sampling described in this section was not to provide a comprehensive assessment of the biomass of prey available to the turnstone on the study site, but rather to monitor any possible seasonal fluctuations in the abundance of major prey species. Such monitoring would be useful for the interpretation of any seasonal changes in individual turnstones´ feeding behaviour (section 6.5). A further objective was to assess which of the prey species were to be found in the different microhabitats, although Marshall´s results, ´spot samples´ (section 6.3) and the invertebrate sampling of four different areas (Chapter 3) also provided this information.

6.4.2 METHODS

The methods associated with invertebrate sampling have been described elsewhere, as have the size categories of the main prey species (section 3.2.2). All samples were taken in the Coastguard area (see Fig. 1.2), where barnacles were not numerous, so whilst these invertebrates were a major turnstone prey elsewhere on the study site, they were rarely eaten at the Coastguard and are not considered further in this section. Samples were taken in the last week of each month in the 1982-83 and 1983-84 winters from several semi-permanent sampling stations, marked by a number painted on rock with white roadline paint. There were three stations per non-"tide edge" microhabitat (see section 6.2 for description of microhabitats): 1-3(AR), 4-6(WAR), 7-9(WR), 10-12(SWR), 13-15(Pebbles), 16-18(Pool), 19-21(BR), 22-24(Sand), 25-27(Wrack/Sand). These stations represented a compromise of a small-scale sampling programme attempting to monitor seasonal fluctuations in an extremely patchy environment (Marshall, 1981). All samples were taken from all stations on the same day.

6.3 RESULTS AND DISCUSSION

The major purpose of the sampling was to provide background information on seasonal fluctuations of the major intertidal prey species taken by the Coastguard birds which were used in the MANOVA analysis of feeding behaviour. Therefore, I have presented only the results of samples containing reasonable numbers of *Hyale*, *Idotea*, *L.obtusata* and *L.littorea*, as these were the predominant prey species eaten by Coastguard birds. Moreover, seasonal changes in invertebrate numbers were relatively the same in both winters, so I have presented detailed results for the 1982-83 winter only.

Hyale was found mainly in WR and SWR microhabitats (brown seaweed covered rocks) where its numbers appeared to be greatest in August and September, falling off to a low in December to February, before rising slightly in March and April (Fig. 6.7). Seasonal trends for *Idotea* were similar (Fig. 6.8). Numbers of small *L.obtusata* (size class 1) followed seasonal changes paralleling those of *Hyale* and *Idotea*, but there were no obvious trends in the numbers of larger individuals (Fig. 6.9). Interestingly though, the numbers of larger *L.littorea* did appear to show similar fluctuations to those of the crustaceans (Fig.6.10). It should be noted, however, that Coastguard birds rarely probed for *L.littorea*; in the Coastguard area

Fig. 6.7a Seasonal changes in the numbers of <u>Hyale</u> (size classes 1-4) in $0.066m^2$ samples collected from microhabitat WR at sampling sections 7 (triangle), ((open circle), 9 (closed circle).

a)

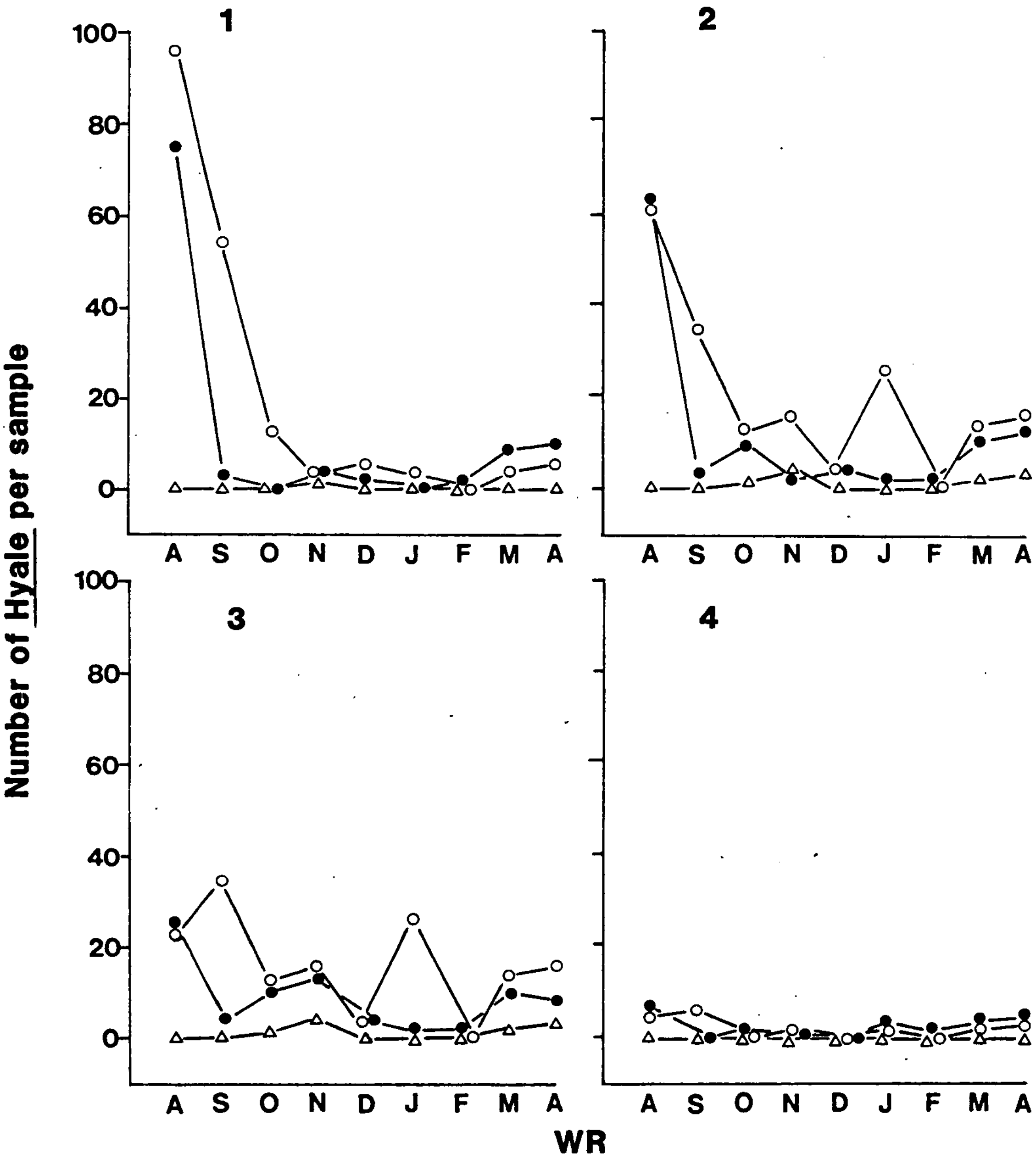


Fig. 6.7b Seasonal changes in the numbers of <u>Hyale</u> (size classes 1-4) in 0.066m^2 samples collected from microhabitat SWR at sampling stations 10 (triangle), 11 (open circle), 12 (closed circles).

b)

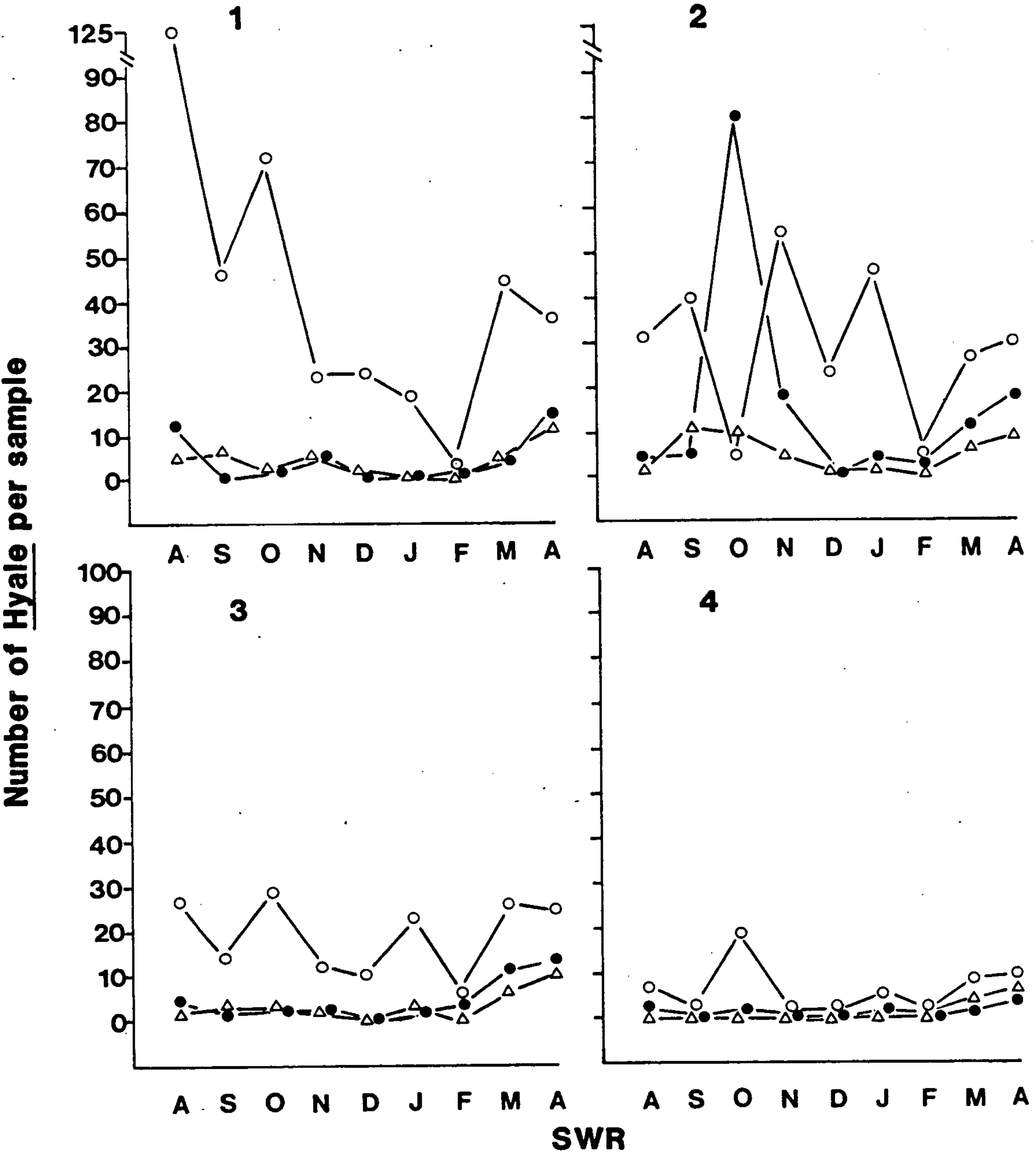
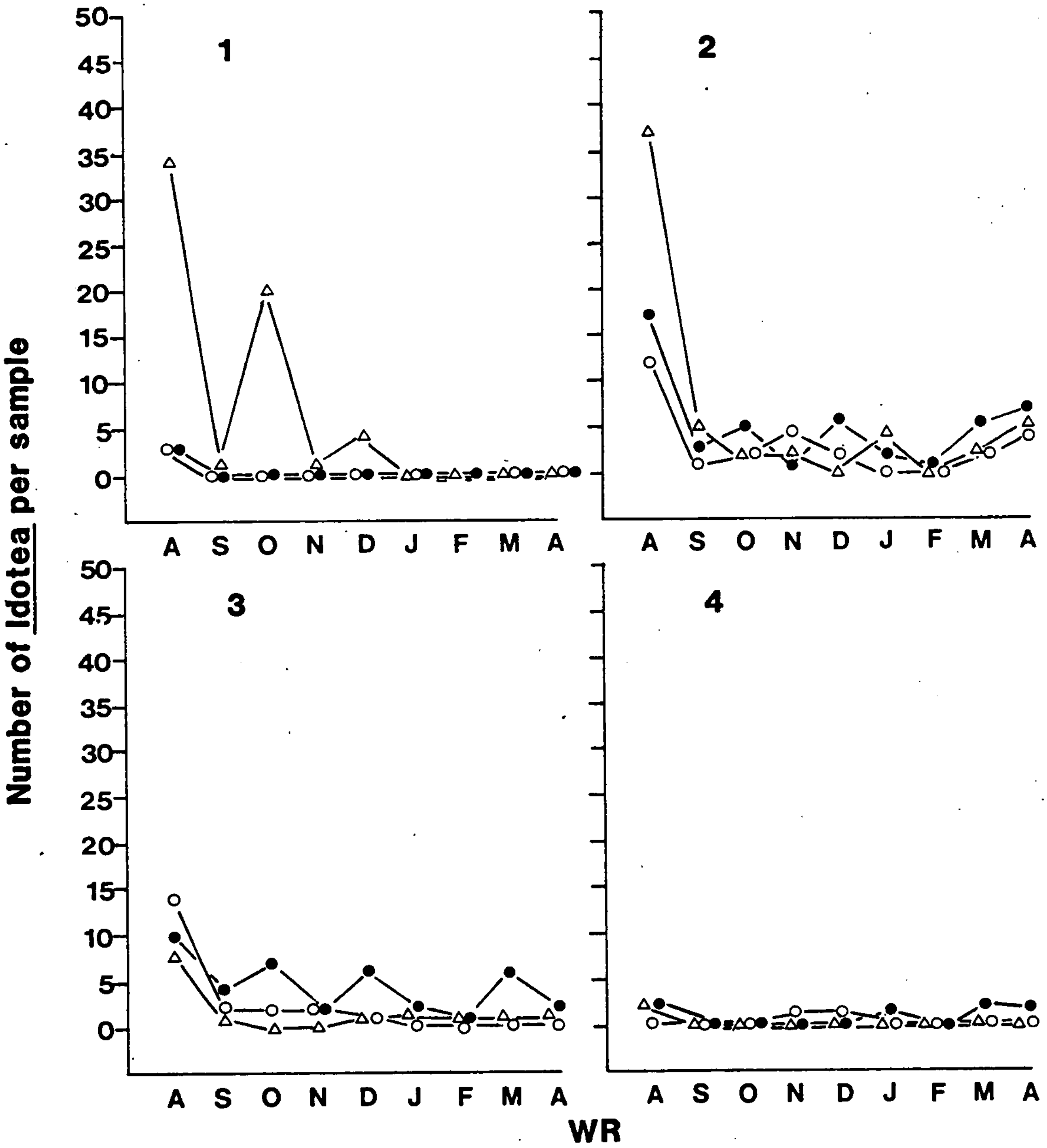

1
2
3
4
125
90
80
70
60
50
40
30
20
10
0
100
Number of Hyale per sample
A S O N D J F M A
SWR

Fig. 6.8a Seasonal changes in the numbers of <u>Idotea</u> (size classes 1-4) in 0.066m^2 samples collected from microhabitat WR at sampling stations 7 (trinagle9, 8 (open circle), 9 (closed circle).

a)



1
2
3
4
Number of Idotea per sample
50
45
40
35
30
25
20
15
10
5
0
A S O N D J F M A
WR

Fig. 6.8b Seasonal chnages in the numbers of <u>Idotea</u> (size classes 1-4) in 0.066m^2 samples collected from microhabitat SWR at sampling stations 10 (triangle), 11 (open circle), 12 (closed circle).

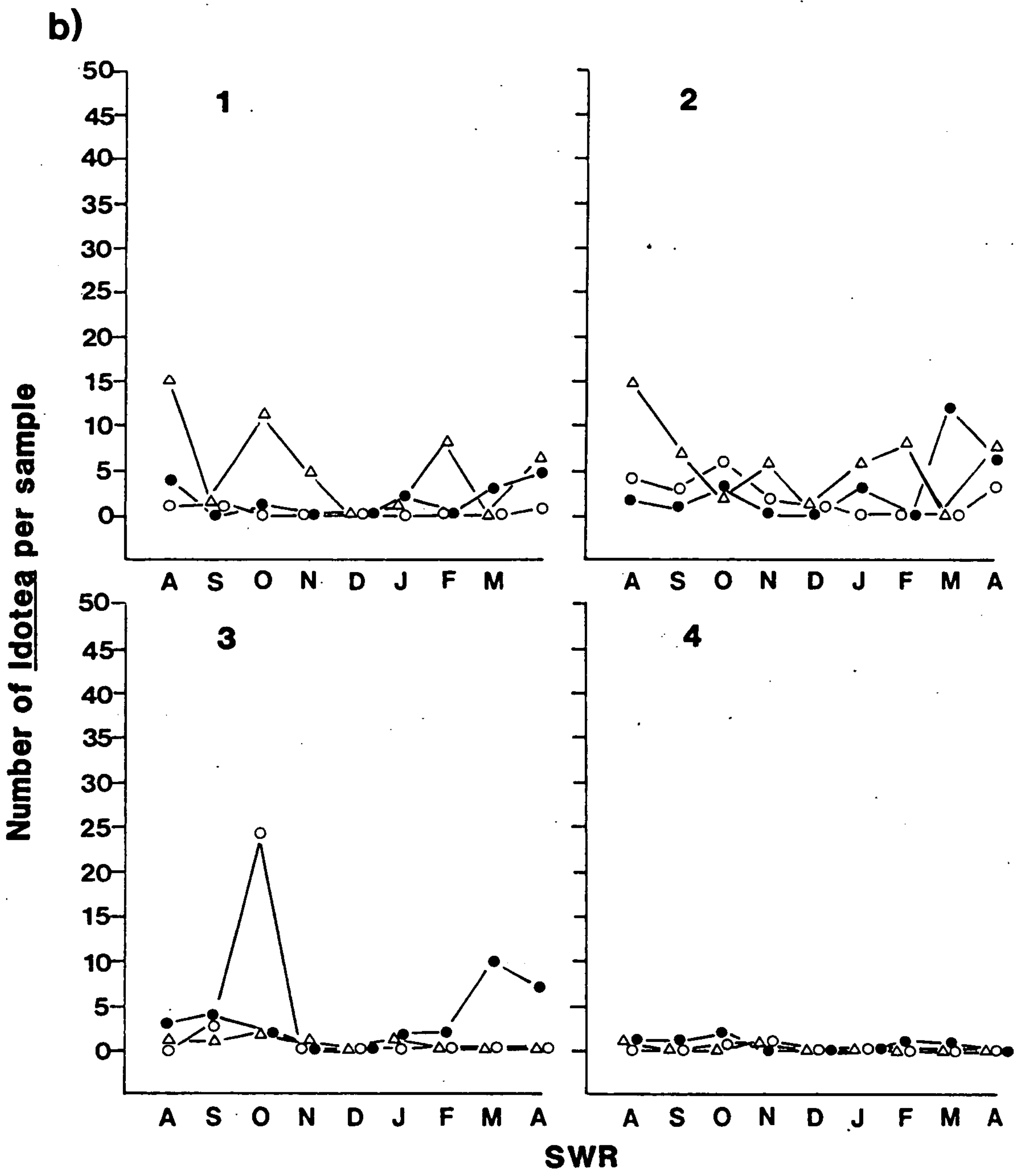
b)
1
2
3
4
Number of Idotea per sample
50
45
40
35
30
25
20
15
10
5
0
A
S
O
N
D
J
F
M
A
SWR

Fig. 6.9a Seasonal changes in the number of *Littorina obtusata* (size classes 1-6) in 0.066m^2 samples collected from microhabitat WR at sampling stations 7 (triangle), 8 (open circle), 9 (closed circle).

a)

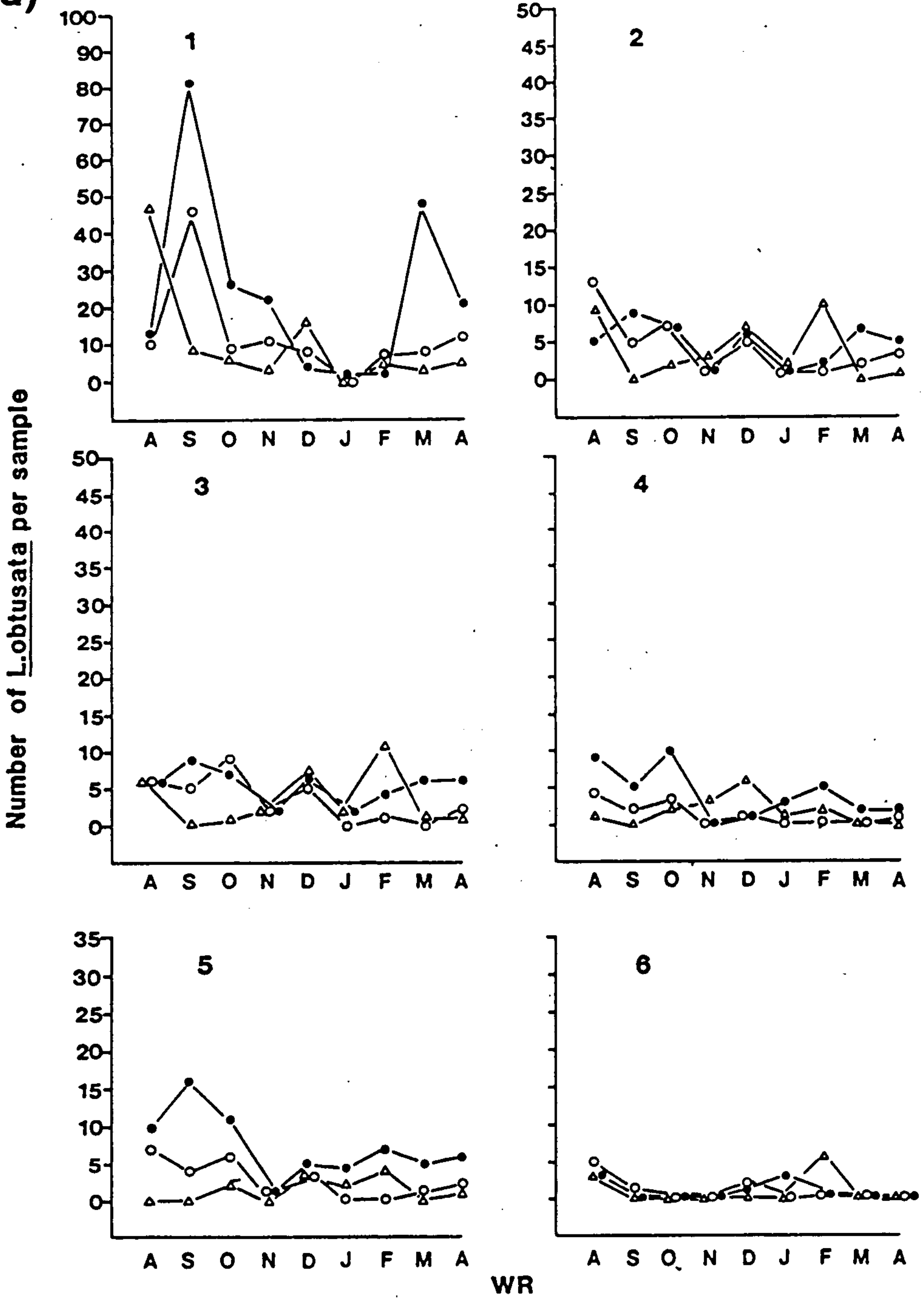

Number of L.obtusata per sample
1
2
3
4
5
6
100
90
80
70
60
50
45
40
35
30
25
20
15
10
5
0
A S O N D J F M A
WR

Fig. 6.9b Seasonal changes in the numbers of _L_._obtusata_ (size calsses 1-6) in 0.066m^2 samples collected from microhabitat SWR at sampling stations 10 (trinagle), 11 (open circle), 12 (closed circle).

b)

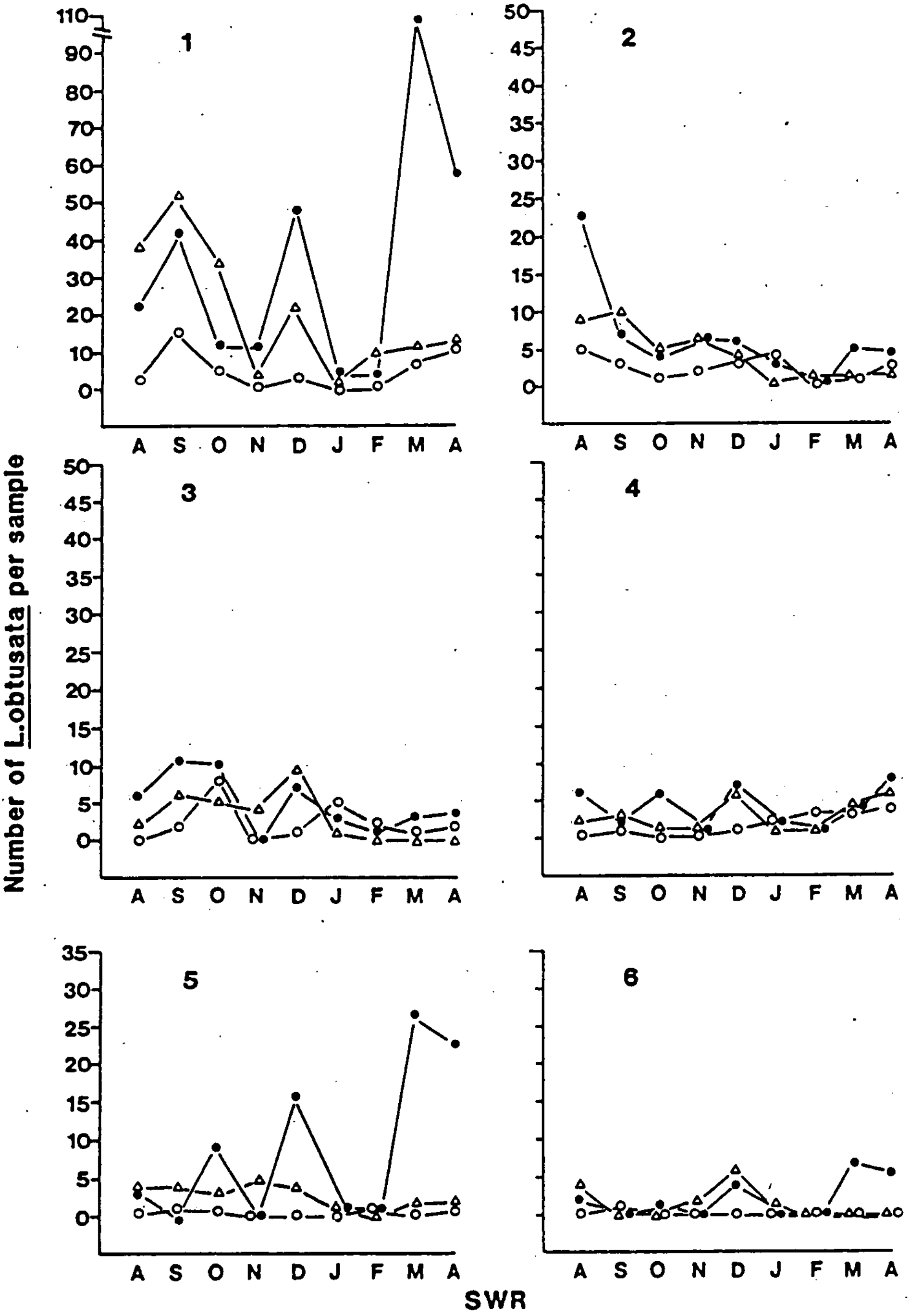
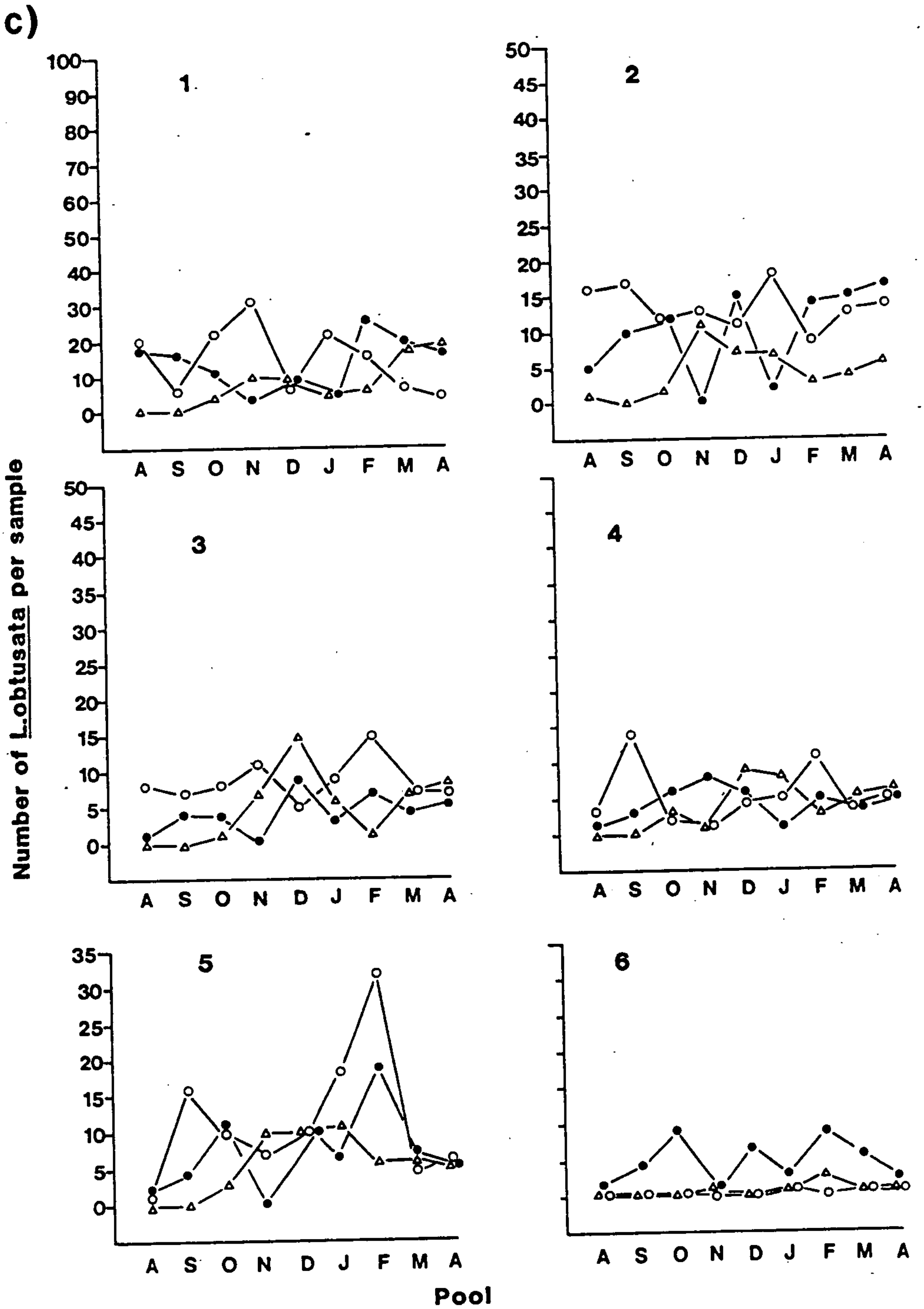

1
2
3
4
5
6
Number of L.obtusata per sample
A S O N D J F M A
SWR
110
90
80
70
60
50
45
40
35
30
25
20
15
10
5
0

Fig. 6.9c Seasonal changes in the number of <u>L</u>.<u>obtusata</u> (size classes 1-6) in 0.066m^2 samples collected from microhabitat pool at sampling stations 16 (triangle), 17 (open circle), 18 (closed circle).


c)
1
2
3
4
5
6
100
90
80
70
60
50
45
40
35
30
25
20
15
10
5
0
A S O N D J F M A
Number of L.obtusata per sample
Pool

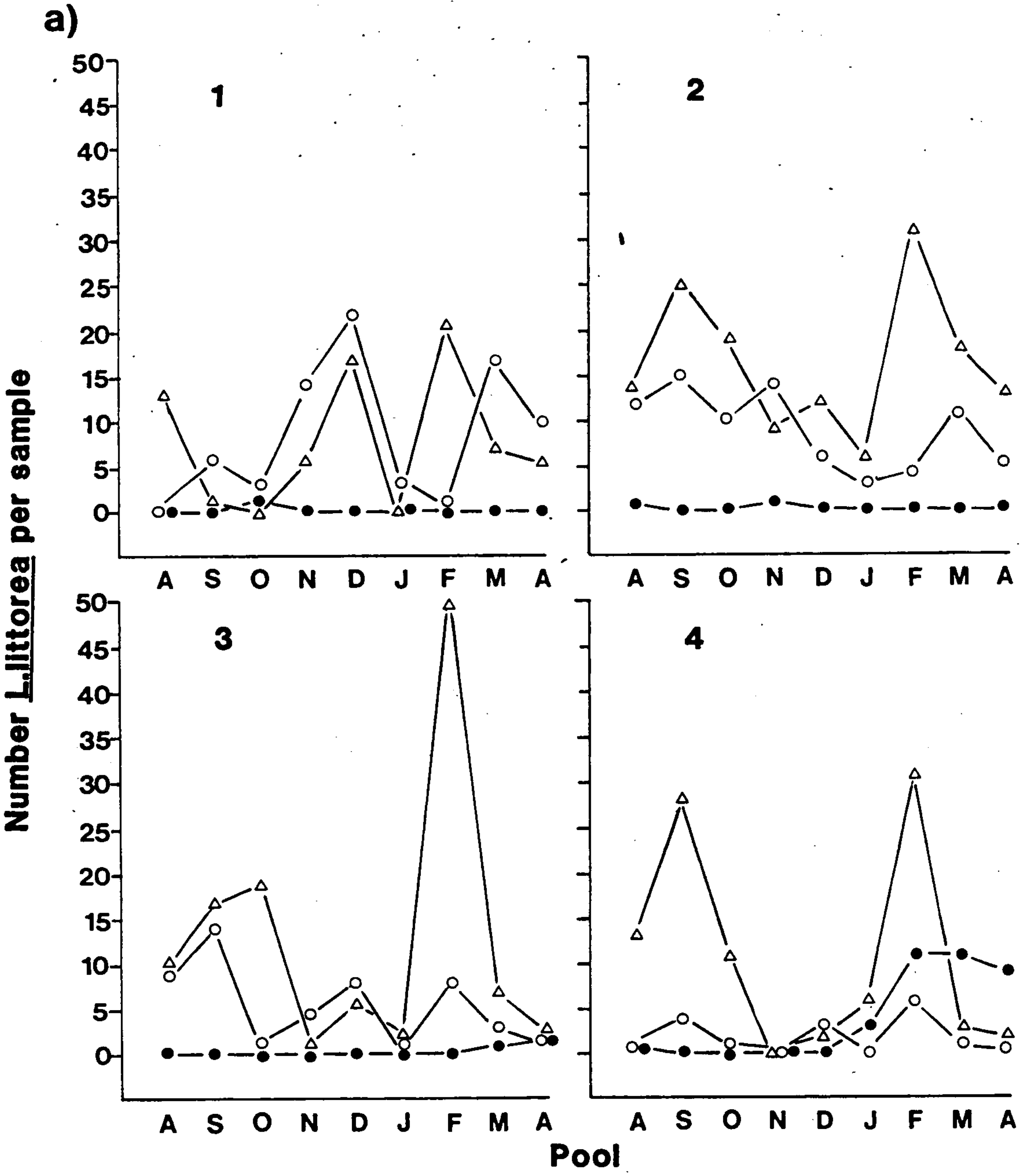
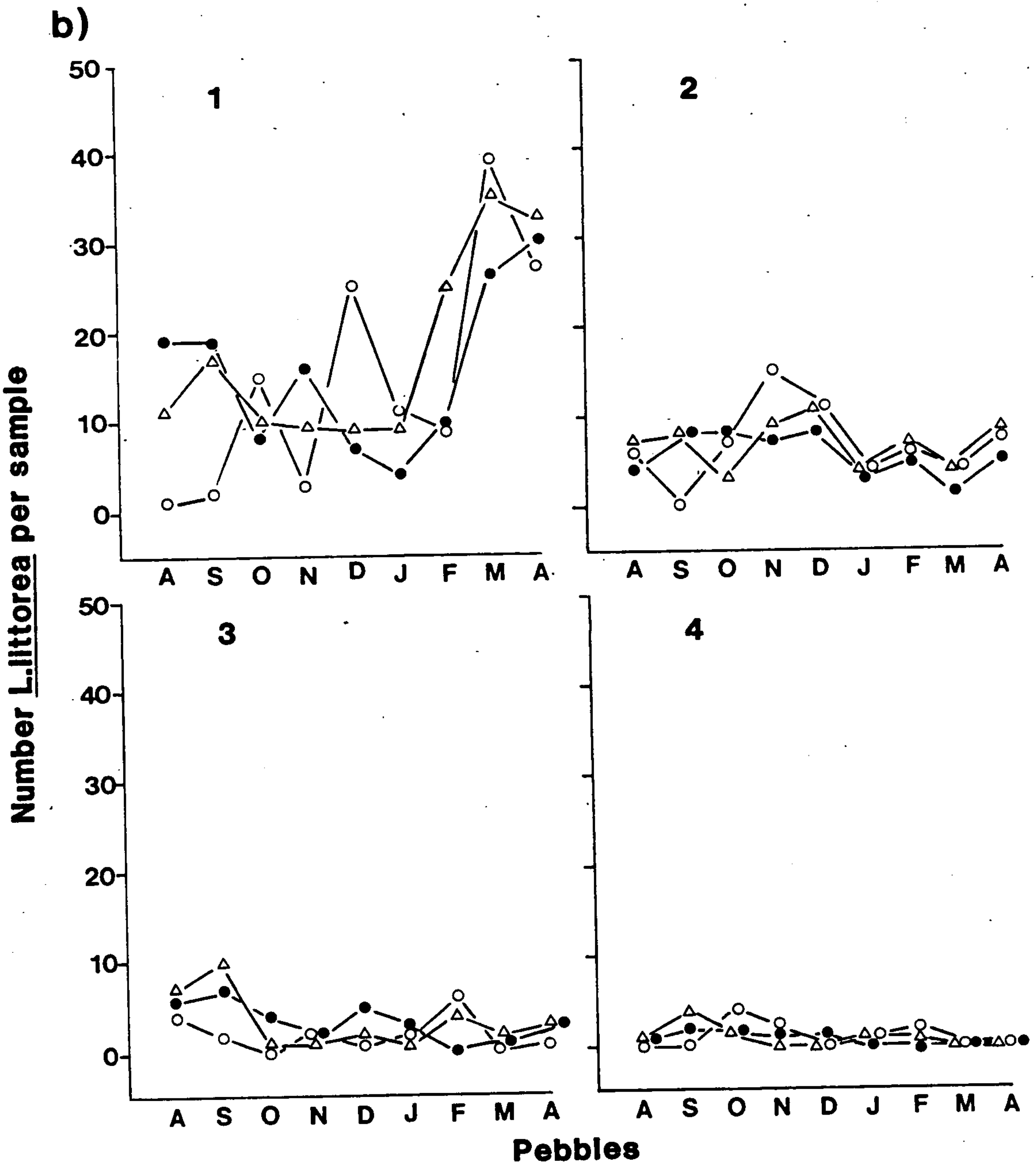

a)
Number L.littorea per sample
1
2
3
4
0
5
10
15
20
25
30
35
40
45
50
A
S
O
N
D
J
F
M
A
Pool

Fig. 6.10a Seasonal changes in the number of *L.littorea* (size classes 1-4) in 0.066m^2 samples collected from microhabitat pool at sampling stations 16 (triangle), 17 (open circle), 18 (closed circle).

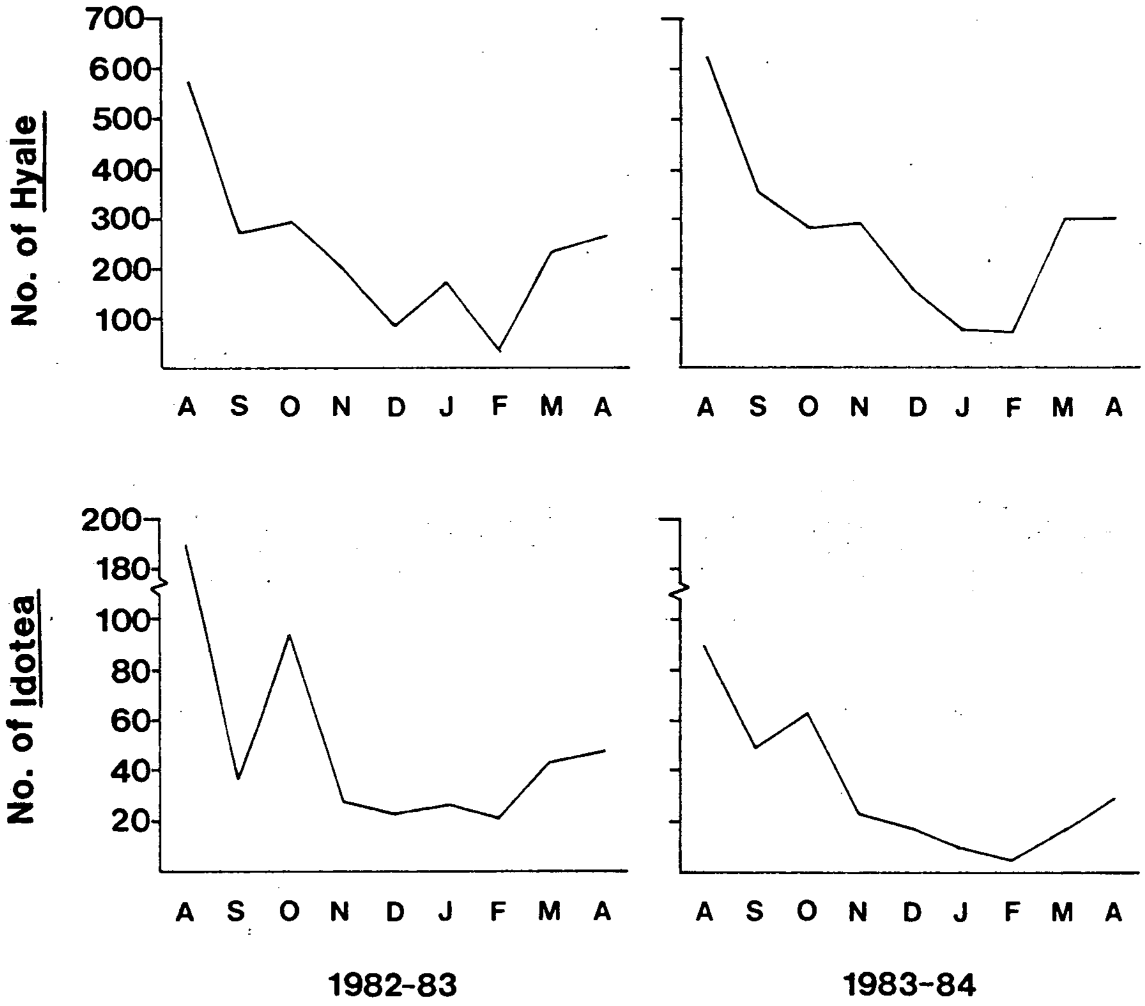
Fig. 6.10b Seasonal changes in the numbers of *L. littorea* (size classes 1-4) in 0.066m^2 samples collected from microhabitat pebbles at sampling stations 13 (triangle), 14 (open circle), 15 (closed circle).

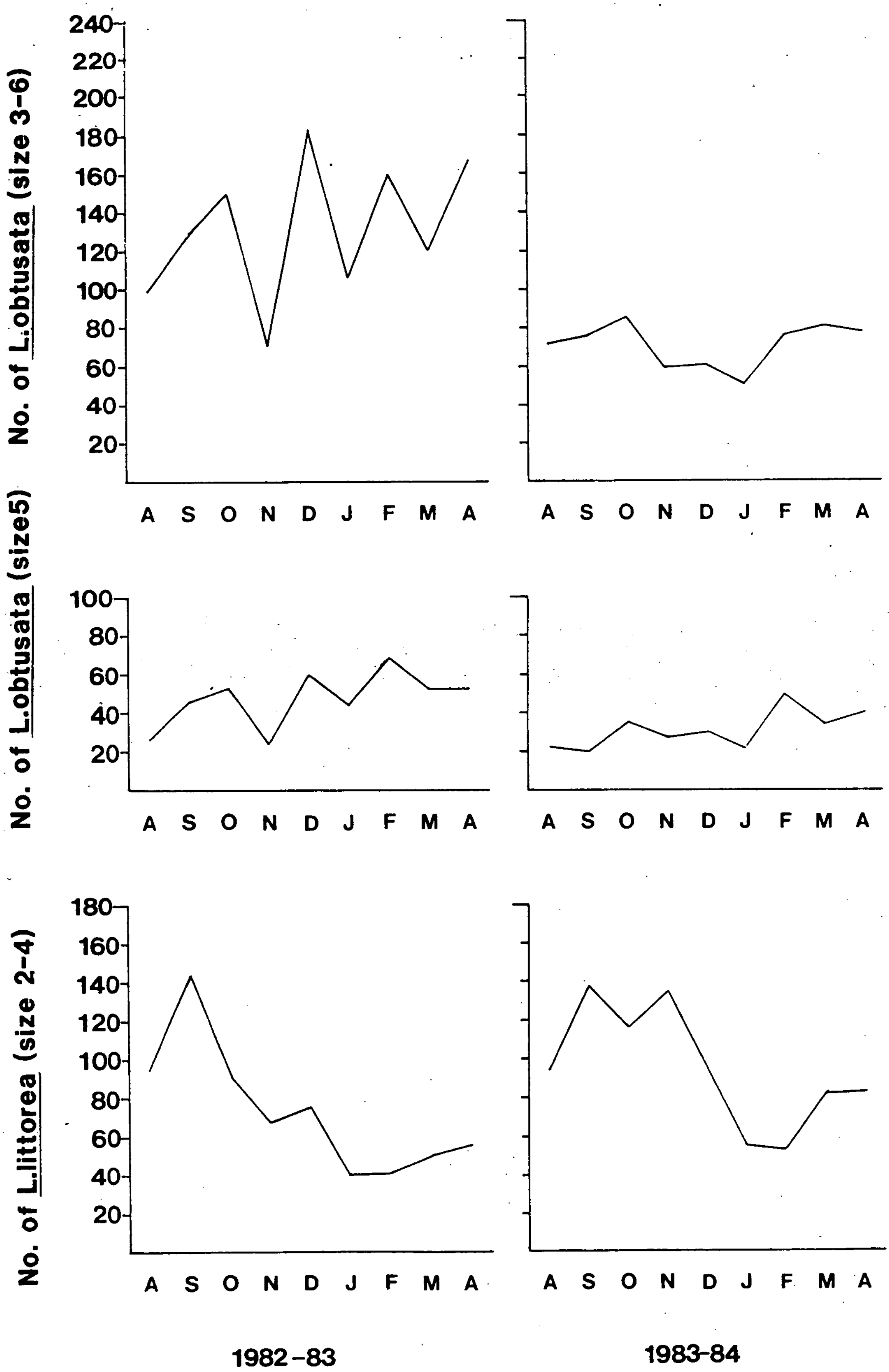

b)
Number L.littorea per sample
0
10
20
30
40
50
1
2
3
4
A
S
O
N
D
J
F
M
A
Pebbles

this gastropod occurred mainly in pools, which were were extremely limited in number and size. In Pebbles small L.littorea predominated, but, again possibly because of the limited coverage that this microhabitat enjoyed at Coastguard, I very rarely saw Coastguard birds eat small littorea.

The main prey of routing turnstone appeared to be Hyale and, to much lesser extent, Idotea (section 6.3). The strong seasonal fluctuations in the numbers of both these invertebrates were similar in the 1982-83 and 1983-84 winter (Fig.6.11). In contrast, the main probing prey at Coastguard, larger L.obtusata, showed no clear within-winter variations in their numbers which remained more-or-less the same,even though between-winters variations appeared to occur (Fig.6.12). The mid winter reduction in the abundance of routing prey coincided with many birds switching from routing to probing (see later, Table 6.16), and so it is tempting to invoke prey abundance as a major determinant of an individual's feeding behaviour although, as I will show later, several other factors also play a large part (section 6.5).

The results of this small-scale sampling programme at Coastguard confirm the seasonal changes in prey abundance noted by Marshall (1981) some nine to ten years earlier at Scoughall, although the mid winter drop in the numbers of routing prey appeared to be much more exaggerated at Coastguard than at Scoughall: a similar result was obtained by my within-year between-areas sampling described in Chapter 3. My results also confirm the findings of many other studies of wintering waders in that in mid winter intertidal prey abundance is at its lowest (e.g. Goss-Custard et al,1977). They also go some way towards explaining why turnstone depend on the


No. of Hyale
700
600
500
400
300
200
100
A S O N D J F M A
A S O N D J F M A
No. of Idotea
200
180
100
80
60
40
20
A S O N D J F M A
A S O N D J F M A
1982-83
1983-84


No. of L.obtusata (size 3–6)
240
220
200
180
160
140
120
100
80
60
40
20
A S O N D J F M A
A S O N D J F M A
No. of L.obtusata (size5)
100
80
60
40
20
A S O N D J F M A
A S O N D J F M A
No. of L.littorea (size 2–4)
180
160
140
120
100
80
60
40
20
A S O N D J F M A
A S O N D J F M A
1982–83
1983-84

strandline more in mid winter and, possibly as a result of birds spending more time there, it may play an indirect role in the increased mid winter predation risk (Chapter 2).

6.5 FEEDING SPECIALISATIONS

6.5.1 INTRODUCTION

Individual differences in feeding behaviour have been noted in a wide variety of species and there is evidence that some of these differences may be related to attributes of sex (e.g. Selander, 1966; Kilham, 1970; Bell, 1982), to attributes of age (e.g. Clark & Gibbons, 1969; Ballinger *et al*, 1977; Gray & Tardif, 1979) or to other individual differences (e.g. Harris, 1965; Norton-Griffiths, 1968; Bryan & Larkin, 1972; Heinrich, 1976). It is only within the last decade that such differences have received much attention: prior to this most interest was centred on species feeding differences and on comparisons of the width of feeding niches which different species occupied (e.g. MacArthur, 1958, 1968; Lack, 1968). However, it has since been pointed out that any definition of a given population´s niche width along a range of food resources consists of two components. The first, the between-phenotype component, reflects differences between individuals in their resource utilisation, and the second, the within-phenotype component, reflects the variability of food resources utilised by the average individual (Roughgarden, 1972, 1974). Such increasing realisation of the importance of individual feeding behaviour in ecological theory has been reflected by an increasing interest in individual differences in evolutionary theory.

The developmant and application of game theory and the concept of alternative strategies has recognised that individual differences in behaviour can occur and the theory attempts to provide functional explanations for such individual differences (e.g. Maynard Smith, 1982). Although normally applied to individual differences in mating behaviour (e.g. Dunbar, 1983), the concept of alternative strategies suggests that three main mechanisms may be responsible for individual feeding preferences. First, a patchy environment may dictate that different behaviours are most appropriate in different patches. Second, an animal´s feeding behaviour may be conditional on its phenotype. Third, a mixture of feeding behaviours with equal pay-offs may be maintained by frequency dependent selection either (i) as a result of individuals being genetically programmed to possess different pure feeding behaviours (pure evolutionarily stable strategy - ESS), or (ii) because each individual has a genetically fixed mixed strategy of feeding behaviours (mixed ESS), or (iii) through individuals assessing how other individuals are feeding (Dawkins, 1980; Davies, 1982; Dunbar, 1983). These mechanisms are not mutually exclusive, but assessing the relative importance of their effects is often quite difficult, particularly in the field (Davies, 1982; Partridge & Green, 1985).

Feeding specialisations also have important consequences for the population dynamics of both predators and prey, as well as for ecological niche theory and evolutionary game theory (Goss-Custard, 1985; Partridge & Green, 1985).

The turnstone obtains its prey using a variety of feeding techniques, and Marshall (1981) suspected that individuals may prefer to use different techniques. One of the aims of my study of wintering turnstone was to examine whether individual specialisations did occur and, if they did, attempt to determine the factors responsible for such individual differences in feeding behaviour.

6.5.2 GENERAL METHODS

6.5.2.1 ASSESSING INDIVIDUAL DIFFERENCES IN TECHNIQUE UTILISATION

Six feeding techniques were recognised: routing seaweed, turning stones, probing, hammer-probing, surface pecking and digging (see earlier). Monitoring individuals′ use of feeding techniques was achieved by repeated instantaneous sampling (Altmann,1974). Upon detecting a feeding flock of turnstone I selected an individual at random and noted its colour ring combination. I then noted the feeding technique the individual used next within 30s of my reading its colour rings, the microhabitat it was feeding in, the identity of its nearest neighbour, the distance in m to its nearest neighbour, the number of birds in the flock of which the focal bird was a member, and the position of the bird on the study site (see Chapter 3). I then moved to the nearest bird I could see to my right of the focal bird and noted the same information. This procedure was repeated until I reached the last bird I could see at the right hand end of the flock, whereupon I shifted my attention to the opposite end of the flock and restarted the procedure with the first bird I came to. However if, as usually occurred, several flocks were in view at one time my sampling ended at the last bird within view to my right and recommenced with the first bird within view to my left. At the beginning of each observation session I noted the date, and the time was regularly recorded during the course of the session, so the height of tide could be estimated later from Admiralty tide tables. If very few birds were in view at a particular position on the study site I moved to another position. All observations were independent as the minimum time between observations of the same bird was about 10min. which was ample time for a bird to switch to another different technique. Observations were collected throughout the study period and at all stages of the tide but analyses were performed only on intertidal data gathered in the 1982-83 and 1983-84 winters. For birds occupying the same intertidal area, agonistic rank was calculated on the basis of dyadic interactions between birds from the same area (see Chapter 4). Individuals´ sex, age and biometrics were assessed or measured as described in Chapter 2.

6.5.2.2 RUNNING COMMENTARIES ON FEEDING BEHAVIOUR

Commentaries on birds´ feeding behaviour were recorded onto tape in the field and later transferred onto a program disc using an Apple II computer linked to a remote keyboard , monitor and disc-drives (Deag, 1983a). Transfer was accomplished by each behaviour being represented by a key on the remote keyboard; by pressing these coded keys the timing and sequence of behaviours were recorded on to a program disc and later transferred from the disc into a data file on the main ERCC (EMAS) computer. Using a ´keytime´ control program (Deag, 1983b) the keypress-time data files were analysed to produce a basic behavioural record for each behaviour´s latency, frequency, duration and rate per minute. A print-out of the basic commentary could also be obtained. The Keytime control program which was used assumed each behaviour (keypress) terminated the previous behaviour (keypress) and in the analysis the final behaviour which occurred was ignored because the termination of the commentary did not always coincide with the termination of a behaviour. However, commentaries were always started when a behaviour was initiated. The behaviours which were recorded and analysed were as follows: walk, run, fly, preen, look-up, supplant, supplanted, peck, flick, bulldoze, probe, turn (stone), hammer-probe, switch (to a new barnacle), dig, swallow. Prior to making each commentary the following information was noted: date, time, identity of focal bird, microhabitat feeding in, identity of nearest neighbour, distance in m to nearest neighbour, number of birds within 10m of focal bird. This information was also transferred onto the disc before Keypressing-in each commentary.

As a check on my accuracy at measuring nearest neighbour distance I estimated the distance (to the nearest metre) between two turnstone decoys placed on an intertidal feeding area by a colleague: my assessment and the total distance as measured (to the nearest metre) by my colleague were then compared later. The decoys were placed at varying distances from each other, at varying positions relative to my own position above the shoreline and at varying distances (up to 300m) from my position. My estimate and the actual distance were the same in 58% of cases and within one metre of the actual distance in 88% of cases and within two metres in 100% of cases (N=50). When I was wrong I did not appear to consistently underestimate or overestimate, but I was more accurate over shorter distances (decoys about 50m or about 100m away from me- 80% estimates were correct, N=20) than over longer distances (decoys about 200m or about 300m away- 43% estimates correct, N=30). However, the distance between the two decoys did not appear to have any bearing on my accuracy. Thus, my estimates appeared to be reasonably accurate and for the purposes for which I used nearest neighbour distance analysis the slight inaccuracies will probably have little effect on my conclusions.

6.5.3 DO INDIVIDUALS SPECIALISE?

As mentioned above in section 6.3.3.1, most birds fed by surface pecking when on beaches (zone A of Marshall, 1981). Although digging in sand (for sandhoppers) was relatively common in late winter (February to April) and, particularly in early winter (September to October) (cf Marshall, 1981, Fig 2.5) and birds sometimes turned stones on pebble beaches or routed on tidewrack, surface pecking was so prevalent that I could detect no evidence of individual specialisations in birds feeding on strandline microhabitats. The situation was notably different for birds feeding in intertidal areas and marked individual differences in feeding technique utilisation were apparent (Table 6.8). For birds within the same intertidal areas, even individuals within a single flock could differ enormously from one another in the feeding techniques used. In addition, there were differences in feeding techniques between birds inhabiting different areas. As noted in section 6.3.3.1 surface pecking occurred only occasionally in intertidal areas and digging never occurred there (see also Marshall, 1981), but for each of the other feeding techniques there were several

TABLE 6.8A

The number of occasions individuals of the Coastguard flock were seen routing (FR), probing (FP) or stone turning (FT) in their home area.

		1982 - 1983			1983 - 1984		
		FR	FP	FT	FR	FP	FT
BGWL	m	13	29	1	24	31	0
BWLY	f?	-	-	-	7	8	0
BWOG	f	5	29	0	9	24	0
BWWO	m	26	31	0	15	28	0
BWWR	f	28	14	1	25	0	0
YBOL	f	19	10	0	33	1	0
YLBG	m	8	4	0	1	1	0
YLGN	f	15	25	1	11	18	0
YLLG	f	8	32	0	4	27	0
BWYL	f	-	-	-	8	2	0
YLOL	m	47	6	0	-	-	-
YLON	m	12	6	0	19	7	0
YLWL	m	70	5	0	33	0	0
YLWN	m	61	7	0	1	0	0
YLWO	f	5	6	0	-	-	-
YNBG	m	34	12	0	-	-	-
YNGB	m	14	25	0	5	30	0
YNOR	f	44	7	0	38	10	0
YNWN	m	34	5	1	10	0	0
YNWO	m	38	25	0	3	1	0
YOBL	?	23	15	0	-	-	-
YOWL	m	17	8	0	17	12	0
YORW	f	28	32	0	7	3	0
YRLG	f	7	3	0	-	-	-
YRM	f	30	0	0	-	-	-
YRWR	m	35	8	0	23	8	0
YWBW	m	42	9	0	36	5	0
YWGB	m	51	16	0	14	17	0
YWNB	m	50	5	0	1	0	0
YWNW	m	69	2	0	30	1	0

TABLE 6.8B.

The number of occasions individuals of the Scoughall-Field Space flock (* excluding experimental period- section 6.5.52) were seen routing (FR), probing (FP) or stone turning (FT) in their home areas.

		1982-1983			1983-1984*		
		FR	FP	FT	FR	FP	FT
BWLW	f	-	-	-	3	0	10
YWWB	f	12	6	2	4	3	1
YWWO	f	7	4	1	15	1	33
YWWR	f	18	3	4	58	3	0
YWWL	m	25	15	0	42	20	0
YWNR	m	8	16	0	22	34	0
YWGN	f	19	11	13	24	4	38
BGYG	m	28	7	0	33	7	0
BGYW	f	7	18	59	10	18	38
YROL	f	2	36	0	6	18	0
YWGW	f	7	20	7	12	20	4
YOWO	f	15	10	28	13	6	22
BWYO	f	26	14	42	22	7	25
YBLG	m	35	16	3	-	-	-
YWLO	m	33	7	6	25	4	3
YWLR	f	9	32	18	8	17	30
YOBN	m	1	44	0	8	82	0
YONO	f	10	88	13	6	72	0
YLNO	f	18	65	16	37	18	9
YNNW	f	9	1	25	24	4	24
YLBG	m	3	23	2	8	34	2
YOWL	m	7	6	0	6	19	0
YLLB	m	31	8	0	40	5	0
YNLG	m	63	9	2	74	10	0
BWWL	m	75	3	5	64	1	4
YLNW	f	13	6	26	10	2	32
YBWL	m	58	5	1	45	3	4
YWOB	m	65	5	2	50	1	0
YLGR	m	22	11	7	32	6	18
YGRW	m	25	23	1	46	18	2
BWRY	m	11	4	1	62	5	1
YOOW	f	16	1	4	10	0	6
YWNL	m	41	50	10	-	-	-
YNNG	m	73	0	10	46	0	0

TABLE 6.8C

The number of occasions individuals of the Car Rocks flock were seen hammer-probing (HP), routing (FR) or probing (FP) in their home area.

		1982 - 1983			1983 - 1984		
		HP	FR	FP	HP	FR	FP
BWYN	m	13	10	6	6	17	6
YGOW	m	17	4	0	3	6	1
YLBR	m	8	6	0	2	10	0
YLNR	m	3	7	2	0	7	1
YLOW	m	15	10	0	5	17	0
YLRN	m	18	5	0	0	8	0
YNBR	?	7	3	0	5	8	0
YNRW	f	2	4	1	6	4	1
YOGW	m	12	2	0	4	8	4
YOWG	f	4	6	3	2	4	0
YRBN	m	9	8	2	3	14	1
YRGL	m	13	3	4	6	2	3
YRNG	m	15	7	1	3	2	0
YRNL	f	6	5	4	4	2	1
YRWL	m	17	10	5	8	13	5
YWNG	m	18	7	0	2	10	1
YWOR	f	4	9	0	5	7	0
YBWB	m	20	3	0	6	2	0
YBOR	m	22	2	0	5	1	0
YRRW	m	14	0	0	8	3	0
YOGN	m	8	2	0	8	11	0

individuals which specialised in its use. Individuals could not, however, be categorised absolutely in terms of their technique utilisation, but rather it would be more accurate to refer to individuals as displaying varying degrees of predilection for each feeding technique. If the utilisation of feeding techniques is considered as a four dimensional space with each technique as an axis then each individual occupied a different position within that space. Although some individuals´ predilections changed between the two winters (and within a winter), many remained more or less the same, and this was confirmed by smaller data sets collected in 1981-82 and 1984-85. It was clear, nevertheless, that individuals were not inflexible in their use of feeding techniques. For example, some Car Rocks birds switched in mid-winter 1982-83 from hammer-probing barnacles to routing (for Hyale mainly), probing (for littorinids mainly) or surface pecking (for smaller barnacles), apparently in response to a reduction in the numbers of large barnacles at the Great Car (Chapter 3). Such seasonal or tidal changes in food availability would render inflexible technique utilisation a distinctly pessimal strategy.

In answer to the question posed at the beginning of this section, it appears that in intertidal areas individual turnstone do specialise to varying degrees in the feeding technique they employ both in a winter and between winters.

6.5.4 POSSIBLE FACTORS INFLUENCING INDIVIDUALS´ FEEDING BEHAVIOUR

The purpose of this section is to outline the rationale underlying the choice of variables whose influence on feeding behaviour was analysed later (section 6.5.5) using a full factorial analysis of variance (ANOVA).

Microhabitat. There is a limited number of microhabitats in which each feeding technique can be used. Birds can only rout in microhabitas containing seaweed, where the main prey is the amphipod <u>Hyale</u>, which is probably unavailable when covered by seawater as it can easily swim away, so routing birds are probably further limited to microhabitats containind 'dry' seaweed (i.e. WR, SWR, AR, WAR). Stone turners are also clearly limited to microhabitats containing small stones (i.e. pebbles, pool). Insofar as hammer probing is used mainly to break into large barnacles, its use will obviously depend on the presence of large barnacles: settlement of barnacle spat appears to be limited in part to areas of strong wave action which prevents settlement of Fucaceae seaweed (Lewis, 1964). Therefore, the use of hammer-probing is probably restricted to 'dry' microhabitats with little growth of seaweeds (i.e. BR, SWR). Probing is probably less restricted, in terms of the diversity of microhabitats it can be used in, than the techniques mentioned above. The main prey taken by probing is the feet of gastropods which are available if the opercula of gastropods are not tightly closed which occurs when the animals withdraw into their shells. Gastropods do appear to withdraw into their shells as an anti-predator tactic but the response is also important in reducing desiccation (Fretter & Graham, 1962; Lewis, 1964): gaping gastropods should be more available and probing birds should tend to feed in microhabitats which are damp or covered in seawater (i.e. WRE, SWRE, ARE, WARE, Pool).

When the distribution of feeding techniques across microhabitats was examined it tended to confirm that certain feeding techniques were restricted to a limited number of microhabitats (Table 6.9). This being the case, the microhabitats which are available to a bird will probably have a strong influence on its feeding behaviour. This is confirmed by the observation that differences between intertidal areas in microhabitat composition were reflected by differences in the feeding techniques which were used there. For example, the Great Car was the only area where there were high densities of large barnacles (and consequently much BR microhabitat), so hammer-probing was frequently used by birds feeding in this area, but was rarely used in other areas. Similarly, the Field Space, with its flat topography (Chapter 1), possessed many shallow pools and stone-littered patches, so it is perhaps not surprising that birds frequently turned stones in this area.

Tide. The tidal cycle is well known as a factor influencing the feeding behaviour of waders (reviews by Burger, 1984; Puttick, 1984; for turnstone see e.g. Fleischer, 1983). Marshall (1981) found that in turnstone at Scoughall probing occurred more often in some areas when the tide ebbed or flowed near high tide, probably because the availability of large littorinids increased. The level of the tide may also affect which microhabitats are available and thereby affect the feeding techniques which individuals use.

Season. As shown in section 6.4 there were marked seasonal changes in the abundance of some prey species on the study site, similar to those found by Marshall (1981). Such seasonal changes in prey availability (and microhabitat availability, section 6.3.3.1) may have an influence on individuals′ feeding behaviour by altering the

TABLE 6.9.

Differential occurrence of feeding techniques in intertidal microhabitats, expressed as proportions. Rout=FR, probe=FP, stone turn=FT, hammer-probe=HP.

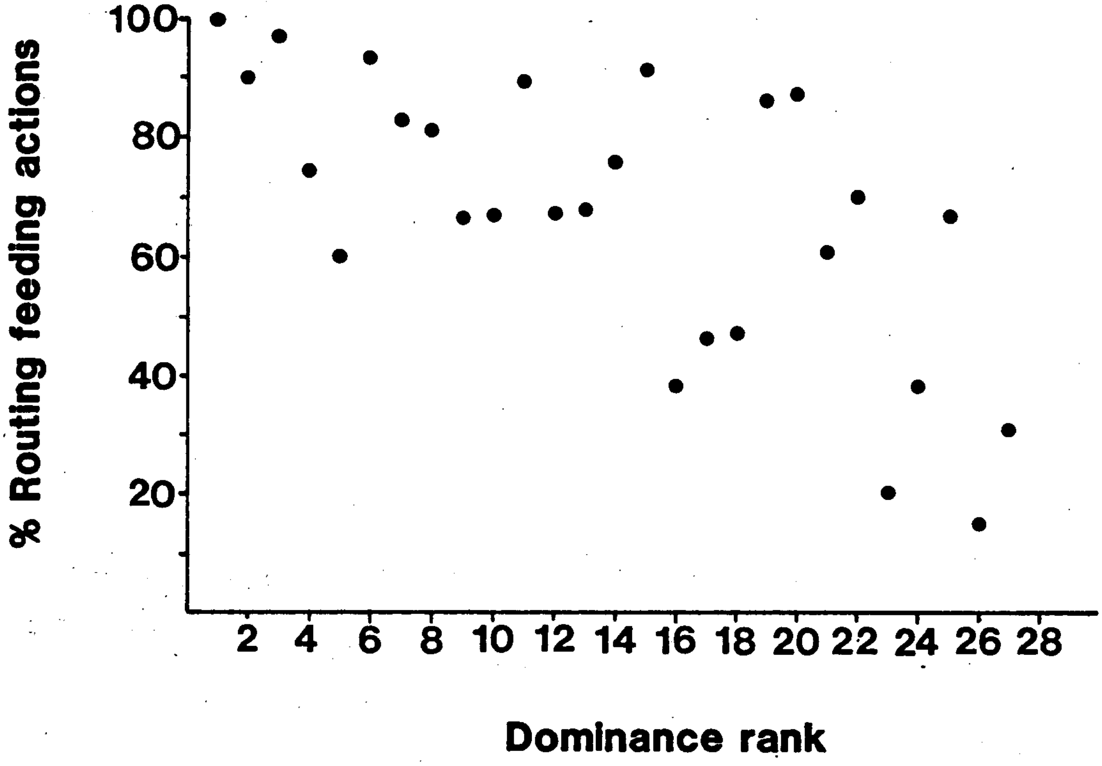
MICRO	FR	FP	FT	HP
1	98	28	0	4
2	1	53	0	0
3	0	1	65	0
4	1	12	35	0
5	0	2	0	92
6	0	4	0	4
N	3742	1826	570	720

MICRO 1= WR,SWR,AR,WAR
MICRO 2= WRE,SWRE,ARE,WARE
MICRO 3= PEBBLE
MICRO 4= POOL
MICRO 5= BR
MICRO 6= BRE

profitability of different feeding techniques at different times of the winter.

Status. In Chapter 4 I suggested that if prey is distributed in patches it is profitable for turnstone to supplant other individuals from feeding sites containing the patchily distributed prey. Whereas the supplanter gains a short-term advantage in intake rate, the supplanted bird incurs a short-term loss in intake rate. If an intertidal technique is used to exploit a prey which is patchily distributed then it might be expected that the intake rate of low status birds using that technique is affected by supplants, aggression and /or avoiding high ranking birds more than that of high status birds. A possible response to such effects of low status might involve birds switching from the technique which renders supplanting a profitable behaviour to other techniques where supplants are not profitable, or even avoiding the aggression-profitable technique altogether. A possible example of such an effect is shown in Fig.6.13. In Coastguard birds the proportion of an individuals´ feeding technique which was routing was negatively correlated with its rank: high ranking birds tended to rout more than low ranking birds. Therefore, status may have an important influence on individuals´ feeding behaviour (see also Chapter 4 and Goss-Custard, 1985).

Sex. Bar-tailed godwits _Limosa_ _lapponica_ show strong sexual dimorphism in bill length (e.g. Prater _et_ _al_, 1977; Cramp & Simmons, 1983), and the sexes appear to feed in different microhabitats (Smith & Evans, 1973) and take different prey (Smith & Evans, 1973; Engelmoer _et_ _al_, 1984). Curlew _Numenius_ _arquata_ also show comparatively strong sexual dimorphism, and the sexes have frequently


% Routing feeding actions
100
80
60
40
20
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Dominance rank

been observed feeding in different ways (Townshend, 1981; Ens & Zwarts, 1980; Elphick, 1979). There are many other avian examples of sex-related foraging differences, including some from species which do not exhibit marked sexual dimorphism (e.g. Morse, 1968; Williamson, 1971; Holmes et al, 1978; Bell, 1982). Thus, the possibility exists that a turnstone's sex influences its feeding behaviour.

6.5.5 ANALYSIS OF FACTORS INFLUENCING FEEDING BEHAVIOUR

6.5.5.1 ANOVA AND INDIVIDUAL DIFFERENCES IN TECHNIQUE PROFITABILITY

The relative importance of the above mentioned variables, microhabitat, tide, season, status and sex, in determining individuals' use of feeding techniques was assessed by several full factorial analyses of variance (MANOVA program of the SPSSX statistical package, Nie et al, 1983). Analyses were performed on three intertidal 'flocks'; Coastguard, South Scoughall and North Scoughall-Field Space using data collected by instantaneous sampling in the 1982-83 and 1983-84 winters (Table 6.10). Four categories of microhabitat were recognised: (1) WR, SWR, AR, WAR; (2) WRE, SWRE, ARE, WARE; (3) pebbles; (4) pool. Each winter was divided into three seasons: (1) July-November; (2) December-February; (3) March- April. The tidal cycle was divided into three categories: (1) 'high' flow tide; (2) 'high' ebb tide; (3) low tide. Tide state (1) encompassed tidal heights between about one hour before intertidal feeding areas were covered (3.1m) until intertidal feeding areas were covered (4.2m). Tide state (2) encompassed tidal heights between the time

TABLE 6.10.

Lists of the birds (in rank order) from each flock which were employed in the MANOVA analyses.

Flock:	CG	NS-FS	SS
	YRM	YWOB	YOBN
	YLWN	BWWL	YNLG
	YWNW	YNNG	YLGR
	YNBG	YWNL	YLLB
	YNWO	YBWL	YWWL
	YLWL	BWRY	YWNR
	YWBW	YWGN	YOWL
	YRWR	YLNW	YLBG
	YBOL	YWLR	
	YLOL	YGRW	
	YLON	YONO	
	YOWL	YLNO	
	YWGB	YWWO	
	YWNB	YWGW	
	YNGB	YOWO	
	BWWO	YOOW	
	YORW	BWYO	
	YNOR	YNNW	
	YNWN	YWLO	
	YLLG	YROL	
	YLGN	BGYW	
	BWWR	BGYG	
	BGWL		

when intertidal feeding areas were first uncovered (4.2m) until about three-quarters of an hour after intertidal feeding areas were uncovered (3.1m). Tide state (3) encompassed all tidal heights lower than 3.1m. Two categories of status were recognised for each flock: high status and low status. Individuals in each flock were arranged in their rank order determined from the summed results of dyadic interactions (Chapter 4). The birds in the upper half of the rank order were designated as high status, the birds in the lower half were designated as low status. Only birds of known sex were included in the analyses: individuals were sexed as described in Chapter 2. Two females, YWWR and YWWB, were excluded from the analysis of the S. Scoughall flock and only males were considered. This was because both females were of low status so it would have been impossible to separate the effects of sex and status if the females were included. By examining only S. Scoughall males, the effect of sex could obviously not be investigated in these individuals.

For birds of each flock I included only those observations collected from an individual feeding in its home intertidal area. Thus, for Coastguard birds I used only observations of feeding techniques collected from those birds in the Coastguard area. Data from both 1982-83 and 1983-84 winters were combined into one data set for each flock.

The three sets of birds fed in rather different areas in terms of microhabitat composition and the opportunity which existed to employ different techniques. In all three flocks very few observations of hammer-probing and surface pecking were noted, and in only the N. Scoughall-Field Space (NS-FS) flock was stone turning observed to any marked degree. In terms of analysis, therefore, one flock (NS-FS) had to be treated differently from the other two, S. Scoughall (SS) and Coastguard (CG), since the NS-FS birds used three feeding techniques whilst the others used only two. In the SS and CG birds I used the % routing observations (with angular transformation) as the dependent variable since % probing observations follows automatically because % rout + % probe = 100. Where three techniques were used, all three techniques were analysed individually (% rout, % probe, % stone turn, all with angular transformation) as the dependent variable. As in the two technique situation, once two have been examined the result for the third follows automatically, but I wanted to look at each technique individually to examine the main sources of variance. The significance of the effect of main variables (i.e. sex, status, microhabitat, etc.) on the use of feeding techniques was assessed by dividing the variable mean square by (residual mean square + mean square of all significant interaction effects involving the variable) (see Sokal & Rohlf, 1969). This produced an F value, the significance of which could be looked up in statistical tables.

Thus, for all three flocks, when I subjected the data to a MANOVA looking at the effects of microhabitat, tide, season, sex (not in SS flock), status and individuals on the feeding technique used, individual differences (denoted in Tables as CONSTANT) emerged as an extremely important variable, having highly significant effects on the use of all feeding techniques in the three flocks (Tables 6.11 - 6.15) This could partly be an effect of individual dominance rank differences (see Fig.6.13) or individual differences in phenotype affecting individuals' feeding skill or dietary requirements.

TABLE 6.11

CG flock: the results of the analysis of variance (MANOVA) on the effects of sex, status, season, tide and microhabitat on % routing, examined across both microhabitats. Main effects: sex-F=1.968, NS; status-F=2.117, NS; season-F=3.145, p<0.05; tide-F=0.875, NS; micro-F=151.058, p<0.001; individual-F=4196.841, p<0.001.

TABLE 6.11

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIG. OF F
RESIDUAL	43821.75759	251	174.58868		
CONSTANT	732720.85943	1	732720.85943	4196.84070	0.0
SEX	2330.77664	1	2330.77664	13.35010	.000
MICRO	480085.24698	1	480085.24698	2749.80748	0.0
SEASON	1098.10100	2	549.05050	3.14482	.045
TIDE	1552.84880	2	776.42440	4.44716	.013
STATUS	3081.36893	1	3081.36893	17.64931	.000
SEX x MICRO	1009.38843	1	1009.38843	5.78152	.017
SEX x SEASON	616.82829	2	308.41414	1.76652	.173
SEX x TIDE	129.62179	2	64.81090	.37122	.690
SEX x STATUS	322.19571	1	322.19571	1.84546	.176
MICRO x SEASON	287.34949	2	143.67475	.82293	.440
MICRO x TIDE	1425.94832	2	712.97416	4.08374	.018
MICRO x STATUS	1281.20146	1	1281.20146	7.33840	.007
SEASON x TIDE	564.84677	4	141.21169	.80883	.521
SEASON x STATUS	81.83946	2	40.91973	.23438	.791
TIDE x STATUS	186.93223	2	93.46612	.53535	.586
SEX x MICRO x SEASON	635.08493	2	317.54247	1.81880	.164
SEX x MICRO x TIDE	25.29622	2	12.64811	.07245	.930
SEX x MICRO x STATUS	90.64186	1	90.64186	.51917	.472
SEX x SEASON x TIDE	324.96597	4	81.24149	.46533	.761
SEX x SEASON x STATUS	30.06162	2	15.03081	.08609	.918
SEX x TIDE x STATUS	40.16747	2	20.08374	.11503	.891
MICRO x SEASON x TIDE	253.52173	3	84.50724	.48404	.694
MICRO x SEASON x STATUS	76.20592	2	38.10296	.21824	.804
MICRO x TIDE x STATUS	148.51133	2	74.25567	.42532	.654
SEASON x TIDE x STATUS	359.21402	3	119.73801	.68583	.561
SEX x MICRO x SEASON x TIDE	200.31809	3	66.77270	.38246	.766
SEX x MICRO x SEASON x STATUS	16.04091	2	8.02045	.04594	.955
SEX x MICRO x TIDE x STATUS	28.96711	1	28.96711	.16592	.684
SEX x SEASON x TIDE x STATUS	184.76096	2	92.38048	.52913	.590
MICRO x SEASON x TIDE x STATUS	142.01723	3	47.33908	.27115	.846
SEX x MICRO x SEASON TIDE x STATUS	0.0	0	.	.	.

TABLE 6.12

SS flock: the results of the analysis of variance (MANOVA) on the effects of status, season, tide and microhabitat (only males) on % routing, examined across both microhabitats. Main effects: status-F=5.275, p<0.025; season-F=1.037, NS; tide-F=0.910, NS; micro-F=104.520, p<0.001; individual-F=157.252, p<0.001.

TABLE 6.12

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIG. OF F
RESIDUAL	54596.31562	63	866.60818		
CONSTANT	136275.47477	1	136275.47477	157.25154	0.0
SEASON	1797.14636	2	898.57318	1.03689	.361
TIDE	1577.88408	2	788.94204	.91038	.408
STATUS	4571.35177	1	4571.35177	5.27499	.025
MICRO	90577.76516	1	90577.76516	104.51986	0.0
SEASON x TIDE	999.06129	4	249.76532	.28821	.885
SEASON x STATUS	721.39891	2	360.69946	.41622	.661
SEASON x MICRO	81.51297	2	40.75649	.04703	.954
TIDE x STATUS	934.91363	2	467.45681	.53941	.586
TIDE x MICRO	421.99597	2	210.99798	.24348	.785
STATUS x MICRO	34.39059	1	34.39059	.03968	.843
SEASON x TIDE x STATUS	1986.67801	4	496.66950	.57312	.683
SEASON x TIDE x MICRO	535.45585	4	133.86396	.15447	.960
SEASON x STATUS x MICRO	746.01663	2	373.00831	.430042	.652
TIDE x STATUS x MICRO	111.66917	2	55.83459	.06443	.938
SEASON x TIDE x STATUS x MICRO	319.29647	3	106.43216	.12281	.946

TABLE 6.13

NS-FS flock: the results of the analysis of variance (MANOVA) on the effects of sex, status, season, tide and microhabitat on % routing, examined across all four microhabitats. Main effects: sex-F=10.976, $p<0.005$; status-F=5.201, $p<0.05$; season-F=0.488, NS; tide-F=0.930, NS; micro-F=27.718, $p<0.001$; individual=F=1238.406, $p<0.001$.

TABLE 6.13

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIG. OF F
RESIDUAL	79477.34757	306	259.72989		
CONSTANT	321651.16271	1	321651.16271	1238.40640	0.0
SEX	48191.75486	1	48191.75486	185.54566	0.0
MICRO	423359.21542	3	141119.73847	543.33268	0.0
SEASON	1799.76494	2	899.88247	3.46469	.033
TIDE	7459.87403	2	3729.93701	14.36083	0.0
STATUS	13718.80383	1	13718.80383	52.81950	0.0
SEX x MICRO	3239.30737	3	1079.76912	4.15728	.007
SEX x SEASON	1487.68284	2	743.84142	2.86390	.059
SEX x TIDE	1138.76710	2	569.38355	2.19221	.113
SEX x STATUS	357.74026	1	357.74026	1.37735	.241
MICRO x SEASON	1558.48707	6	259.74785	1.00007	.425
MICRO x TIDE	4205.23508	6	700.87251	2.69847	.014
MICRO x STATUS	1364.47227	3	454.82409	1.75114	.157
SEASON x TIDE	2051.94429	4	512.98607	1.97508	.098
SEASON x STATUS	353.46980	2	176.73490	.68046	.507
TIDE x STATUS	905.79417	2	452.89708	1.74372	.177
SEX x MICRO x SEASON	2619.92330	6	436.65388	1.68118	.125
SEX x MICRO x TIDE	4039.00932	6	673.16822	2.59180	.018
SEX x MICRO x STATUS	288.34985	3	96.11662	.37006	.775
SEX x SEASON x TIDE	1291.92701	4	322.98175	1.24353	.292
SEX x SEASON x STATUS	73.40174	2	36.70087	.14130	.868
SEX x TIDE x STATUS	377.84297	2	188.92148	.72738	.484
MICRO x SEASON x TIDE	4200.29278	12	350.02440	1.34765	.191
MICRO x SEASON x STATUS	2143.29131	6	357.21522	1.37533	.224
MICRO x TIDE x STATUS	1294.14528	6	215.69088	.83044	.547
SEASON x TIDE x STATUS	2472.12264	4	618.03066	2.37951	.052
SEX x MICRO x SEASON x TIDE	1379.43390	5	275.88678	1.06221	.381
SEX x MICRO x SEASON x STATUS	1523.99751	3	507.99917	1.95587	.121
SEX x MICRO x TIDE x STATUS	2384.81176	3	794.93725	3.06063	.028
SEX x SEASON x TIDE x STATUS	1515.08984	4	378.77246	1.45833	.215
MICRO x SEASON x TIDE x STATUS	3524.25223	10	352.42522	1.35689	.200
SEX x MICRO x SEASON TIDE x STATUS	4748.55122	3	1582.85041	6.09422	.000

TABLE 6.14

NS-FS flock: the results of the analysis of variance (MANOVA) on the effects of sex, status, season, tide and microhabitat on % stone turning, examined across all four microhabitats. Main effects: sex-F=8.878, p<0.005; status-F=0.001, NS; season-F=2.823, NS; tide-F=1.808, NS; micro-F=16.748, p<0.001; individual-F=1077.841, p<0.0001.

TABLE 6.14

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIG. OF F
RESIDUAL	110271.49351	306	360.36436		
CONSTANT	388415.42941	1	388415.42941	1077.84086	0.0
SEX	59151.58311	1	59151.58311	164.14382	0.0
MICRO	451269.11774	3	150423.03925	417.41930	0.0
SEASON	14573.50962	2	7286.75481	20.22052	0.0
TIDE	8863.48348	2	4431.74174	12.29795	0.0
STATUS	.18606	1	.18606	.00052	.982
SEX x MICRO	15918.43830	3	5306.14610	14.72439	0.0
SEX x SEASON	779.27465	2	389.63732	1.08123	.340
SEX x TIDE	489.70204	2	244.85102	.67945	.508
SEX x STATUS	380.20309	1	380.20309	1.05505	.305
MICRO x SEASON	7348.94621	6	1224.82437	3.39885	.003
MICRO x TIDE	6565.53513	6	1094.25585	3.03653	.007
MICRO x STATUS	193.94431	3	64.64810	.17940	.910
SEASON x TIDE	2565.59011	4	641.39753	1.77986	.133
SEASON x STATUS	510.30554	2	255.15277	.70804	.493
TIDE x STATUS	126.33694	2	63.16847	.17529	.839
SEX x MICRO x SEASON	1546.08576	6	257.68096	.71506	.638
SEX x MICRO x TIDE	549.44887	6	91.57481	.25412	.957
SEX x MICRO x STATUS	809.53778	3	269.84593	.74881	.524
SEX x SEASON x TIDE	2828.97748	4	707.24437	1.96258	.100
SEX x SEASON x STATUS	61.31874	2	30.65937	.08508	.918
SEX x TIDE x STATUS	262.74516	2	131.37258	.36455	.695
MICRO x SEASON x TIDE	7147.04063	12	595.58672	1.65273	.077
MICRO x SEASON x STATUS	444.23874	6	74.03979	.20546	.975
MICRO x TIDE x STATUS	508.79124	6	84.79854	.23531	.965
SEASON x TIDE x STATUS	657.92424	4	164.48106	.45643	.768
SEX x MICRO x SEASON x TIDE	4980.52886	5	996.10577	2.76416	.018
SEX x MICRO x SEASON x STATUS	50.41083	3	16.80361	.04663	.987
SEX x MICRO x TIDE x STATUS	1214.58348	3	404.86116	1.12348	.340
SEX x SEASON x TIDE x STATUS	41.08687	4	10.27172	.02850	.998
MICRO x SEASON x TIDE x STATUS	1577.84236	10	157.78424	.43785	.927
SEX x MICRO x SEASON TIDE x STATUS	20.89687	3	6.96562	.01933	.996

TABLE 6.15

NS-FS flock: the results of the analysis of variance (MANOVA) on the effects of sex, status, season, tide and microhabitat on % probing,examined across all four microhabitats. Main effects: sex-F=0.058, NS; status-F=23.012, p<0.001; season-F=2.133, NS; tide-F=0.348, NS; micro-F=13.593, p<0.001; individual-F=757.653, p<0.001.

TABLE 6.15

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIG. OF F
RESIDUAL	180687.13792	306	590.48084		
CONSTANT	447379.46087	1	447379.46087	757.65279	0.0
SEX	505.97230	1	505.97230	.85688	.355
MICRO	343543.70712	3	114514.56904	193.93444	0.0
SEASON	10394.14132	2	5197.07066	8.80142	.000
TIDE	1458.08974	2	729.04487	1.23466	.292
STATUS	13588.05592	1	13588.05592	23.01185	0.0
SEX x MICRO	18989.18570	3	6329.72857	10.71962	0.0
SEX x SEASON	3691.18389	2	1845.59195	3.12557	.045
SEX x TIDE	210.78190	2	105.39095	.17848	.837
SEX x STATUS	.62066	1	.62066	.00105	.974
MICRO x SEASON	5599.81428	6	933.30238	1.58058	.152
MICRO x TIDE	9024.52856	6	1504.08809	2.54723	.020
MICRO x STATUS	1506.08654	3	502.02885	.85020	.467
SEASON x TIDE	1727.28094	4	431.82023	.73130	.571
SEASON x STATUS	951.87751	2	475.93875	.80602	.448
TIDE x STATUS	1478.52187	2	739.26093	1.25196	.287
SEX x MICRO x SEASON	1146.32571	6	191.05429	.32356	.924
SEX x MICRO x TIDE	3456.77938	6	576.12990	.97570	.442
SEX x MICRO x STATUS	1181.85596	3	393.95199	.66717	.573
SEX x SEASON x TIDE	3000.70163	4	750.17541	1.27045	.282
SEX x SEASON x STATUS	6.84643	2	3.42322	.00580	.994
SEX x TIDE x STATUS	636.02438	2	318.01219	.53856	.584
MICRO x SEASON x TIDE	8386.38521	12	698.86543	1.18355	.294
MICRO x SEASON x STATUS	2089.27867	6	348.21311	.58971	.739
MICRO x TIDE x STATUS	2609.46607	6	434.91101	.73654	.621
SEASON x TIDE x STATUS	2996.40016	4	749.10004	1.26863	.282
SEX x MICRO x SEASON x TIDE	6217.87620	5	1243.57524	2.10604	.065
SEX x MICRO x SEASON x STATUS	1948.83332	3	649.61111	1.10014	.349
SEX x MICRO x TIDE x STATUS	3766.58029	3	1255.52676	2.12628	.097
SEX x SEASON x TIDE x STATUS	1232.78655	4	308.19664	.52194	.720
MICRO x SEASON x TIDE x STATUS	4920.52480	10	492.05248	.83331	.597
SEX x MICRO x SEASON TIDE x STATUS	4429.82912	3	1476.60971	2.50069	.060

Another extremely important source of variance in all three flocks was microhabitat, which had a highly significant effect on the use of all three feeding techniques. As mentioned in the previous section, the reason for this seems obvious as certain feeding techniques can only be used in certain microhabitats. The availability of microhabitats will consequently have an important influence on which techniques an individual turnstone uses.

Interestingly, on their own tide and season did not have a significant effect on the use of feeding techniques, except for a marginally significant effect of season in the CG birds. This result may have been due to chance (one in twenty results will be significant due to chance alone), or it may have been a genuine effect. Seasonal changes in prey abundance (particularly _Hyale_-routing prey) appeared to be most marked at CG, this may have forced birds, independent of other variables, to switch from routing to probing in mid-winter (season 2) (Chapter 3; section 6.4; Table 6.16). Apart from this possible significant effect at the Coastguard, season alone had very little effect anywhere, apart form a few patchy interaction effects, which suggests that there are seasonal changes, but their effects are not consistent and depend, for example, on sex or microhabitat. The results also show that there was no consistent effect of tide on all birds so, for example, as the tide rose, every bird did not start probing. However, tide was involved in some interesting interaction effects; for instance, in all cases except SS, tide interacted with microhabitat in its effect on feeding technique utilisation. In other words, the effect of tide depended on the microhabitat being used, or equivalently, the effect of microhabitat depended on the stage of the tide. For

TABLE 6.16.

Table of seasonal changes in the use of feeding techniques by individual turnstone. See text for details of seasons.

	% FR (FR/(FR + FP) x 100%		
Bird	season 1	season 2	season 3
YLGN	64	38	28
YNBG	100	40	67
YNOR	97	62	78
YNWO	77	33	53
YWBW	80	88	93
YLON	87	55	56

example, a rising tide creates more ´islands´ in areas covered by Fucoid seaweeds from which turnstone probed for littorinids in tide edge microhabitats (microhabitat 2) (see also Marshall, 1981). Furthermore, on an ebbing tide birds feeding near to the tide edge (as turnstone tend to do - Marshall, 1981) encounter damper seaweed than on a flowing tide, hence gaping littorinids are more likely to occur on an ebbing tide, so the profitability of probing is probably increased at this stage of the tide.

Status and sex both had important effects on the use of feeding techniques, but these effects varied from flock to flock. For instance, if all the data for CG are considered, neither variable had a significant effect whereas in NS-FS both sex and status had significant effects on the use of two of the three feeding techniques, and in SS status had a significant effect (sex was not examined in this flock). The occurrence or non-occurrence of the effects of the sex and status may well have been related to which microhabitats were available and the particular techniques involved, as evidenced by significant interactions between sex and microhabitat, and status and microhabitat in several cases, suggesting that the effect of sex and status depended in part on microhabitat. This problem can be examined further by looking separately at those microhabitats that permit the use of more than one technique.

For example, in CG microhabitat 1 allows both probing and routing, whereas in microhabitat 2 birds only probed. If all the data for CG are examined sex and status were not significant, but their effects depended on microhabitat (as evidenced by significant interactions with both). However, when a MANOVA was carried out only for microhabitat 1, both sex and status became highly significant, so where there was a choice, both sex and status had a major effect on which technique was used, low ranking birds and females probing more often (Table 6.17). There are two possible reasons for this result:

(a) individual differences in competitive ability; routing is the preferred technique but low ranking birds´ access to the technique is limited by high ranking birds. That this is at least partly true is suggested by the effect of status. The effect of sex could also be partly a consequence of a status effect because within status categories males have a higher average rank than females.

(b) It is also possible that females are better at probing than males because of some phenotypic foraging performance difference.

Several other lines of evidence suggest that routing was the preferred technique but that low status reduced birds´ opportunities to use it. First, the intake rate of routing low status birds (intermittent routers) and high status birds (regular routers) were not significantly different when no aggression occurred, showing that there was no phenotypic effect on routing profitability (Table 6.18). Secondly, aggression between routing birds was comparatively common compared with birds employing other feeding techniques and when a birds´ feeding behaviour before and after it was supplanted were compared (see section 4.3.4.1 for methods), intake rate, feeding rate and feeding efficiency (swallows/feeding actions) were significantly reduced as a result of being supplanted ($p<0.0001$, $p<0.001$, $p<0.0001$ respectively). Conversely, when a routing bird supplanted another router it significantly increased its intake rate, feeding rate and feeding efficiency ($p<0.0001$, $p<0.01$, $p<0.0001$ repectively) (Table 6.19). Low status birds are more likely to incur the costs of being

TABLE 6.17

CG flock: the results of the analysis of variance (MANOVA) on the effects of sex, season, tide and status on % routing , examined within microhabitat 1. Main effects: sex-F=10.113, p<0.005; status-F=16.159, p<0.0001; season-F=2.405, NS; tide-F=6.012, p<0.005.

TABLE 6.17

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIG. OF F
RESIDUAL	42457.01087	154	275.69488		
CONSTANT	1213231.42987	1	1213231.42987	4400.63105	0.0
SEX	2788.14161	1	2788.14161	10.11314	.002
SEASON	1325.90258	2	662.95129	2.40466	.094
TIDE	3314.78849	2	1657.39425	6.01170	.003
STATUS	4455.01415	1	4455.01415	16.15922	.000
SEX x SEASON	1054.60995	2	527.30498	1.91264	.151
SEX x TIDE	82.89337	2	41.44668	.15034	.861
SEX x STATUS	165.58358	1	165.58358	.60060	.440
SEASON x TIDE	684.57715	4	171.14429	.62077	.648
SEASON x STATUS	167.57733	2	83.78866	.30392	.738
TIDE x STATUS	389.59222	2	194.79611	.70656	.495
SEX x SEASON x TIDE	436.47950	4	109.11987	.39580	.811
SEX x SEASON x STATUS	7.59213	2	3.79606	.01377	.986
SEX x TIDE x STATUS	127.06106	2	63.53053	.23044	.794
SEASON x TIDE x STATUS	609.24560	3	203.08187	.73662	.532
SEX x SEASON x TIDE x STATUS	118.63012	2	59.31506	.21515	.807

TABLE 6.18.

Mean intake rates of high and low status birds whilst routing. Observations of high and low status birds taken consecutively from the same flock (N=30). Wilcoxon matched pairs signed ranks test, p=0.229

	Routing intake rate	
	x	SD
High status	2.97	1.78
Low status	3.56	2.58

TABLE 6.19.

Median values of number of swallows and feeding actions made by turnstone in a median time period, (a) before and after being supplanted by another turnstone, (b) before and after supplanting another turnstone whilst routing in seaweed.

(a) Supplanted by another bird

Time period (s)	No. of swallows		No. of feeding actions	
	before	after	before	after
27	1	0	17	11

(b) Supplant another bird

Time period (s)	No. of swallows		No. of feeding actions	
	before	after	before	after
30	1	2	11	12

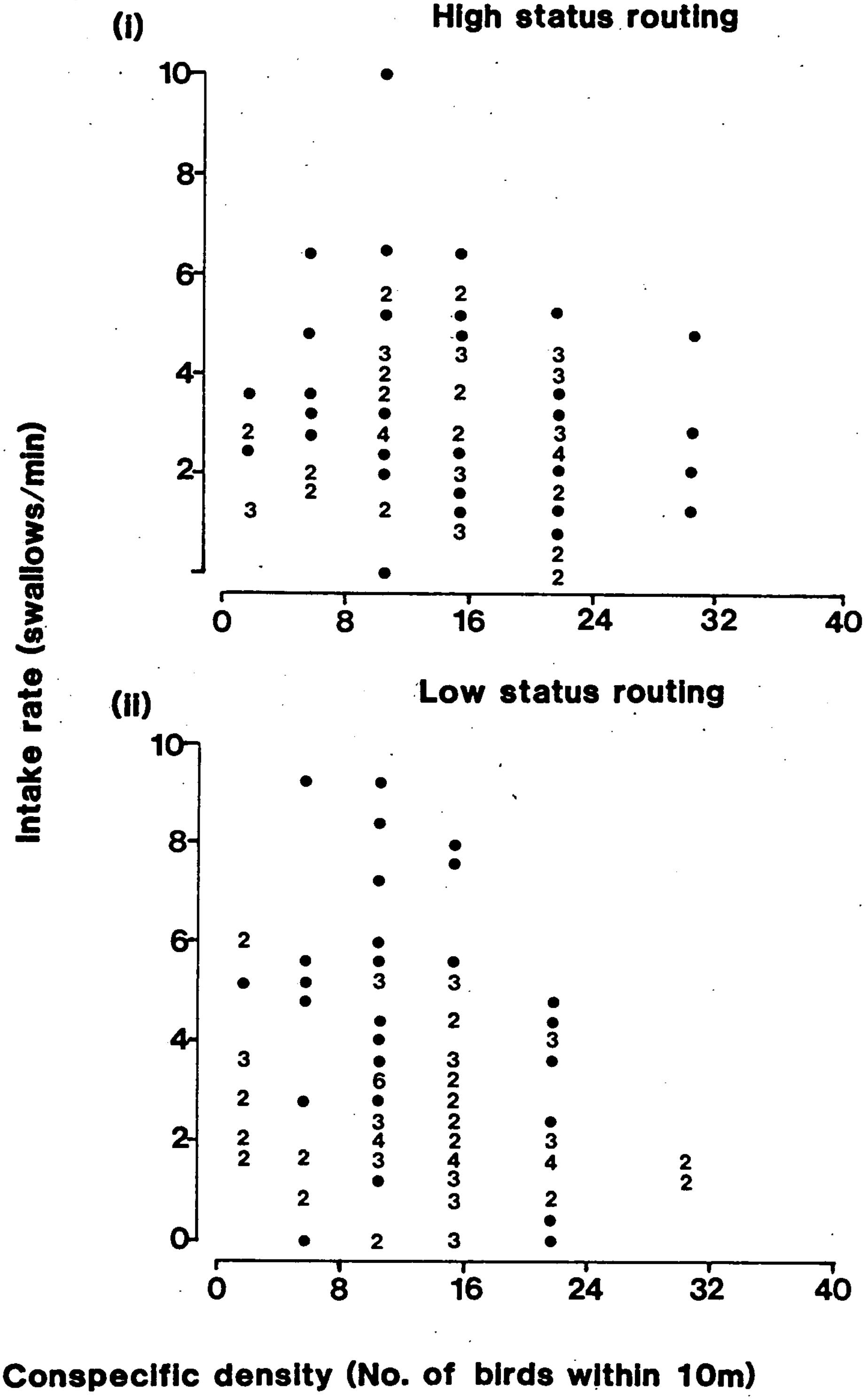
supplanted, whilst high status birds are more likely to enjoy the benefits of supplanting. Thirdly, low status birds suffered interference when routing whereas high status birds did not (Fig. 6.14a).

Interestingly, also within microhabitat 1 for CG birds, tide had a significant effect. That tide only had an effect within a single microhabitat (1) suggests that the tide had an effect on the profitability of the two techniques within microhabitat 1. This effect may well have been due to the greater dampness of microhabitat 1 on ebb tides making littorinids more vulnerable to probing birds (see earlier).

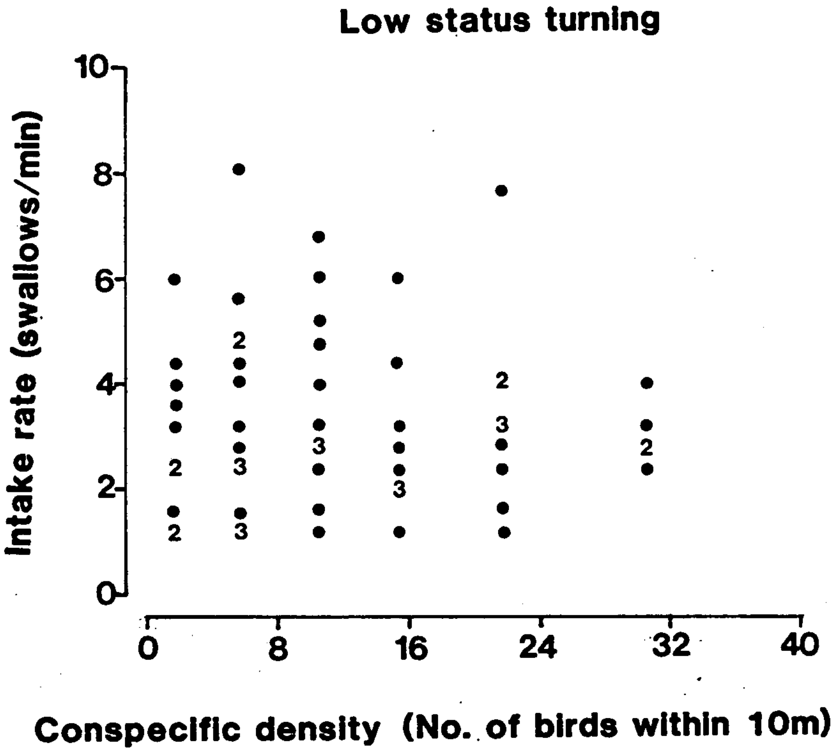
The SS flock lived in very similar circumstances to the CG flock in terms of the microhabitats available (1 and 2) and the techniques used (routing and probing). Interestingly, however, unlike the CG flock the whole SS flock data set showed a significant effect of status, but when I examined the effects of variables within microhabitat 1 status was no longer significant (Table 6.20). I suspect that the underlying reason for the differences between the two flocks is that in CG birds there was a wider rank spectrum in microhabitat 1 compared with that in SS birds, so in CG birds the effect of status is obvious within a microhabitat but not between microhabitats whereas in SS birds to get a full rank spectrum both habitats must be considered.

For the whole NS-FS data set, sex affected % rout and % stone turn, whilst status had a massive effect on % probe and a small but significant effect on % routing (Tables 6.13 & 6.15). In all three feeding techniques the effect of sex depended on microhabitat. To examine further the effects of status and sex, I looked at

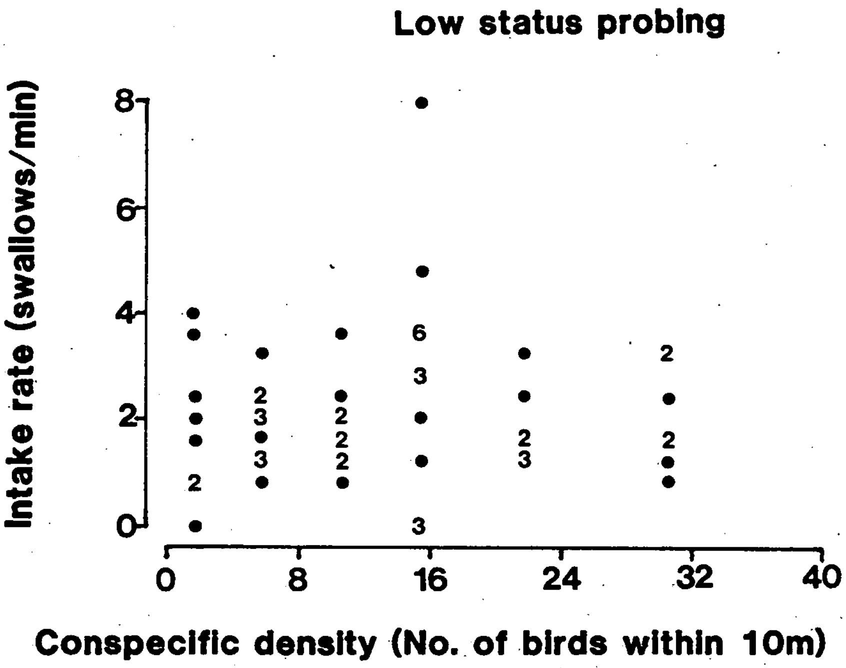
(a)


(i)
High status routing
(ii)
Low status routing
Intake rate (swallows/min)
0
2
4
6
8
10
0
8
16
24
32
40
Conspecific density (No. of birds within 10m)

(b)


Low status turning
Intake rate (swallows/min)
10
8
6
4
2
0
0
8
16
24
32
40
Conspecific density (No. of birds within 10m)
2
2
2
3
3
3
3
3
2
3
2

(c)



Low status probing

TABLE 6.20

SS flock: the results of the analysis of variance (MANOVA) on the effects of status, season and tide on % routing (only males), examined within microhabitat 1. Main effects: status-F=0.011, NS; season-F=0.107, NS; tide-F=0.192, NS; individual-F=167.367, $p<0.001$.

TABLE 6.20

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIG. OF F
RESIDUAL	54596.31562	39	1399.90553		
CONSTANT	234298.18469	1	234298.18469	167.36714	0.0
SEASON	300.26836	2	150.13418	.10725	.899
TIDE	538.71223	2	269.35611	.19241	.826
STATUS	15.17616	1	15.17616	.01084	.918
SEASON x TIDE	1593.81973	4	398.45493	.28463	.886
SEASON x STATUS	998.08032	2	499.04016	.35648	.702
TIDE x STATUS	1606.34584	2	803.17297	.57373	.568
SEASON x TIDE x STATUS	2341.42418	4	585.35604	.41814	.795

microhabitats where more than one feeding technique was possible. In microhabitat 1 (routing and probing possible) neither sex nor status had an important effect (Table 6.21). This result was the same as that for SS birds, and the reasons were probably also the same; only a narrow rank spectrum tended to be found in microhabitat 1.

Within microhabitat 4, where both probing and turning stones was possible, sex had an important effect but status did not. This result was due to females turning stones more often than males (e.g. Table 6.22; section 6.5.3), which suggests that due to phenotypic differences females were more inclined to turn stones than were males. It was most unlikely that females were excluded or prevented from probing by males because when either stone turning or probing, low status females did not suffer from interference (Fig. 6.14b,c). Although this may have been because conspecific density did not acurately reflect stone turner density or prober density, it does show that within the range of conspecific densities experienced by stone turning or probing birds on the study site, interference did not occur. I very rarely saw a bird which was probing or turning stones being supplanted, which is in agreement with the former result and the observation that status did not have an effect on the use of probing or stone turning feeding techniques in microhabitat 4. Compared with males, females were also comparatively more successful at turning stones than probing, and whilst this difference was not significant it was in the direction predicted by the notion that phenotypic differences affected the profitability of stone turning (Table 6.23). Since only individual males which happened to be particularly skillful at stone turning may have employed the technique there is no reason why the apparent differences between the

TABLE 6.21

NS-FS flock: the results of the analysis of variance (MANOVA) on the effects of sex, status, season and tide on % routing, examined within microhabitat 1. Main effects: sex-F=1.017, NS; status-F=2.413, NS; season-F=0.684, NS; tide-F=0.348, NS; individual-F=1413.442, p<0.001.

TABLE 6.21

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIG. OF F
RESIDUAL	71662.44224	123	582.62148		
CONSTANT	823501.62664	1	823501.62664	1413.44192	0.0
SEASON	3047.29008	2	1523.64504	2.61515	.077
TIDE	3106.08773	2	1553.04387	2.66561	.074
STATUS	5371.07815	1	5371.07815	9.21881	.003
SEX	4540.24564	1	4540.24564	7.79279	.006
SEASON x TIDE	2039.59120	4	509.89780	.87518	.481
SEASON x STATUS	1318.78821	2	659.39410	1.13177	.326
SEASON x SEX	2488.73445	2	1244.36723	2.13581	.123
TIDE x STATUS	51.92250	2	25.96125	.04456	.956
TIDE x SEX	4476.10763	2	2238.05382	3.84135	.024
STATUS x SEX	49.32131	1	49.32131	.08465	.772
SEASON x TIDE x STATUS	3919.74068	4	979.93517	1.68194	.158
SEASON x TIDE SEX	2503.8048	4	625.77012	1.07406	.372
SEASON x STATUS x SEX	486.42863	2	243.21432	.41745	.660
TIDE x STATUS x SEX	.19717	2	.09859	.00017	1.000
SEASON x TIDE x STATUS x SEX	4930.44088	3	1643.48029	2.82084	.042

TABLE 6.22

NS-FS flock: the results of the analysis of variance (MANOVA) on the effects of sex, status, season and tide on % probing, examined within microhabitat 4. Main effects: sex-F=14.893, p<0.001; status-F=0.638, NS; season-F=3.565, p=0.034; tide-F=3.363, p=0.040; individual-F=111.039, p<0.001.

TABLE 6.22

SOURCE OF VARIATION	SUM OF SQUARES	DF	MEAN SQUARE	F	SIG. OF F
RESIDUAL	93482.96881	69	1354.82563		
CONSTANT	150437.82078	1	150437.82078	111.03851	0.0
SEASON	9659.09548	2	4829.54774	3.56470	.034
TIDE	9111.24844	2	4555.62422	3.36252	.040
STATUS	864.16217	1	864.16217	.63784	.427
SEX	20177.76040	1	20177.76040	14.89325	.000
SEASON x TIDE	5886.27013	4	1471.56753	1.08617	.370
SEASON x STATUS	237.31290	2	118.65645	.08758	.916
SEASON x SEX	641.58209	2	320.79104	.23678	.790
TIDE x STATUS	1233.55944	2	616.77972	.45525	.636
TIDE x SEX	422.04148	2	211.02074	.15575	.856
STATUS x SEX	462.53441	1	462.53441	.34140	.561
SEASON x TIDE x STATUS	398.08084	3	132.69361	.09794	.961
SEASON x TIDE SEX	8864.02977	3	2954.67659	2.18085	.098
SEASON x STATUS x SEX	70.08978	2	35.04489	.02587	.974
TIDE x STATUS x SEX	2013.09346	2	1006.54673	.74293	.479
SEASON x TIDE x STATUS x SEX	19.22568	1	19.22568	.01419	.906

TABLE 6.23.

Mean intake rate of males and females probing (FP,N=40) or turning stones (FT,N=38) $X^2=0.0008$, df=1,p>0.05.

Sex	Mean intake rate	
	FP	FT
Male	2.05	4.84
Female	2.27	5.19

sexes should have been significant.

In all flocks an effect of status on individuals' feeding behaviour occurred invariably in situations where the two possible techniques were routing and probing, and this suggests that competition for the use of routing, rather than a phenotypic effect on routing profitability, explained the use of routing. This was evidenced by there being no significant difference in routing profitability between high and low status birds in the absence of supplanting behaviour, and the effect of sex on the use of routing in this case can be explained by the low mean status of females within each status category. In contrast, in a situation where probing and stone turning were the only two viable techniques status was unimportant and phenotypic differences between individuals probably determined feeding technique utilisation, females seemingly being more successful at turning stones than males.

When running commentaries on feeding birds using either a routing, probing or stone turning technique are broken down into their composite behaviours using Keytime (Deag , 1983b) some important differences between the techniques emerge (Table 6.24). These results give some indications as to why aggression in the form of supplants and defending feeding sites is more common in routing birds (I very rarely saw a probing or stone turning bird involved in aggression), and hence why status has important effects on the use of this technique. First, routing birds spent less time walking, indicating that their prey occurred at higher densities than did probing or stone turning prey. However, routing birds had a lower rate of walking bouts and had longer inter-walk bout lengths suggesting that their prey was more clumped and patchily distributed.

TABLE 6.24.

Behavioural parameters associated with routing (FR), probing (FP) and turning stones (FT). All measures taken from birds in the same flock.

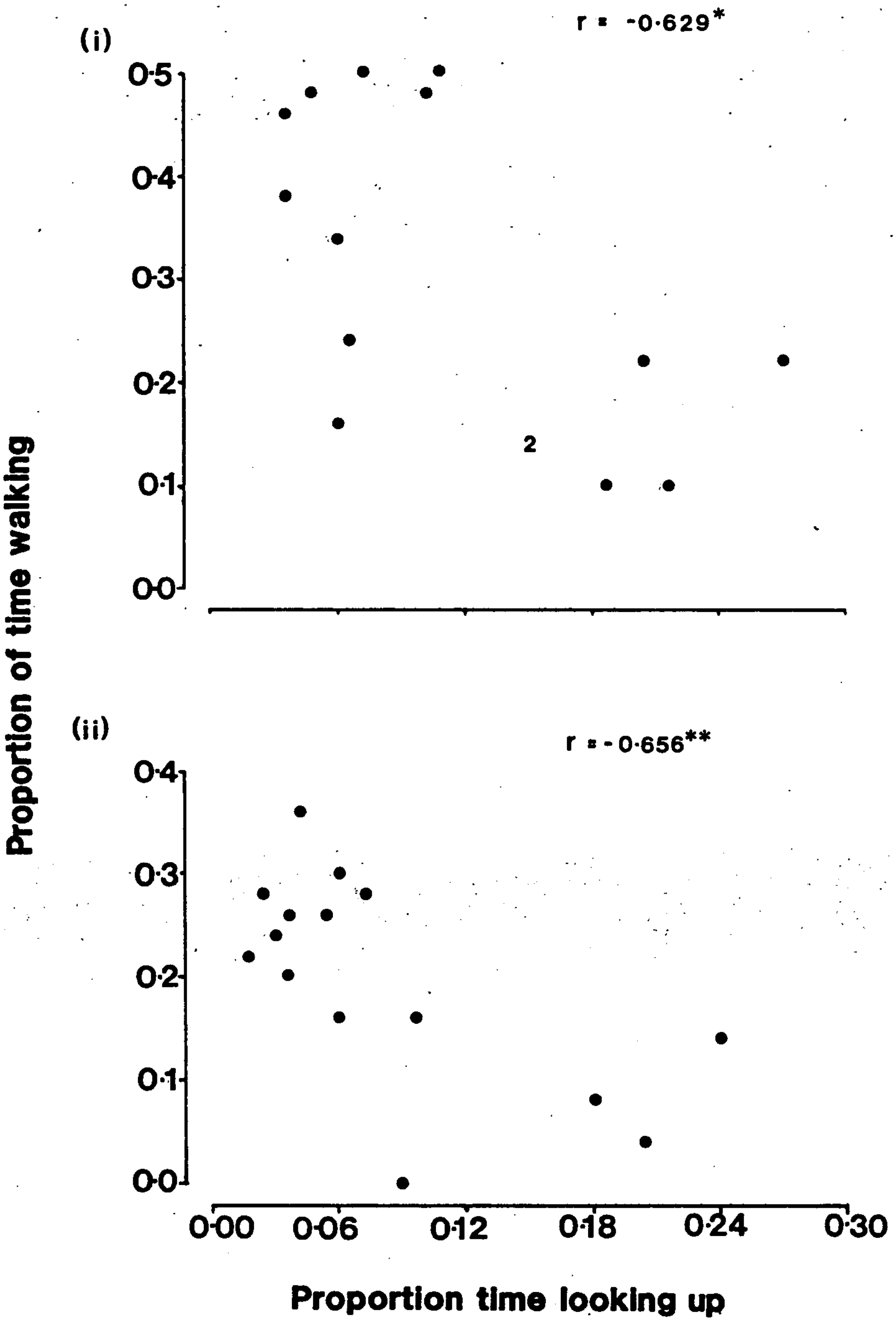
	FR		FP		FT	
	x	SD	x	SD	x	SD
Nearest neighbour distance (m)	1.95	0.00	2.91	1.85	3.37	1.93
Proportion time spent walking	0.18	0.13	0.53	0.19	0.34	0.17
Walking bouts per minute	3.16	1.56	7.97	2.05	7.86	4.57
Swallows per minute	2.50	1.52	2.18	1.42	3.29	1.81
Look ups per minute	3.61	2.33	1.60	1.55	1.32	1.43
Proportion time looking up	0.19	0.36	0.05	0.06	0.03	0.03
Look up duration	1.72	0.90	1.26	1.36	0.64	0.65

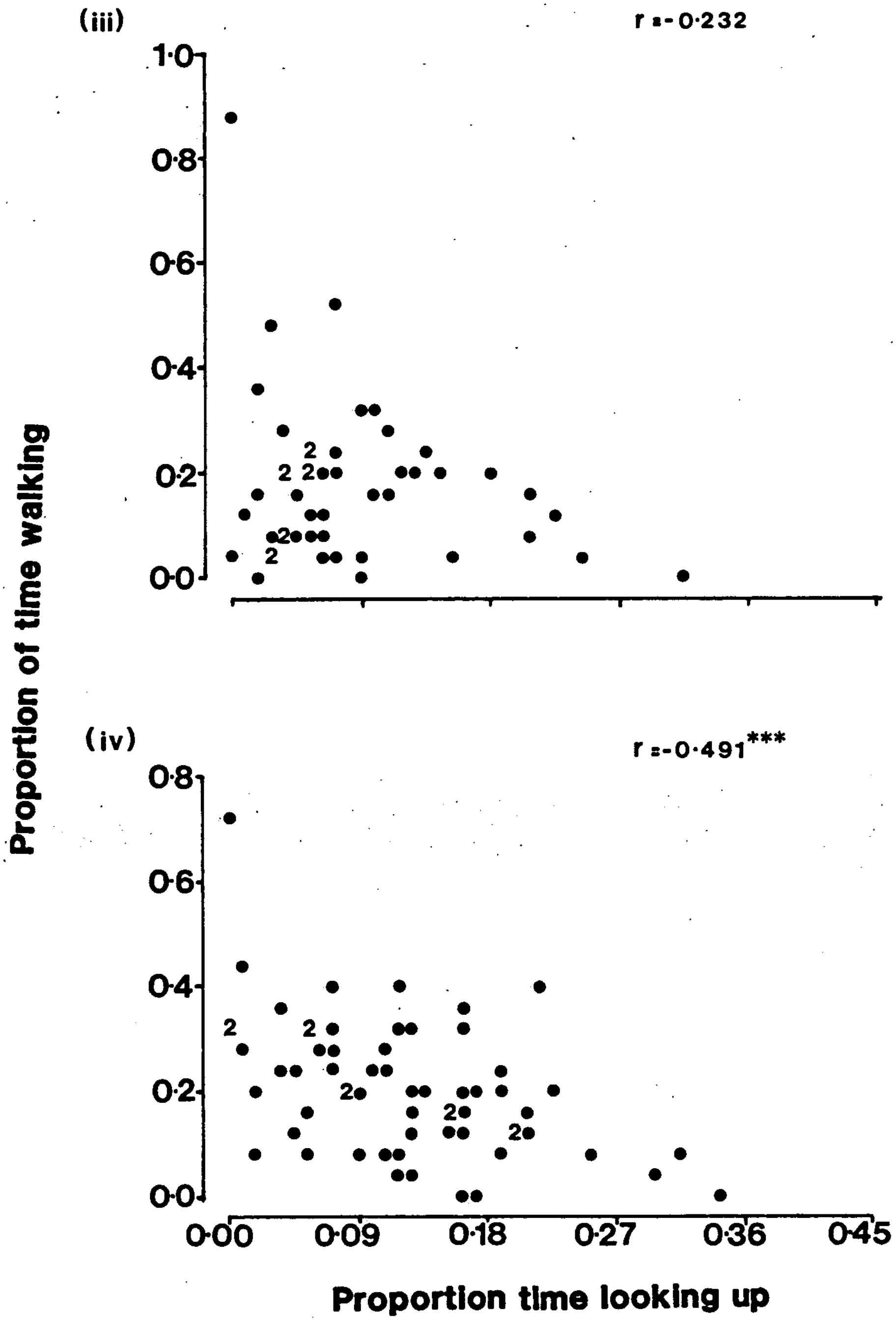
Perhaps as a consequence of their covering a larger area while feeding , probing birds and stone turning birds were further away from their nearest neighbours than were routing birds. They also spent less time looking up but because they spent more time walking they could potentially spend more time looking out for predators. That there is a trade-off between time spent looking up and walking is suggested by the negative relationship between proportion of time spent looking up and time spent walking in routing birds (Fig. 6.15). At a given conspecific density aggression between routing birds was significantly greater than between birds using the other two techniques (Table 6.25). These results are consistent with the argument put forward in Chapter 4, namely that when prey is patchily distributed and when the density of prey (patches) is high then supplanting is profitable, so aggression is greater. Differences in the distribution of prey exploited by the three techniques would seem to be the most likely reason for the differences in the aggression levels associated with each technique, and therefore with the differences in the effect that status has on the use of each technique.

6.5.5.2 REMOVAL EXPERIMENT

To assess further the effects that high status birds may have had on the feeding behaviour of other birds I removed some of the birds from the NS-FS flock. Under an NCC licence four individuals, YNNG, YWOB, YWGN, YLNW, were captured using cannon-nets on 5 Feb 1984 and were taken back to the Zoology Dept. roof aviary where they were held until their release at Scoughall on 5 Mar 1984. YNNG and YWOB

Fig. 6.15 Proportion of time spent looking up plotted against proportion of time spent walking for routing birds at different conspecific densities) (i) 36-45, (ii) 26-35, (iii) 19-25, iv) 13-18, (v) 8-12, (vi) 3-7, (numbers of birds in flock), r is the correlation coefficient, *p<0.05, **p<0.01, ***p<0.001.


(i)
r = -0·629*
0·5
0·4
0·3
0·2
0·1
0·0
2
(ii)
r = -0·656**
0·4
0·3
0·2
0·1
0·0
0·00
0·06
0·12
0·18
0·24
0·30
Proportion of time walking
Proportion time looking up


(iii)
r =-0·232
1·0
0·8
0·6
0·4
0·2
0·0
Proportion of time walking
(iv)
r =-0·491***
0·8
0·6
0·4
0·2
0·0
0·00
0·09
0·18
0·27
0·36
0·45
Proportion time looking up

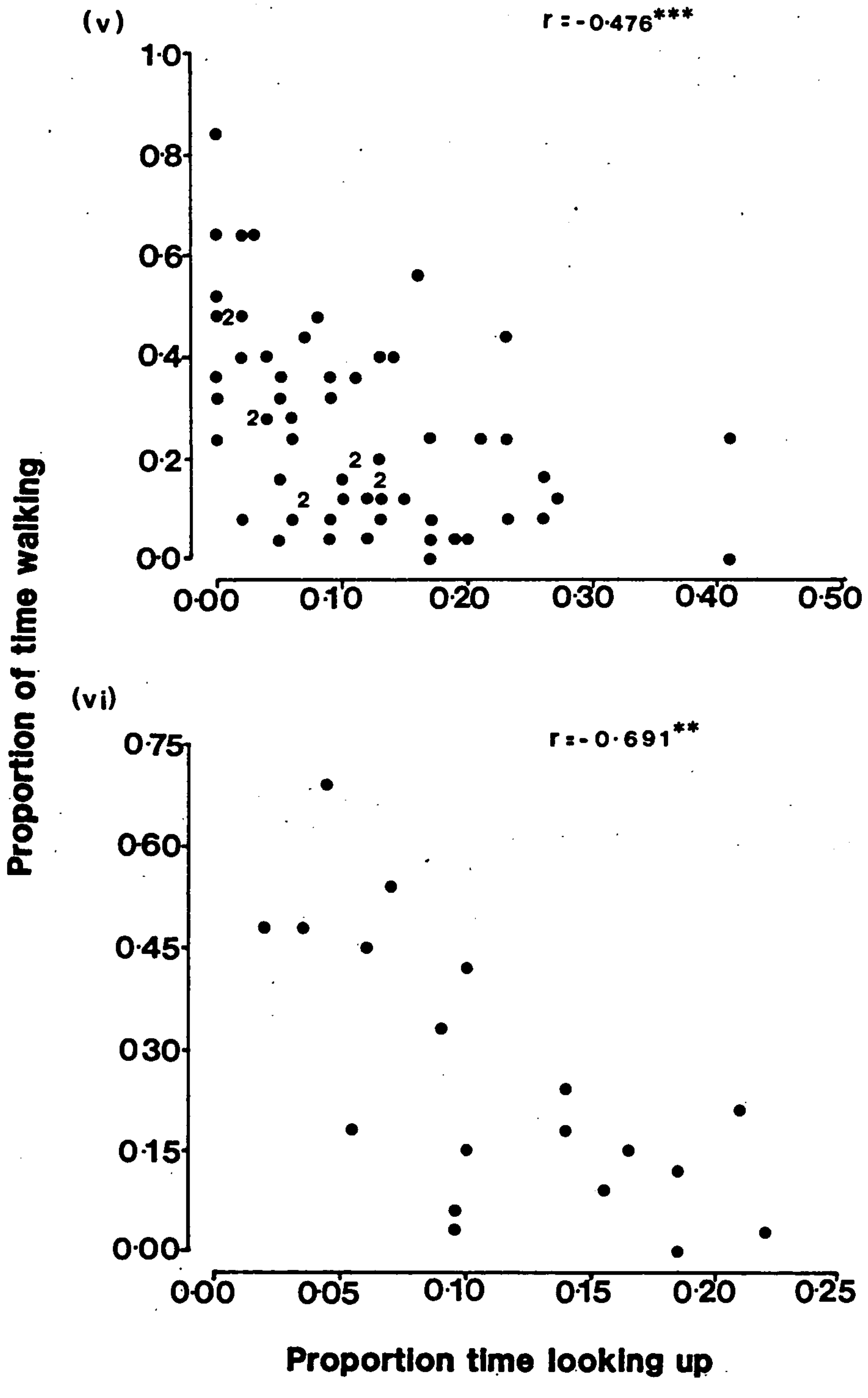

(v)
r = -0·476***
1·0
0·8
0·6
0·4
0·2
0·0
0·00
0·10
0·20
0·30
0·40
0·50
2
(vi)
r = -0·691**
0·75
0·60
0·45
0·30
0·15
0·00
0·00
0·05
0·10
0·15
0·20
0·25
Proportion of time walking
Proportion time looking up

TABLE 6.25.

(a) Number of aggressive interactions which routing (FR), probing (FP) and stone turning (FT) birds were involved in when feeding in the same flock. (b) Probability levels resulting from Wilcoxon signed ranks tests comparing aggression rates associated with different techniques (N=38). *** p<0.001, NS not significant.

(a) Number of aggressive interactions/min

	x	SD
FR	0.90	0.67
FP	0.03	0.12
FT	0.16	0.37

(b)

	FP	FT
FR	***	***
FP		NS

were high ranking males and routing specialists, whereas YWGN and YLNW were high ranking females which used all three techniques but used probing least (Table 6.8). The effect of the removal of these individuals on the remaining birds' feeding behaviour was assessed by monitoring individuals' use of feeding techniques by instantaneous sampling (see General Methods) one month before, during and one month after the removal.

The frequencies with which NS-FS individuals used each of the three techniques before the removal, during the absence and after the return of their four flockmates are shown in Table 6.26. Some individuals appeared to change their feeding behaviour as a result of the removal (e.g. YLGR, YGRW) whilst others did not (e.g. YONO, YWGW). Overall, there were no significant differences between birds' use of feeding techniques as a result of the removal, although there was a tendency for individuals to increase their use of routing and to decrease their use of stone turning during the removal compared with before the removal (Table 6.26).

According to the suggestion that competition with high ranking birds limits low ranking birds' use of routing, the removal of two (YWOB and YNNG) of the four high ranking males should have caused low ranking birds to rout more often. Whilst there was a tendency for this to occur, overall there was no mass switch of low ranking birds to the routing technique. Given the strength of the evidence presented earlier which indicated that an individual's access to the routing technique is influenced by its status, there are several possible reasons for this apparently contradictory result. These are:

(a) several factors other than status (e.g. microhabitat, individual

TABLE 6.26A

Number of occasions birds from the NS-FS flock were seen routing (R), probing (P), or turning stones (T) in their home area before, during and after the removal of four flockmates.

	BEFORE			DURING			AFTER		
	R	P	T	R	P	T	R	P	T
m BWWL	21	1	1	15	0	1	23	0	1
m YBWL	14	1	0	19	0	0	11	0	2
m YLGR	6	1	4	8	0	2	10	1	5
m BWRY	5	1	3	8	1	4	7	0	3
m YGRW	10	5	0	11	0	0	9	3	1
f YWLR	1	4	5	1	5	8	1	2	8
f YONO	1	18	0	0	13	0	0	18	0
f YLNO	12	5	2	15	5	1	18	6	3
f YWGW	3	6	2	3	8	3	2	5	1
f YWWO	6	0	12	8	1	15	11	0	9
f YOWO	7	2	13	5	3	9	6	1	9
m YWLO	8	1	1	9	1	0	6	1	1
f BWYO	5	2	6	6	2	9	6	3	8
f YNNW	11	0	13	7	0	5	8	1	9
f YROL	2	5	0	3	8	0	4	11	0
f BGYW	1	3	10	3	4	12	4	4	14
m BGYG	7	1	0	8	2	0	10	0	0

TABLE 6.26B

Summary of Wilcoxon matched pairs signed ranks tests of significance for differences between the feeding techniques used by NS-FS birds before, during, and after the enforced absence of four flock-mates. N = number of signed ranks, T = smaller number of like-signed ranks, p = associated probability level, NS = not significant.

	BEFORE vs. DURING REMOVAL			DURING vs. AFTER REMOVAL		
	N	T	p	N	T	p
% ROUT	16	32.5	NS	14	44	NS
% PROBE	14	40.5	NS	13	41.5	NS
% TURN	11	11.5	NS	14	28	NS

differences) affect an individual´s use of routing and in the present experiment too few ´routers´ were removed;

(b) as in (a) but the removal period of one month was too short to have a major influence;

(c) through positive reinforcement individuals may acquire the appropriate foraging skills and digestive capabilities for their own intertidal diet to a point where it becomes disadvantageous to switch rapidly to a different suite of feeding behaviours and/or diet. There is some evidence that gut morphology and digestive efficiency is related to diet, the implication being that changes in diet may lead to short term reductions in digestive efficiency until digestive morphology and physiology have adapted to the new diet (reviewed in Partridge & Green, 1985) Familiarity or experience in the use of feeding techniques undoubtedly increases the profitability of those techniques (Partridge & Green, 1985; section 6.6 and references therein).

In the present study I suspect that all three possibilities, a, b, and c, may have had an influence on the result of the removal experiment, although c may have been of greatest importance. For example, the tendency for individuals to increase their use of routing in the absence of higher ranking birds appeared to occur at the expense of their use of stone turning. Similar prey were obtained using these two techniques, i.e. small littorinids and amphipods, so the cost in reduced digestive efficiency of switching techniques will have been least for these two techniques. Moreover, it should be expected that females should be less likely to switch techniques than should males in the absence of higher ranking birds. The rationale of this argument can be explained by the following example. If a higher ranking male dies then all remaining birds rank increases by one. In the following winter, however, a third winter male, formerly subordinate to most females, becomes dominant over them and assumes a position at the bottom of the adult male rank order (see Chapter 4): the rank of females drops by one but that of adult males remains the same. If adult females switched foraging tactics in response to the death of the high ranking male they would have to revert to their earlier tactics in response to the new presence of a higher ranking third winter male. In contrast, adult males′ rank is not affected by the third male so if they switched tactics on the death of the high ranking male they would not have to revert to their original foraging behaviour. The cost of switching techniques after the death or removal of high ranking birds will therefore be less for adult males than for adult females in the long run. Thus, it is interesting to note that four out of seven males showed an increase in the use of routing during the removal experiment (i.e. % rout greater during removal than either before or after) whereas only two out of ten females did (Table 6.26). The two individuals which showed the most marked increase in routing during the removal (YGRW and YLGR) were both males.

When Milinski (1982) presented pairs of sticklebacks Gasterosteus aculeatus with Daphnia of two size classes as prey, the inferior competitors ate fewer large Daphnia than superior competitors even though large Daphnia were more profitable. When foraging alone, the inferior competitors still ate less large Daphnia than superior competitors (see also Barnard & Brown, 1981, for similar findings with shrews Sorex araneus). However, in contrast, Coates (1980) found that although damselfish Dascyllus aruanus of low competitive rank ate small prey in the presence of superior competitors, in their absence they switched to larger prey. Similarly, in downy woodpeckers Picoides pubescens the sexes often differ markedly in foraging behaviour with females feeding more on large branches, tree trunks and at lower levels in the canopy. When males were removed from an experimental woodlot, the females switched to male-like foraging behaviour (Peters & Grubb, 1983). The foraging response of subordinate individuals to the removal of socially dominant competitors clearly differs in different species. Quite why these species differences occur requires further study, but the answer may well lie in the relative costs of switching foraging tactics.

6.5.6 GENERAL DISCUSSION AND CONCLUSIONS

Clearly, the factors which determine a turnstones' winter feeding behaviour are complex. However, one factor which is probably not important is cultural inheritance. The cross-fostering experiments of Norton-Griffiths (1968) suggest that young oystercatchers learn the feeding techniques of their parents (although see Goss-Custard & Sutherland, 1984; Swennen et al, 1983, for further information on oystercatcher specialisations). In contrast to oystercatchers, young turnstone are not fed by their parents on the breeding ground and feed predominantly by surface pecking (chironomids) (Nettleship, 1973; Whitfield, in press; unpubl. data). At Valassaaret in Finland I never saw young turnstone use any other feeding technique apart from surface pecking, even after fledging.

Nevertheless, one factor which does appear to be important is the environment. The microhabitat a bird is feeding in and the availability of microhabitats have a large influence on feeding technique utilisation in winter. Although of much less importance, tidal, and to a lesser extent, seasonal effects also appear to exist, acting primarily through interactions with other variables, particularly microhabitat. At higher tidal levels and in mid-winter some turnstone switched to probing, probably because of a change in the relative profitabilities of routing and probing prey, and this often entailed a switch in the microhabitat they were feeding in. That a turnstone´s feeding behaviour is partly conditional on the environment is perhaps not surprising given the large range in environmental conditions which they face during the course of a winter.

Individual phenotypic differences, apart from those associated with status and sex, also appear to have a major influence on winter feeding behaviour. These phenotypic differences may be the product of genotype, physiology, morphology and learning, but it is impossible in a field study to determine the relative importance of such factors. Bill morphology would perhaps seem to be an obvious candidate as a factor affecting phenotypic differences in feeding behaviour, but there appeared to be no obvious correlation between bill length and feeding technique utilisation, and matters were not taken further since any correlation would be impossible to interpret, partly because a turnstone´s bill length is probably determined in part by the way it feeds (Chapter 2). For example, birds which hammer-probe for barnacles probably suffer from increased abrasion of the bill rhampotheca and may well have more rapid compensatory rhampothecal growth. However, it would be difficult to say whether an increased growth rate was due to increased rhampothecal stimulation through use of the technique or was due to a genuine physiological predisposition. Similarly, if hammer-probers have shorter bills than other technique specialists, a short bill could be a cause or an effect of hammer-probing. The study of Swennen et al (1983) on oystercatcher bills shows that feeding technique affects bill form in this species. Individual differences in foraging skills, caused by genetic effects and/or learning, are probably important components of individual phenotypic differences (e.g. Partridge, 1976).

Status also accounted for a significant proportion of the variance in feeding technique utilisation and the evidence suggested that an individual´s feeding behaviour was partly conditional on its status. Turnstone appeared to compete with each other to feed by routing, with poorer competitors being forced by and/or avoiding superior competitors to adopt probing or stone turning techniques. To measure the costs incurred by poor competitors of using less preferred techniques is extremely difficult: measuring pay-offs experienced by different individuals or strategies in any field study is notoriously problematical (e.g. Davies, 1982). Several factors must be considered in any cost-benefit analysis of the different techniques.

Intake rate. The sizes of prey items taken by routing are smaller than those taken by probing, consequently the chances that I missed some swallows of prey was greater for routing birds. I did not check this possibility quantitatively by observing captive birds routing or probing under simulated field conditions, but my observed estimates of the number of quarter mealworms taken by captive turnstone matched reasonably well with the actual number taken as determined by counting the prey before and after each observation period (Table 6.27). In the field, even when turnstone swallowed very small prey (e.g. small oligochaetes) it was possible to see swallowing actions because they usually lifted their heads whilst swallowing (cf Groves, 1978).

Energetic content of prey. If wintering waders attempt to maximise their energy intake (e.g. Puttick, 1984) a prime requisite in any cost-benefit analysis of feeding behaviour is to measure the energy content of the prey (e.g. Pienkowski _et al_, 1984). When different prey species are taken using different techniques it is important to determine which parts of a prey item are not digested and exclude them from calculations. The possibility that the energetic value of prey may change seasonally and that such seasonal changes may differ between prey species must also be borne in mind.

Digestive efficiency. It is very likely that turnstone have preferences for particular techniques at least partly because of preferences for particular prey. I suspect that turnstone prefer to rout because it is the most effective method of obtaining amphipods. Harris (1979) also suggested that turnstone may prefer amphipods. Stone turners eat both amphipods (_Gammarus_ sp.) and small littorinids (mainly _L.littorea_) but they appear to prefer _Gammarus_. When I have turned over stones in areas where turnstones feed, on the bottom of almost every single stone were several suitably sized littorinids, yet turnstone certainly did not ingest prey each time they turned over a stone and I frequently saw them ignore apparently suitable littorinids. They also ingested littorinids at the expense of

TABLE 6.27.

Comparison between the observed numbers of half mealworms taken by a focal captive turnstone in 15 minutes and the actual number, as determined by counting half mealworms before and after 10 observation sessions.

Mean Observed	Mean Actual
14.0	15.4

Gammarus when both were exposed by stone turning, and apart from this evidence that stone turners prefer amphipods when presented with a choice between the two prey species (as do routers), that turnstone turn over stones at all also suggests that they prefer Gammarus: small littorinids are numerous in the open whereas Gammarus are not. If Gammarus is the preferred prey, the prey selection of stone turners is consistent with the notion that preferred prey should always be eaten when encountered but less preferred prey should only be taken when preferred prey are scarce to meet the energy requirements of the predator, irrespective of the less preferred prey´s abundance (Pyke et al, 1977). Small littorinids may be preferred less because ingestion of too many may cause a digestive bottleneck (Kenward & Sibly, 1978; Sibly 1981). Although littorinids may be retained in the gizzard as grinding material, their disproportionate representation in pellets suggested they may have taken a comparatively long time to digest (see section 6.3.4). They are probably energetically costly to digest too if the shells need to be broken open for maximal digestive efficiency of the animal inside. Turnstone only take littorinids from the bottom of stones and by doing so they make sure that having turned over a stone they are swallowing a living animal rather than an empty shell, thereby minimising the cost of any potential digestive bottleneck. Zwarts and Wanink (1984) suggest that curlews avoid eating small clams Mya arenaria because they may cause a digestive bottleneck.

Gibbula opercula were ingested by probing birds at low tidal levels yet they were present in pellets voided at high tide, suggesting that gastropod feet also take a comparatively long time to digest. By contrast, amphipods appeared to be very rapidly digested.

Similarly, redshank digest the amphipod *Corophium volutator* more rapidly than the gastropod *Hydrobia ulva* (Goss-Custard, 1969). Greater digestive efficiency may be one reason why turnstone prefer amphipods.

Dietary requirements and parasitic infection of prey. Prey characteristics other than energetic yield may affect prey choice and preferences. It is assumed that adequate nutrient supplies are probably obtained by wintering waders in the course of fulfilling their energy requirements (e.g. Pieǹkowski *et al*, 1984). This may well be true but no study has yet been carried out to determine the dietary requirements of waders: it is becoming increasingly obvious that several herbivorous animals select food on the basis of its biochemical composition as well as its energetic content (Arnold & Hill, 1972; Waterman, 1984). By eating animal foods with a high protein content biochemical considerations may be of little importance to waders but it is worth considering if different prey species are taken by different techniques. The results of Goss-Custard (1979b) suggest that redshank may prefer *Corophium* over *Nereis* for non-energetic reasons, although Goss-Custard (1979) argues that nutrient differences are probably of negligible influence. Differences in the extent of parasitic infection both within and between prey species may influence prey preferences (evidence for the role of parasite loading in prey choice reviewed by Goss-Custard, 1984).

Night feeding. It is possible that birds may rehearse techniques during the day in readiness for their use at night, and the payoffs associated with techniques in the day may be different from those at night. It is becoming increasingly obvious that many waders feed at night (reviewed by Puttick, 1984; Goss-Custard, 1984). Intake rates usually appear to be lower at night (but see Dugan, 1981; Pienkowski et al, 1984) particularly if the birds feed by sight (Evans, 1976), and many visually feeding waders switch to touch feeding at night (e.g. Goss-Custard, 1969). All of the feeding techniques employed by turnstone are predominantly visual and Evans (1976) has stated that turnstone do not feed at night. Turnstone appeared to leave the study site at night (Marshall, 1981; pers. obs.); some of them may have spent the night on the Isle of May where increased night counts of turnstone have been noted (M. Nicoll, pers. comm.). Turnstone have frequently been seen feeding at night on the Isle of May (K. Brockie, pers. comm.), which raises the possibility that different techniques have different profitabilities at night. Several rocky shore animals are more active by night (Gepetti & Tongiori, 1967; Kitching & Ebling, 1967) but how this affects the night feeding behaviour of turnstone is unknown, as is the importance of night feeding to this species.

Energetic costs of feeding techniques. The behavioural components of each technique are very different and so the energetic costs may also be different. For example, compared with routing both probing and stone turning involve more walking but fewer feeding actions. It is difficult to measure the energetic costs of feeding in waders but internal telemetry may provide some hope for the future (Ferns et al, 1980).

Predation risk. Compared with routing birds both probing and stone turning birds spend more time with their heads raised and so can potentially spot an approaching predator earlier, but they are also usually further away from their nearest neighbour and so may be more likely to be captured once a predator has attacked a flock. There are many confounding variables, such as status, age, and the sites where attacks take place, which makes it very difficult to assess the mortality associated with each feeding technique.

Sexual phenotypic differences appear to make stone turning profitable to females than to males. Quite what this difference is was not determined, although the larger size of females or their slightly longer bills may have some bearing.

Thus, phenotypic effects, both in terms of competitive ability and feeding skill, are clearly important in determing the feeding behaviour of turnstone. Microhabitat and environmental effects are also important, probably because creating spatially variable opportunities allows for the use of different feeding techniques. At this point there is no reason to suppose that there is an ESS type mixture of alternative feeding strategies (e.g. see Dawkins, 1980), since birds do not appear to create opportunities for the use of other feeding techniques by picking one.

6.6 AGE-RELATED FEEDING BEHAVIOUR

6.6.1 INTRODUCTION

Young birds generally have a higher mortality than adults (Lack, 1954) and almost without exception this pattern of differential mortality is found in waders (Boyd, 1962; Goss-Custard, 1980; Evans, 1981; Evans & Pienkowski, 1984). For example, juvenile waders of four species had higher winter mortality than adults on the present study site (Whitfield, 1985: Appendix 1). Such age-related differences may be mediated by juveniles being unable to maintain a high enough energy intake, thereby making them more susceptible to periods of food shortage or harsh conditions (Heppleston, 1971; Clark, 1982), or to predation (Whitfield, 1985; Chapter 2). Ashmole (1963) has suggested that starvation may be a major factor contributing to increased juvenile mortality and also implied that young birds are less efficient foragers than adults (for a recent possible example, see Grieg-Smith, 1985). Age-related foraging differences have since been demonstrated in a number of species, including herons and egrets (Recher & Recher, 1969b; Siegfried, 1972; Quinney & Smith, 1980), terns and gulls (Dunn, 1972; Buckley & Buckley, 1974; Verbeek, 1977; Searcy, 1978) and waders (Groves, 1978; Puttick, 1979; Burger, 1980). Groves (1978) found that in turnstone on autumn migration there were differences in the feeding efficiency of adults and juveniles, because juveniles foraged at a lower rate and had a lower intake rate. The differences held when birds were foraging on either barnacle-covered rocks or tidal flats. Along with other authors, she suggested that if inexperience is the main source of the observed inefficiency of juveniles then these differences should attenuate with time, although she mentioned the possibility that adults represent a class of individuals which remain after selection against the most inefficient juveniles. The two possibilities are not mutually exclusive.

In this section I assess whether age-related feeding differences occurred in turnstone on the study site and whether these differences attenuated with time.

6.6.2 METHODS

The methods which were used have been described earlier in this chapter (section 6.5). Running commentaries on focal birds' feeding behaviour were recorded on tape and later transferred to computer using Keybehaviour (Deag, 1983a) and analysed using Keytime (Deag, 1983b). A commentary made on an adult was always preceded by or followed by a commentary made on a juvenile; usually a juvenile in the same flock. The majority of intertidal observations were made on birds feeding in the Coastguard area, although all observations of birds hammer-probing for barnacles were collected from the Great Car area. Commentaries of birds surface pecking in the strandline microhabitats TEWS and TES were recorded at several sites, but mainly at the Coastguard. Birds were aged by plumage characteristics, or by age-specific colour-ring combinations (Chapter 2). Unless otherwise stated, all observations were collected in the 1982-83 winter.

6.6.3 RESULTS

I have presented a detailed breakdown only of the feeding behaviour of adults and juveniles which were routing: in terms of the number of behavioural components this technique was more complex than the other techniques from which I gathered sufficient data to discern seasonal changes (i.e. probing, hammer-probing, surface pecking). For the present analysis I ignored all commentaries in which the focal bird was involved in a supplant: I did this to minimise the effects that aggression had on inter-quartiles and feeding behaviour. The data appeared to be normally distributed so I have presented results as means and standard errors. However, observations of juveniles and adults were paired (see Methods) so I have used

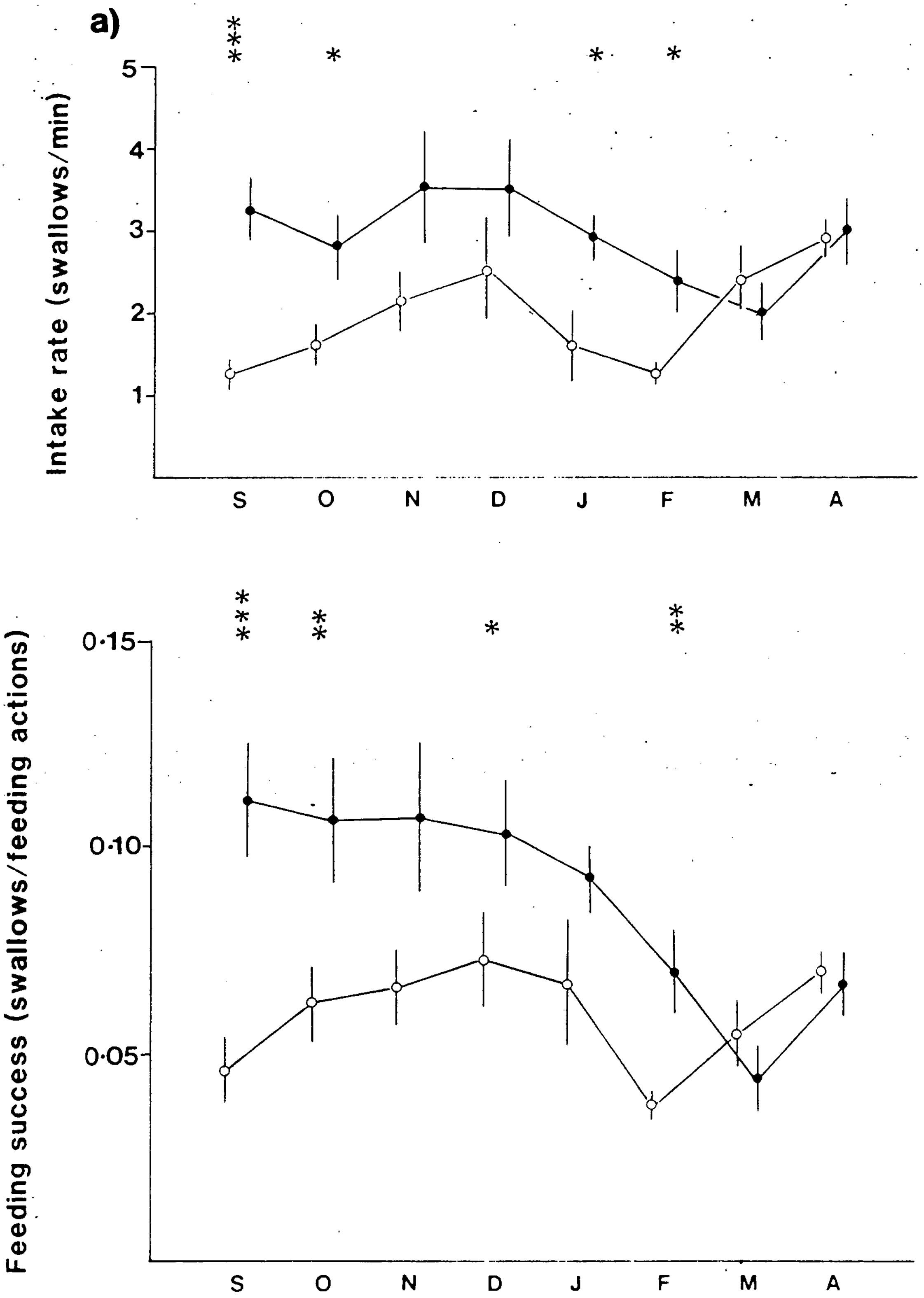
Wilcoxon matched pairs signed ranks tests to assess the significance of age-related differences. The behaviour used during routing by juveniles and adults were markedly different at the beginning of the winter but these differences attenuated over the course of the winter (Fig. 6.16). The intake rates of juveniles were significantly lower than adults´ until March and April when there was no significant difference, and the feeding success (rate of swallows/rate of feeding actions) of the two age classes showed a similar pattern (Fig. 6.16a). Juveniles had higher rates of flicking than adults until December; from then on flicking rates were similar. The bulldozing rates showed similar seasonal attenuations but those of juveniles were initially lower than adults (Fig. 6.16b). The proportion of time spent walking by juveniles was higher than adults´ at the beginning of the winter but again the differences were usually non-significant from December onwards (Fig.6.16c). There were no consistent age differences in look up rates, but for the two other measures of vigilance (proportion of time spent looking up, geometric mean look up bout length) juveniles tended to spend less time looking up and to look up in shorter bouts than did adults in early winter, but by mid-winter the differences were negligible (Fig. 6.16d).

Seasonal changes in intake rate of juveniles and adults using other feeding techniques are shown in Fig. 6.17. In every technique juveniles had lower initial intake rates than adults, but the month when these disparities disappeared differed. When surface pecking, juveniles became as successful as adults in November; when hammer-probing and probing they became as successful in December.

Juvenile turnstone progressively lose some of their distinctive buff-edged wing coverts during the course of the winter (Prater <u>et</u>

Fig. 6.16a Seasonal changes in intake rate (mean ± SE) and feeding success for adults (closed circles) and juveniles (open circles) when routing. *p<0.05, **p<0.01, ***p<0.001.

Fig. 6.16b Seasonal changes in pecking, bulldozing and flicking rates (mean ± SE) for adults (closed circles) and juveniles (open circles) when routing. *p<0.05, ***p<0.001.


a)
***
*
*
*
Intake rate (swallows/min)
5
4
3
2
1
S
O
N
D
J
F
M
A
***
**
*
**
Feeding success (swallows/feeding actions)
0·15
0·10
0·05
S
O
N
D
J
F
M
A

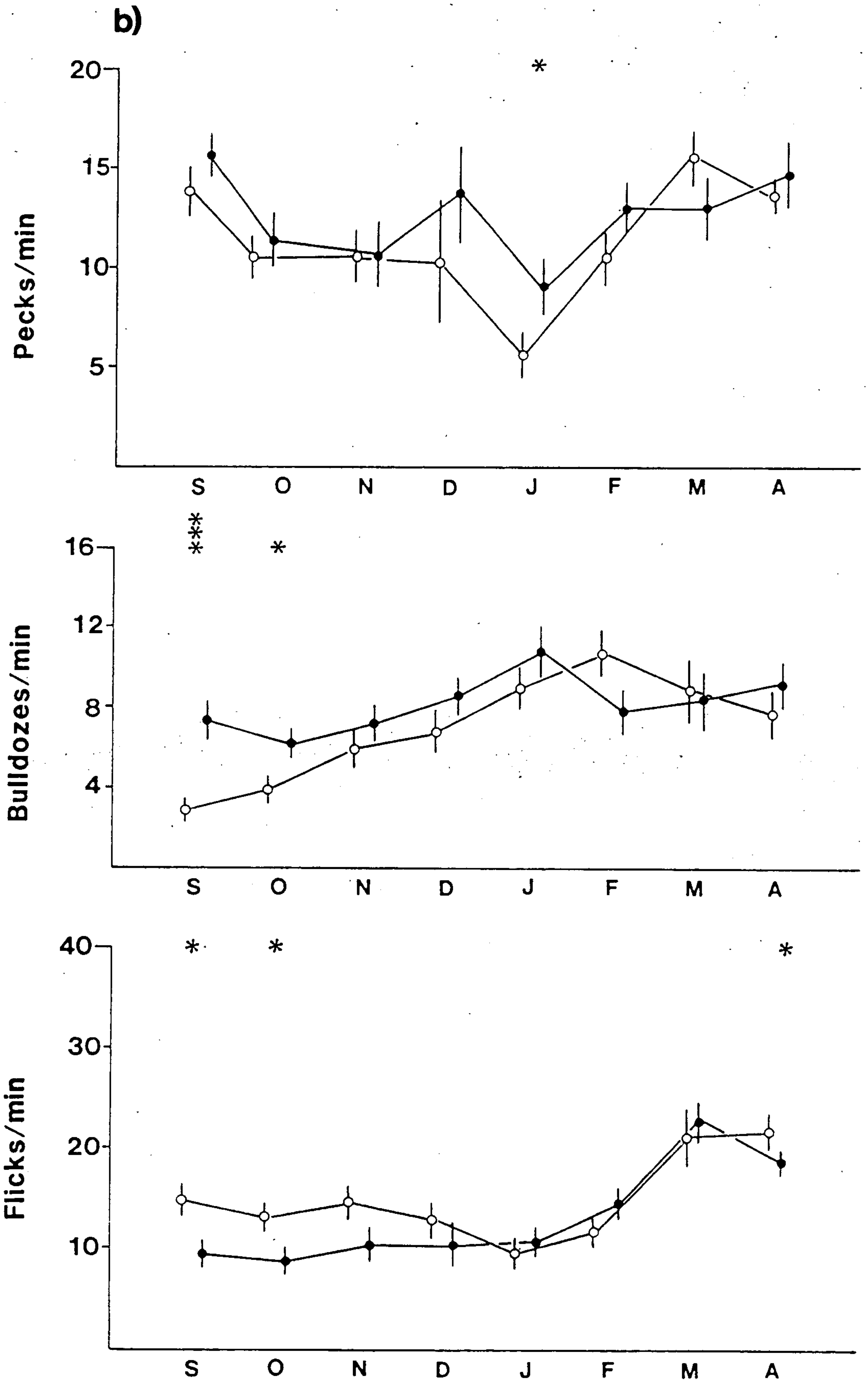
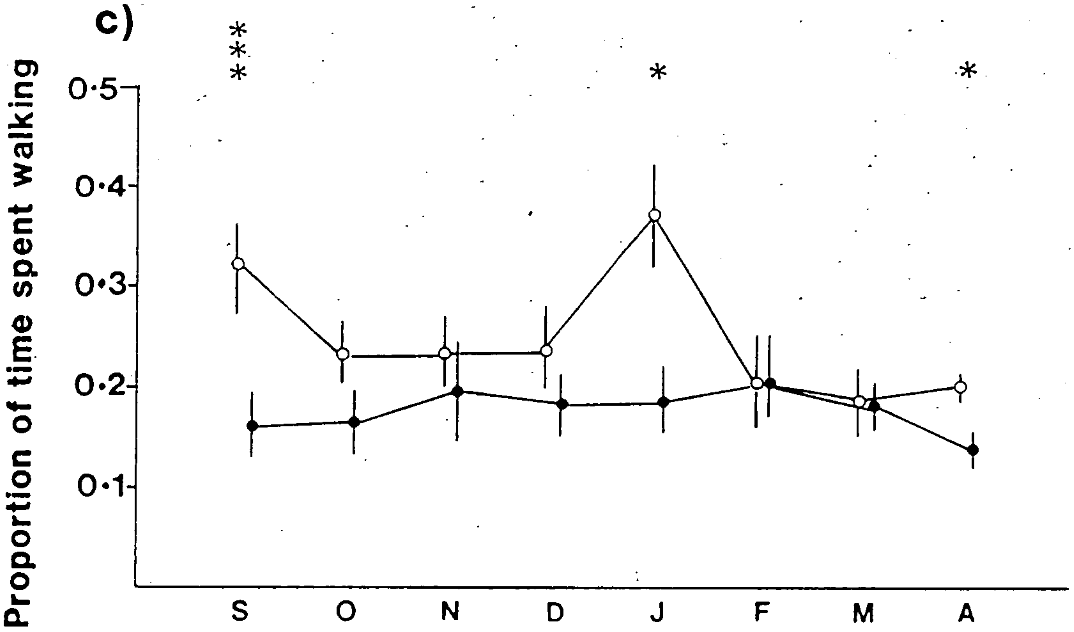
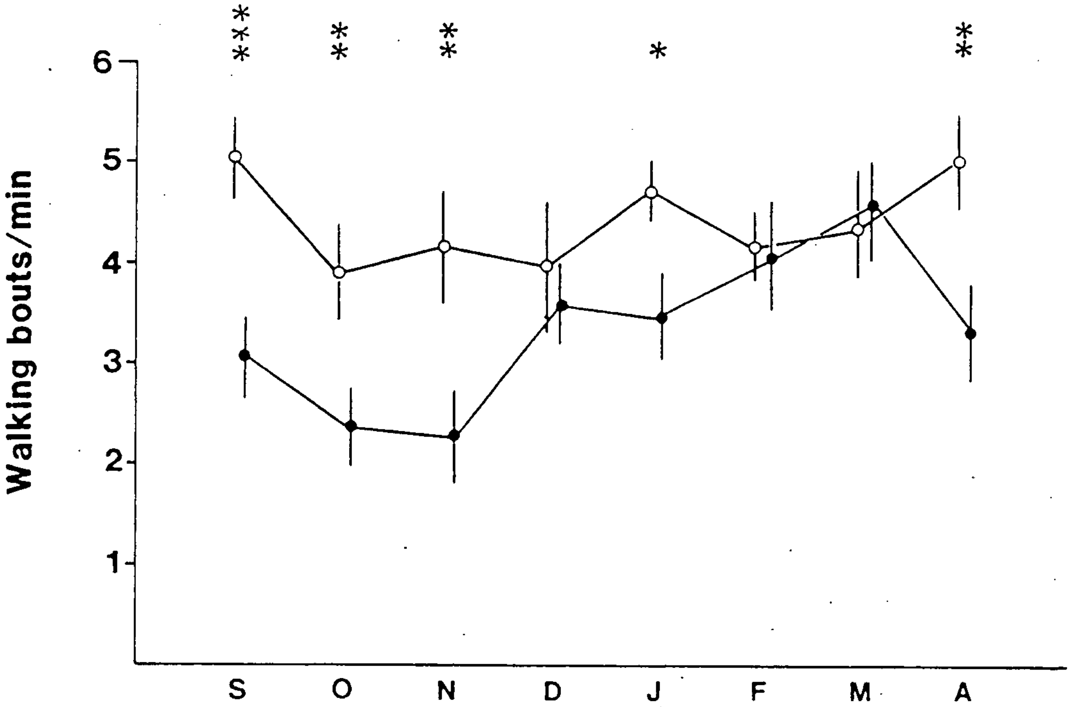

b)
Pecks/min
20
15
10
5
*
S O N D J F M A
Bulldozes/min
16
12
8
4
***
*
S O N D J F M A
Flicks/min
40
30
20
10
*
*
*
S O N D J F M A

Fig. 6.16c Seasonal changes in the proportion of time spent walking, and rates of walking bouts (mean ± SE) or adults (closed circles) and juveniles (open circles) when routing. *p<p}05, **$p<0.01$, ***$p<0.001$.

Fig. 6.16d Seasonal changes in look up rate, proportion of time spent looking up, and geometric mean look up duration (mean ± SE) for adults (closed circles) and juveniles (open circles) when routing. *$p<0.05$, **$p<0.01$.


c)
Proportion of time spent walking
0·5
0·4
0·3
0·2
0·1
S
O
N
D
J
F
M
A
***
*
*


Walking bouts/min
6
5
4
3
2
1
S
O
N
D
J
F
M
A
***
**
**
*
**

d)

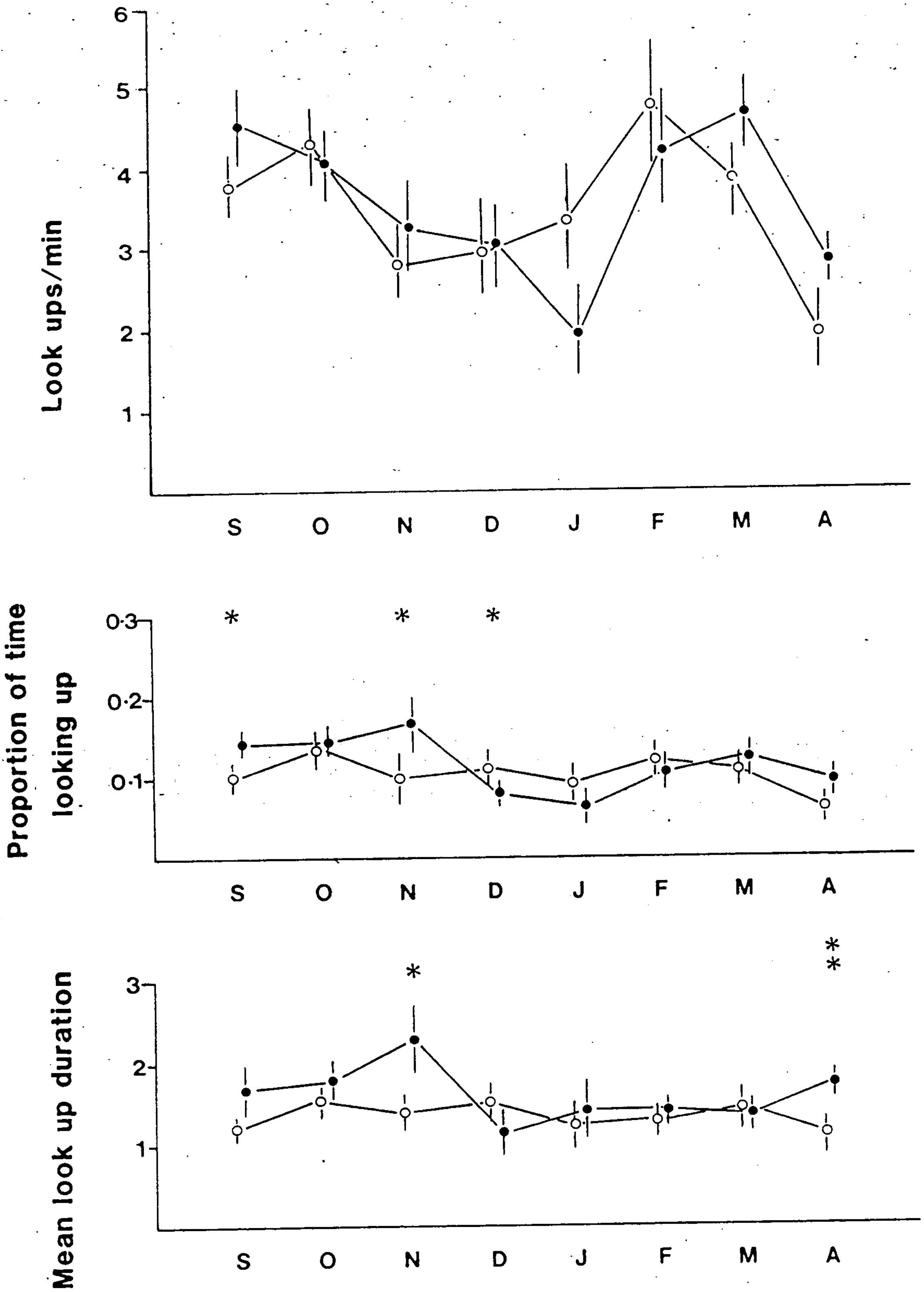
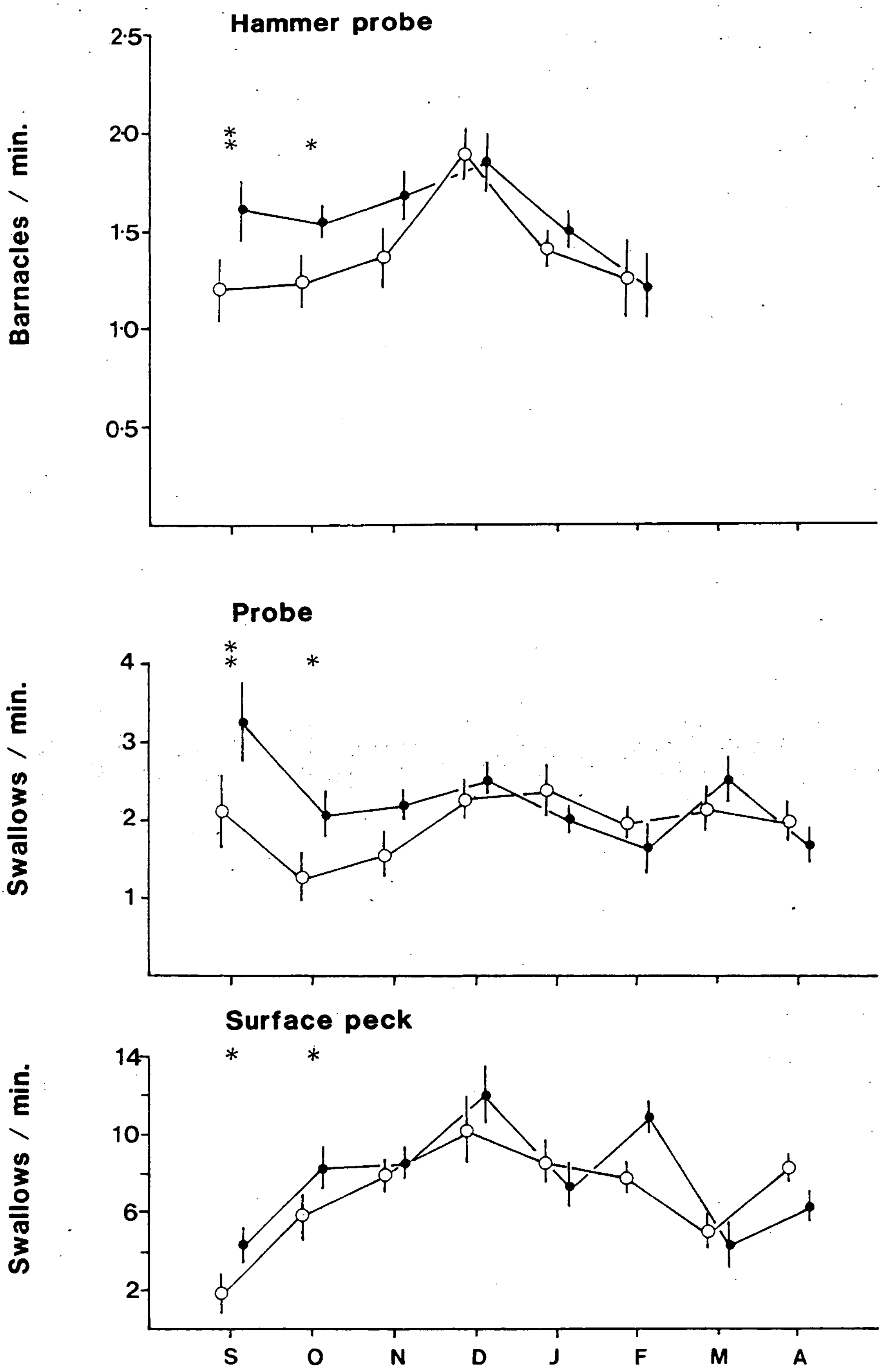

Look ups/min
6
5
4
3
2
1
S
O
N
D
J
F
M
A
Proportion of time looking up
0·3
0·2
0·1
*
*
*
S
O
N
D
J
F
M
A
Mean look up duration
3
2
1
*
**
S
O
N
D
J
F
M
A

Fig. 6.17 Seasonal changes in intake rates for adults (closed circles) and juveniles (open circles) when hammer-probing, probing and surface pecking. *$p<0.05$, **$p<0.01$.


Hammer probe
Barnacles / min.
2·5
2·0
1·5
1·0
0·5
**
*
Probe
Swallows / min.
4
3
2
1
**
*
Surface peck
Swallows / min.
14
10
6
2
*
*
S
O
N
D
J
F
M
A

al, 1977) making it potentially more difficult to discriminate between adults and juveniles later in the winter. It is possible, therefore, that the apparent attenuation of age-related differences in feeding behaviour was caused by an increasing number of birds being aged incorrectly. This did not appear to be the case, however, as the slight seasonal increase in the number of incorrectly aged birds could not account for the observations of seasonal changes in feeding behaviour (Table 6.28).

6.6.4 DISCUSSION

In September juvenile turnstone had lower intake rates and lower feeding success than did adults. These disparities gradually lessened as the winter progressed and they had virtually disappeared after two to three months in surface pecking, probing and hammer-probing birds, or after six months in routing birds. The attenuation of age-related differences in foraging success appeared to be mainly due to learning in juveniles. Juveniles were probably as site-faithful as adults (Chapter 3), so most intertidal observations were collected from the same groups of birds, which rules out any possibility that seasonal changes in feeding behaviour were due to watching different birds whose foraging skills also differed. Four colour-ringed juvenile turnstone were regularly watched over several months, and each one's foraging success increased. Several turnstone which for several months fed by hammer-probing switched to routing in December and January: relative to adults these juveniles fed with lower success than did the juveniles which had been routing since September. This suggests that

TABLE 6.28

Seasonal changes in the accuracy of ageing turnstone in the field. A colour-ringed bird was judged to have been correctly aged if an assessment of its age in the field agreed with an assessment made in the hand. Birds were aged in the field before their colour-ring combinations were visible.

	O	N	D	J	F	M	A	TOTAL
N AGED	42	21	32	28	27	55	31	236
N CORRECT	42	19	29	26	25	49	27	217
% CORRECTLY AGED	100	91	91	93	93	89	87	92

learning through increased experience with a technique was more important than maturation in producing the increased foraging success of juveniles.

Changes in the behaviour of routing juveniles appeared to reflect the learning process. At the beginning of the winter, compared with adults, juveniles spent more time walking, fed in more food patches (i.e. had higher rates of walking bouts), and flicked seaweed more often but bulldozed seaweed less often. They also spent less time looking up, but had their heads raised for longer than did adults because they spent comparatively more time walking. These results suggest that juveniles were not efficient at recognising good feeding patches and/or could not feed efficiently in those feeding patches. By flicking too much and bulldozing too little it was probable that fewer prey items were exposed when juveniles routed in seaweed.

By December juveniles' routing behaviour was very similar to adults' yet their intake rates were still lower. This may have been because (a) they could still not recognise good feeding sites, or (b) they were forced to feed in poorer sites by the aggression of adults when feeding in good sites, or (c) they avoided the good sites because of the presence of adults. Juveniles using other feeding techniques appeared to be able to assess the quality of feeding sites by December, which indicates that possibility (a) may have been of minimal importance, although it is possible that it was more difficult to assess a good routing site. Aggression rates were higher for routing than for other techniques which, even though I excluded observations containing supplants, lends support to hypotheses (b) and (c). If lower status most affected the intake rates of juveniles when prey was at low densities, then the increased intake rates of juveniles in March and April can be explained by increases in prey density at this time of the year (section 6.4).

Although the lower foraging experience of juveniles could be a factor involved in producing age-related mortality in early winter (until around December), for the rest of the winter other factors are probably more important. Such factors could include juveniles' inexperience at avoiding predators and juveniles' low social status (see Chapters 2 and 4). If juveniles take smaller prey items than adults by virtue of their inexperience then their biomass intake rates may have been lower for longer periods than indicated by my measures of intake rates. However, I have no reason to believe that juveniles did take smaller items (but see Puttick, 1978, for curlew sandpipers). Juvenile waders are usually smaller than adults (Prater _et al_, 1977) and taking smaller prey is likely to be a consequence of a smaller bill size rather than inexperience. For example, shorter-billed male purple sandpipers take smaller prey than longer-billed females (Feare & Summers, 1985).

CHAPTER 7

GENERAL DISCUSSION

The primary objectives of a wintering turnstone are to survive and be in good condition at the end of a winter, and to achieve this it must eat and avoid being eaten. Consequently, the influence of food and predation on the behaviour and ecology of turnstone is a reccurring theme throughout this thesis. In this final chapter I will consider the evidence that food and predation have influenced the social organisation of turnstone.

Many waders have been shown to defend territories in winter (e.g. Myers _et_ _al_, 1979a) but neither in this study nor in others (Myers _et_ _al_, 1979a; Marshall, 1981; Altenburg _et_ _al_, 1982; Metcalfe, 1984) have turnstone been observed defending territories. If the expression of territoriality depends on the costs and benefits of defending a site (Brown, 1964), then it would seem likely that the costs to turnstone of defending a resource site exceed the benefits. Three factors seem important in determining the payoffs associated with non-breeding territoriality in waders: (1) predation, (2) conspecific density, and (3) nature of food. Increased predation risk seems to increase the costs of defending a territory, presumably because of the increased vulnerability of solitary territory holders. For example, in winters when merlins are resident at Bodega Bay, California, sanderlings cease defending high tide territories and join flocks (Myers, 1980). Although the turnstone at the study site were obviously subjected to frequent sparrowhawk attacks throughout the study period, it is unlikely that this inhibited territory formation. The absence of territoriality at other sites where predator regimes were probably different suggests that predation pressure was not responsible for the lack of territoriality. Intruder density has a negative effect on territory size in wintering sanderling (Myers et al, 1979b) and, possibly, in breeding turnstone (Whitfield, in press: Appendix 2). At high intruder densities, sanderling may abandon defence (Myers et al, 1979a), but I find it difficult to imagine that conspecific density was always so high that it precluded territorial defence in wintering turnstone. Individuals were occasionally seen feeding solitarily yet if approached by other birds they made no attempt to prevent conspecifics feeding nearby. Feeding turnstone follow the ebbing tide out (Harris, 1979; Marshall, 1981; pers. obs.). The tidal instability of prey availability may make it unprofitable to defend an area which soon becomes less suitable than other sites nearer to the tide edge. Tidal stability of defended sites is a common feature of wintering wader territoriality (Myers et al, 1979a; Myers, 1984), and at Scoughall redshank most commonly defended pools as territories (pers. obs.).

Even if the potential payoffs are always too low to warrant territorial defence, a feeding turnstone is faced with two options: feed alone or feed in a flock. Flocking is usually considered as a consequence of predation benefits rather than feeding benefits for several reasons, such as (1) the observation that waders (including redshank at Scoughall) abandon territories and form compact flocks when a predator appears (Myers et al, 1979a; Myers, 1984); (2) flocking reduces vigilance levels, implying that flock members ´feel safer´, and so allows increased feeding time (Fleischer, 1983; Metcalfe, 1984a, b; Myers, 1984); (3) flocking reduces predation risk (Page & Whitacre, 1975; Kus, cited by Myers, 1984); (4) flocking often depresses foraging rates (reviews by Goss-Custard, 1980, 1985).

As turnstone at Scoughall feed closer to cover, and therefore incur higher predation risks (Whitfield, 1985: Appendix 1), flock density increases (Marshall, 1981; compare intertidal data in Chapter 6 with strandline data in Chapter 4). Redshank density also increases nearer to cover (i.e. on the strandline) at Scoughall (Mullin, 1985). However, wader density is known to increase in relation to food density (e.g. Rands & Barkham, 1981), which given the frequent high prey densities and enhanced intake rates on the strandline (Chapters 4 and 6), may explain the higher flock density there, as might the decreased space in which to feed (Marshall, 1981). Nevertheless, the possible relationship between turnstone density and predation risk is supported by the observation that flock density increases immediately after a sparrowhawk attack or appearance (unpubl. data).

Some individuals′ intake rates were depressed by flocking when using certain feeding techniques in some microhabitats as a result of interference effects (Chapters 4 and 6). This suggests that flocking does not increase feeding rates of turnstone , but rather that it can have detrimental effects on feeding (although payoffs probably varied with status). Goss-Custard (1970) has suggested that the dispersion of waders reflects a compromise between the costs of flock feeding and the benefits of reduced predation risk. He argues that all waders could benefit by flocking, but those that use feeding techniques which are prone to interference are forced to spread out in loose groups. Visually feeding redshank are prone to interference and form loose flocks, whereas touch feeding redshank are not affected by interference and form compact flocks (Goss-Custard, 1976). Similarly, touch feeding knot live in dense flocks while visual feeding ringed plovers Charadrius hiaticula usually live in loose flocks or as solitary individuals (Goss-Custard, 1970).

Blick (1980 cited by Goss-Custard, 1985), on the other hand, has argued that individuals or species which are visual feeders have their heads up regularly whilst searching for prey and so have less need to flock to increase vigilance.

Turnstone on the study site used only visual feeding methods, but different techniques were associated with different vigilance levels and different dipersion patterns (Chapter 6). There was clearly a relationship between the amount of time a bird has its head up while searching for prey (proportion of time spent walking) and the amount of time a bird interupts its feeding to look up (proportion of time spent looking up): this is consistent with Blick´s hypothesis. Nearest neighbour distance was greater in probing birds than in routing birds. Therefore, Blick´s hypothesis predicts that probing birds should have their head up for longer than routing birds, whereas Goss-Custard´s hypothesis predicts that probing birds are more prone to interference. The data were consistent with Blick´s hypothesis but contradicted Goss-Custard´s, since probing birds spent more time with their head up and were less prone to interference than were routing birds (Chapter 6). It is worth remembering, however, that probing prey density was lower than routing prey density (Chapter 6) so technique differences in nearest neighbour distance may simply be a response to prey density difference: probing birds must cover a greater area to obtain their prey and so are more likely to be further away from their nearest neighbour.

Increased site tenacity appeared to be promoted by increased stability of food supplies (Chapter 2): this echoes the postulated relationship between territoriality and stability of prey availability mentioned earlier. It also conforms to the suggested ecological basis for intra- and inter-specific differences in itinerancy made by Evans (1981) and others (review in Myers, 1984).

Very little data is available on the stability of wader flock membership but there is a tantalising suggestion that itinerancy, flock stability and the form of competitive interactions are intercorrelated, but separating cause from effect will be difficult until more information is acquired from a greater number of species. The dunlin and the sanderling are more itinerant than the turnstone (Myers, 1984; Symonds et al, 1984; this study) and also appear to have no or very weak individual associations, in contrast to turnstone (Myers, 1983; Shanewise & Herman, 1979; this study). Turnstone compete for food via stable dominant/subordinate relationships, whereas sanderling and dunlin probably do not (this study; Myers, 1983; Bradley, 1982). It is possible that increased instability of food supplies leads to greater itinerancy, which makes individual associations more difficult to maintain, and relatively high flock stability is a prerequisite for the formation of stable dyadic relationships (Chapter 5). Alternatively, the nature of food type and/or distribution may allow frequent displacements of conspecifics from feeding sites or food theft (Chapter 4), which, to minimise the cost to individuals of escalated interactions with unfamiliar birds, selects for increased flock stability and site faithfulness to facilitate the maintenance of constant dominance/subordinate relationships (Balph, 1979). These alternatives are not mutually exclusive and each one may act in conjunction with the other, but their relative importance in determining the social systems of wintering waders, if they are important at all, remains to be discovered.

Large gaps still exist in our knowledge of the factors influencing the social organisation of wintering waders, and attempting to fill these gaps should be an objective of future research.

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APPENDICES

Appendix 1.

RAPTOR PREDATION ON WINTERING WADERS IN SOUTH-EAST SCOTLAND

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ABSTRACT

Predation on overwintering waders was investigated during the winters of 1982-83 and 1983-84 at a rocky shore and a small estuary in S.E. Scotland. Probably all the waders which were found after being eaten were killed by raptors; mammalian predation and death due to severe weather were of minimal importance in comparison to the effects of raptor predation. Sparrowhawks were probably the major predators of waders at both sites. Owls also took some waders at both sites. Differences were found between the rocky shore and the estuary in the species of raptors which were seen (more Peregrines and Merlins seen on the estuary) and in the numbers of wader kills which had been plucked and eaten on open ground (more open ground pluckings, indicative of Peregrines and Merlins, found on the estuary). It is suggested that Peregrines and Merlins took more waders at the estuary due to their preference for hunting over large open expanses. Winter mortality rates due to predation varied between species of waders: at the rocky shore the Redshank suffered the heaviest winter mortality (20% and 16%) whilst on the estuary the Ringed Plover had the highest winter mortality (19%). At both sites no large waders such as Curlews and Oystercatchers died as a result of predators and in these species other factors, such as severe weather or starvation, appeared to be a greater source of mortality. Significantly more juvenile Redshanks, Turnstones and, probably, Dunlin and Ringed Plovers were found eaten than was expected from the age-composition of their respective populations. In the Redshank and Turnstone several differences in the behaviour of juveniles and adults were discovered which may have made juveniles more vulnerable to predation.

Page & Whitacre (1975) have shown that raptor predation can be an important factor in the population dynamics of several wader species overwintering in California. For example, in one winter they estimated that about 21% of the Dunlin (*Calidris alpina*) population was eaten by raptors. Kus *et al* . (1984) have extended Page & Whitacre's findings and demonstrated that raptors may also produce age-related differences in mortality in the Dunlin by eating more juveniles than would be expected from their representation in the population. However, several authors have stated that the effects of raptor predation on British wintering waders are probably negligible (e.g. Evans 1976; Goss-Custard 1979; Prater 1979) despite the lack of any relevant study. Townshend (1984), reviewing several aspects of possible effects of predation on waders, presented few data but stressed the need for further studies on predation on waders.

This paper aims to assess the impact that raptor predation may have on overwintering waders at two sites in S.E.Scotland over two winters by examining: (1) the proportion of wader populations found eaten; (2) age-related differences in mortality and associated age-related differences in wader behaviour; and (3) seasonal, between- year and between-site variations in raptor predation.

STUDY SITE AND METHODS

The study areas, 48 km east north east of Edinburgh on the East Lothian coast, were a rocky shore at Scoughall and a small estuary at Tyninghame (Fig.1). At Scoughall the rocky coastline is bordered mainly by open farmland interspersed with small deciduous woods and occasional narrow strips of conifers. Sea-buckthorn (*Hippophae rhamnoides*) borders much of the shoreline. The shore of Tyninghame estuary is surrounded by mixed woodland, mature coniferous plantations and sand dunes.

The study took place in the " winters " (August to April) of 1982-83 and 1983-84. All species of waders were counted each month, at Scoughall from August to April and at Tyninghame from September to March. Waders less than one year old were termed juveniles and older birds termed adults. The juvenile:adult ratio was estimated for several species of waders using plumage characteristics (Prater *et al*. 1977) viewed through a 15-60X telescope. With the aid of a hide I could often view birds from close distances (on numerous occasions from less than 15m) and this facilitated ageing individuals in the field. Juveniles of all species which were aged progressively lost some of their distinctive "juvenile" feathers throughout a winter, and until December, when the majority of juvenile feathers were replaced by "adult" feathers, this produced a characteristic "patchy" apearance of the scapulars and wing coverts of juveniles when seen in the field. From December onwards most juvenile Turnstones (*Arenaria interpres*) retained some visible juvenile wing coverts, and they often had less black on the breast and paler legs than adults. Bill colour and appearance of tertials were the main criteria used in ageing Redshanks (Tringa totanus) (Prater et al. 1977). Assessment of the age of colour-marked Turnstones and Redshanks in the field agreed in 92% (n=236) and 91% (n=72) of instances, respectively, with those made in the hand when the birds were caught. These checks on my ability to age in the field occurred after colour-ringing. Turnstones were aged before I could see their colour-ring identity as this frequently occurred when they fed in seaweed or behind rocks. Similarly, some Redshanks were aged as they fed in leg-depth pools, and although others were aged when I could see their colour rings, I did not know the ring combinations of adults and juveniles. Juvenile Ringed Plovers (Charadrius hiaticula) usually had thinner breast bands than adults and retained a few worn juvenile scapulars until spring. Juvenile Dunlin usually retained a few juvenile outer median coverts until early spring but this species proved to be comparatively difficult to age later in the season because most Dunlin normally fed at greater distances from the hide. Gromadzka & Przystupa (1984) have noted that some adult Dunlins possess buff fringed coverts rather than the "normal" grey fringed adult coverts and so may be mistakenly identified as juveniles. Despite this problem, of the large numbers of Dunlins wintering in Britain which so far have been examined (including many on the Firth of Forth), extremely few adults with buff fringed coverts have been discovered (Clark 1984) and ageing Dunlins in the field is possible even on large estuaries (Clark 1983). Even if some adult Dunlins were wrongly classed as juveniles in the present study, this should only make the test for age related mortality more conservative. However, only the juvenile:adult ratio estimates for the Turnstone and the Redshank can be regarded as reliable because I could not check independently my accuracy in ageing Dunlin and Ringed Plovers in the field. I have not used the results of cannon-netted samples to estimate the age composition of wader populations because catches were often heavily biased towards juveniles (see also Pienkowski & Dick 1976; Goss-Custard et al. 1981).

I attempted to assess the number of birds dying on the study site by carefully looking for corpses and other remains. In 1982-83 Scoughall was searched about every 4-5 days whereas a part of Tyninghame was searched only five times in the entire " winter " period. In 1983-84 Scoughall was searched every week and almost all of Tyninghame was searched every month (Fig.1). Some plucked feathers of small passerines may not have been found but, because searches were frequent, there was unlikely to have been seasonal variation in the efficiency of detecting them. Repeated searches by independent observers suggested that at Scoughall very few, if any,wader remains will have been missed but at Tyninghame some remains were probably undiscovered (especially on the mudflats and saltmarshes). However, searching efficiency was not checked quantitatively. Remains of the same species found in two places at the same time have been classified as two individual remains only if an identifiable feature was common to both e.g. right outer primary feather, or right leg. Any individual wader found dead could usually be aged by examining the wing feathers left by the predator or by referring to ringing records if the bird had been ringed. The date of death was estimated from the state of the remains (see Newton and Marquiss 1982) and the date of the preceding search at that site. All remains were collected to avoid confusion with later finds.

Each set of pluckings or remains was ascribed to one of the following categories:

A. Corpse eaten in cover (i.e. in a wood or undergrowth), on or less than 1.5m above the ground (e.g. on tree stump, fallen tree); cleanly plucked feathers; any bones picked clean of flesh; wing feathers either plucked cleanly or still left on wing bones.

B. As in A but corpse eaten on the ground in the open (i.e. >5m away from cover).

C. As in A but corpse eaten on a wooden post in the open.

D. Corpse eaten up a tree (>1.5m above ground); cleanly plucked feathers but very few found; some flesh remaining on any bones found.

E. Corpse eaten in cover; feathers removed by biting through shafts; remains have "messy" appearance and may not be completely eaten; uneaten parts have "chewed" appearance.

F. As in E but corpse eaten in the open.

G. Corpse found on strand line, either intact or partially eaten.

These categories encompassed the state and position of all remains which were found and were later used to identify the probable cause of death of each corpse. All diurnal raptors cleanly pluck their prey and neatly tear the flesh from the bones. Sparrowhawks normally eat their prey on or near the ground in cover (M.Marquiss pers. comm.; A.Heavisides pers. comm.; pers. obs.) (Category A). On the other hand, Peregrines usually eat their prey on the ground in the open (Baker 1967; Ratcliffe 1980; M.Marquiss pers. comm.) (Category B). Merlins normally eat their prey in the open (Newton _et al_. 1984; A.Heavisides pers. comm.; pers. obs.) (Categories B and C), often plucking their prey on fence posts (Page & Whitacre 1975; Kus _et al_. 1984; pers. obs.) (Category C). Owls normally attempt to swallow their prey whole or in large portions, leaving fewer plucked feathers and less "neat" remains compared to diurnal raptors (e.g. Welty 1963) (Category D). Since mammalian predators usually chew their prey, feathers are bitten through the shafts and remains have a "messy" appearance (Categories E and F). I estimated the numbers of waders dying by starvation or through the effects of severe weather by searching for intact or scavenged corpses on or near the strand line (Goss-Custard et al. 1977; Davidson & Clark 1982) (Category G).

Mean weights of prey species were taken from Ratcliffe (1980) and from local ringing records. When estimating the weight consumed from each prey item 10% was subtracted from the mean species weight to approximate what was not eaten (Ratcliffe 1980; unpublished data, this study).

I noted all mammalian and avian predators seen. Checks for predators were not systematic but there was no seasonal variation in the time spent in the field when observations of predators were made. When raptors (Falconiformes and Strigiformes) attacked waders i.e. flew at flocks or individual waders, I noted whether the attack was succcessful and where the prey was positioned on the littoral zone prior to the attack. If a successful attack was initiated against a wader flock I also attempted to note the position of the captured waders in relation to other flock members.

Whenever possible I estimated the juvenile:adult ratio in flocks of waders feeding on the strand line at Scoughall, particularly when the tide was lower down the shore. When a raptor appeared near these waders I also attempted to count the number of juvenile and adult waders which remained on the ground rather than taking flight, as my earlier subjective observations suggested that the former individuals were more vulnerable to predation. I also compared the age-composition of flock peripheries with flock centres by ageing the ten individuals on the ends of flocks (five each end) and ten randomly selected from the centre. In addition I measured the distance in bird lengths to the nearest adult neighbour for both adult and juvenile Turnstones when feeding at high tide.

RESULTS

PREDATORS SEEN AND REMAINS FOUND

The most commonly seen raptors at both Scoughall and Tyninghame were Sparrowhawks (81% and 51% of sightings respectively), but both Merlins and Peregrines were seen more often at Tyninghame than at Scoughall. Mammalian predators also appeared to be common in the study area (stoats were seen regularly, foxes occasionally and fox faeces were found on numerous occasions) (Table 1). Sparrowhawks (always female in the 23 observations where sexing was possible) were seen to attack waders on thirty-three occasions at Scoughall and on ten occasions at Tyninghame. Three Peregrine attacks on waders were witnessed at Tyninghame as was one Merlin attack. Kestrels were never seen attempting to catch waders, but may have done so (see Discussion). Stoats were seen on the littoral zone at Scoughall on four occasions, but neither stoats or foxes were seen attacking waders.

On several occasions I flushed raptors from their prey or saw a raptor catch a wader and then waited until the raptor had consumed its prey. In these cases I could be sure of the predator which was responsible for each set of remains. The remains of thirteen waders known to have been eaten by Sparrowhawks were all ascribed to

Category A; those of two waders known to have been eaten by Peregrines fell into Category B; one wader eaten by a Merlin could be placed into Category B and another into Category C; and two waders eaten by Tawny Owls were ascribed to Category D. Category D remains were usually associated with owl pellets, suggesting predation by owls. These observations, together with similar findings of other workers (see Methods), provided information of use in identifying the cause of death of other corpses.

I found very little evidence which suggested that scavenging of corpses occurred to any significant extent. Wood Pigeons were regularly shot and not collected by local people, but very few were subsequently scavenged. During an auk "wreck" in the winter of 1982-83, very few corpses were scavenged and even then the scavenging of each body was incomplete. Most other strand line corpses were also unmarked and usually remained so if I did not pick them up. It is likely, therefore, that all remains classified in Categories A-F were the result of direct predation rather than scavenging, and I have assumed that all remains in Categories A-F were "kills".

Most remains of waders were ascribed to Categories A-F (88% Scoughall; 83% Tyninghame), whilst very few waders (12% Scoughall; 17% Tyninghame) were found in a condition which suggested that they had died as a result of starvation,severe weather etc. (Category G). These results suggest that most remains of waders were the result of predation.

The remains of thirty-six species of birds were found after being eaten by predators at Scoughall and Tyninghame (Table 2). The five main prey species by numbers were Redshank, Starling, Linnet, Blackbird, and Song Thrush; and by weight, Redshank, Wood Pigeon, Starling, Blackbird, and Turnstone.

I found only four Wood Pigeons which appeared to have been eaten by foxes judging by the bitten off feathers, and two Wood Pigeons which were probably handled by both a raptor and a fox (there were neat triangular notches out of the pigeon's sternum but some feathers had been bitten off). However, no remains of waders were ascribed to Categories E and F (bitten feathers and "messy" remains), so it is probable that no wader was eaten by a mammalian predator. It seems reasonable to assume, therefore, that all predated waders, and the vast majority of non-waders, were killed by raptors.

Most wader kills fell into Category A (clean pluckings in cover); 82% at Scoughall, 74% at Tyninghame. More clean pluckings of waders were found in the open (Categories B and C) at Tyninghame (24%) than at Scoughall (4%). Conversely, more remains in Category D (eaten up a tree, few plucked feathers) were found at Scoughall (14%) than at Tyninghame (2%) (Table 3). These results suggest that Sparrowhawks were responsible for most predation, and therefore most mortality, of waders at both sites. Furthermore, it appears that some waders were taken by Peregrines and Merlins (mainly at Tyninghame) and by owls, especially at Scoughall.

MORTALITY OF WADERS

The first wader remains of the "winter" were found in the last week of September in 1982 and in the first week of October in 1983. In both winters the last remains were found in the last week of March. Thus, deaths of waders occurred only during October to March and I have confined my analysis to this period. It is known from observations of colour-ringed birds that Turnstones at Scoughall and Tyninghame can be considered as a single resident population, so counts and mortality data from both areas have been combined. For those species eaten by predators, peak wader counts are presented in Fig. 2. Ringing indicated that the Redshanks at Scoughall probably represented a largely resident population with probably some movement to and from Tyninghame, but the extent of movements and turnover of the wader prey species at Tyninghame was not known. It is important to realise that the extent of population turnover may affect mortality estimates. The counts suggest that in 1982-83 the size of the Scoughall Redshank and Turnstone populations varied little, so I have estimated mortality levels based on population sizes of 140 and 250 respectively;

$$\text{i.e. mortality} = \frac{\text{total no. of remains found}}{\text{population size}} \times 100\%$$

In all other cases I have estimated mortality by the following calculation:

$$\text{mortality} = \sum \frac{\text{no. of individuals found dead in month x}}{\text{peak count in month x}} \times 100\%$$

Mortality levels could not be estimated at Tyninghame 1982-83 due to the small area which was searched for kills.

For those wader species which were preyed upon, estimates of the proportions taken are shown in Table 4. Of all the wader species at Scoughall, Redshanks suffered the heaviest winter mortality from predation (20% and 16%). Similarly at Tyninghame many Redshanks were eaten by predators (15%), but here Ringed Plovers suffered the highest rate of predation (19%). At both sites, probably no Curlews or Oystercatchers died as a result of predation, and at Tyninghame , no Bar-tailed Godwits (Limosa laponnica) were eaten by predators.

In both winters most strand line corpses (Category G) which were examined were had low weights and drastically reduced pectoral muscles suggesting they had died of starvation. Some corpses, particularly Oystercatchers, had deformed or broken limbs which may have indirectly caused death. In the 1983-84 winter most strand line corpses appeared within two weeks after a period of comparatively severe weather suggesting that the cold weather had indirectly caused death. At Scoughall in the 1982-83 winter only Curlews and Oystercatchers died as a result of starvation (2% winter mortality for each species). In 1983-84 winter mortality due to starvation and severe weather appeared to occur only in the Redshank (1%) and the Oystercatcher (3%). At Tyninghame in the 1983-84 winter, evidence of mortality due to starvation and severe weather was found in four species: Oystercatcher (1%), Curlew (1%), Grey Plover (2%), and Redshank (2%).

AGE-RELATED MORTALITY OF WADERS

The proportion of juveniles in all wader populations appeared to remain about the same throughout each winter (Fig. 3). Mean values of % juveniles in the population were as follows: Scoughall 1982-83 - Redshank 40%, Turnstone 17%; Scoughall 1983-84 - Redshank 32%, Turnstone 18%; Tyninghame 1983-84 - Ringed Plover 29%, Dunlin 35%, Redshank 42%. Mortality was age-related, with significantly more juvenile waders found eaten by raptors than would be expected from the mean age-composition of the relevant populations (Table 5).

AGE-RELATED WADER BEHAVIOUR AT SCOUGHALL

Sparrowhawks were successful at capturing waders in seven (21%) of the thirty-three attempts observed. Thirty of these attempts

(91%), including the seven successful ones, were made on birds on the strand line rather than on birds feeding lower down the shore. Of the four occasions when the position of the prey individual could be noted with confidence, three waders were taken from the ground after most of the flock had taken flight and one was captured in flight away from the main body of the flying flock. In the Redshank and Turnstone, the only two species to regularly feed in large numbers on the strand line, there were significantly more juveniles present there at low tide than would be expected from the age-composition of the respective populations (Redshank: flk size x = 15.7^{+}1.8 S.E., Juv x = 12.3^{+}1.5 S.E., N=12; Turnstone: flk size x = 9.2^{+}1.9 S.E., Juv x = 6.3^{+}0.8 S.E., N=10) (individual Fisher's Exact Probability Tests: chi-squared combined probabilities test; Redshank $p<0.001$ and Turnstone $p<0.001$). Juvenile Redshanks and Turnstones were also significantly more likely than adults to remain on the ground rather than take flight after the appearance or attack of a Sparrowhawk (individual Fisher's Exact Probability Tests: chi-squared combined probabilities test; Redshank $p<0.01$ and Turnstone $p<0.001$: Table 6). Within high tide feeding flocks of both wader species, significantly more juveniles were found on the ends rather than the centre of flocks (Redshank: flk ends Juv x = 7.6^{+}0.7 S.E., flk centre Juv x = 3.7^{+}0.5 S.E., N=9; Turnstone: flk ends Juv x = 6.7^{+}0.5 S.E., flk centre Juv x = 1.3^{+}0.3 S.E., N=21) (Wilcoxon Matched Pairs Signed Ranks Test; Redshank $p<0.01$ and Turnstone $p<0.01$). Juvenile Turnstones were also significantly further away from the nearest adult neighbour than were other adults (Kolmogorov-Smirnov Two-sample Test; $p<0.001$: Fig. 4). No data were collected for the Redshank in this respect but subjective impressions suggested a similar situation also existed in this species.

SEASONAL VARIATIONS IN RAPTOR DIET

There was a marked seasonal variation in the proportion of waders found eaten by raptors over a winter, regardless of whether the results are considered by number of prey items or as weight of prey eaten (Fig. 5). Wader mortality was generally greatest in December and January and was lowest in February and March. The same pattern was evident regardless of site or year. In contrast, there was no marked seasonal trend in the estimated weight of prey eaten over a winter on the study areas (Fig. 6). However, at Scoughall over twice as much prey was eaten in the 1982-83 winter compared to the 1983-84 winter.

DISCUSSION

There are several problems with trying to ascribe individual eaten remains to a particular predator species; for example, the hunger of the predator may have considerable bearing on the state of the remains; many predators probably eat carrion or scavenge remains, and kleptoparasitism between predators may occur. However, because many predators usually deal with their prey in different ways it is possible, with reservations, to gain an idea of which predators were responsible for certain categories of kill-types which are based on the appearance and position of the remains.

Most waders found eaten by predators were classified into Category A (clean pluckings in cover) (82% at Scoughall, 74% at Tyninghame) and thus seem likely to have been the result of Sparrowhawk predation. Indeed most non-waders (91% at Scoughall, 90%

at Tyninghame) were also found eaten in the manner typical of a Sparrowhawk. Sparrowhawks were the most frequently seen raptor at both study sites and were seen attacking waders on the greatest number of occasions. It seems reasonable, therefore, to conclude that the Sparrowhawk was the major predator of waders, and was responsible for most wader mortality on the study site.

Most of the clean pluckings found eaten in the open (Categories B and C) were probably the result of Peregrine or Merlin predation. This result suggests that these two raptors captured more waders at Tyninghame (24% of all "kills") where they were seen frequently (Table 2), than at Scoughall (4%). I also suspect that the only two waders eaten in the open at Scoughall were the result of Kestrel predation as along with several pellets consisting entirely of fragments of beetles,I found the pluckings at a regular roosting site of a female Kestrel. Moreover, for several reasons Merlin and Peregrine "kills" were far less likely to have been found at Tyninghame than at Scoughall. Firstly, an intensive study of the Turnstone was carried out at Scoughall so I was more likely to incidentally discover any kills on the open shore at this site. Also, many more people visited Tyninghame, so more kills were likely to have been removed before I discovered them, and far more open areas, i.e. the mudflats , were not searched at Tyninghame and because of this I undoubtedly missed many kills, as indicated by my regularly finding several plucked wader feathers which were probably not moulted feathers, washed up on the high tide line at the estuary. It may be that the hunting technique of Sparrowhawks, relying on surprise attacks from cover (Tinbergen 1946; Newton & Marquiss 1982), is less suited to the more open estuarine habitat whilst the

Peregrine and the Merlin, preferring open expanses (Ratcliffe 1980; Brown 1976), are more effective when hunting on estuaries.

The absence of evidence for predation on waders by mammalian predators contrasts with the results of Townshend (1984), who suggested that foxes could be important predators of waders on some sites, basing his conclusion on an estimated 11% fox predation of a cohort of radio-tagged Grey Plovers at Teesmouth. Townshend excluded from his analysis those birds which died during the first week after capture because of possible after-effects of handling. Thus Townshend's estimate is based on the assumption that all the remaining birds subsequently behaved normally. The fact that Plovers were cached and that some of the cached birds were of very low weight (D.Townshend pers. comm.) suggests that foxes found them either easy to catch or find dead. This casts some doubt on to Townshend's assumption that radio-tagging did not affect the likelihood of death. This assumption needs to be tested, especially since Sargeant _et_ _al_. (1973) suggested that American Teal _Anas_ _discors_ carrying radio transmitters were more susceptible to predation by mink _Mustela_ _vison_ (see also Gilmer _et_ _al_. 1974). Despite this difficulty in interpreting the data, there is likely to be variation between sites in the importance of mammalian predation.

The proportion of winter mortality of several smaller wader species (less than 180g: Redshank and smaller) resulting from starvation and severe weather was low in comparison to that due to raptor predation. For larger waders, however, such as Curlews or Oystercatchers, I found that starvation and severe weather caused more deaths than raptor predation. Mortality of waders in Britain due to the effects of weather appears to vary both between areas and between years, with mild winters producing relatively few deaths (Davidson and Clark 1983) but severe winters producing quite spectacular mortality in some estuaries (Clark 1982a). Given the relative infrequency of severe winters in recent decades and the recovery of several raptor populations over the last ten years (e.g. Newton & Haas 1984; Ratcliffe 1984) it may well be that in at least some areas predation is a greater and more consistent source of mortality in some smaller wader species.

At Scoughall waders commonly fed on the strand line, mainly at high tide, often feeding on all stages of the seaweed fly (Coelopa spp.) in the rotting washed up seaweed. These waders seemed particularly vulnerable to attack by Sparrowhawks, the main predators at Scoughall, so the amount of time a wader spent on the strand line probably affected its likelihood of death. For example, compared with other species the Redshank had the highest winter mortality due to predation and was seen feeding on the strand line on most occasions. In contrast, Purple Sandpipers had very low winter mortality due to predation and rarely fed on the strand line, even at high tide when they fed or roosted on an offshore islet. At other sites Purple Sandpipers commonly feed on the strand line at high tide (R.Summers pers. comm.; pers. obs.) and such regional behavioural differences could possibly produce regional mortality differences. Other possible factors affecting predation on wintering waders between given years or sites include the size of local wader populations, the tenure of residency of individual predators, the size of local breeding predator populations and annual fluctuations in their breeding success (see also Townshend 1984). It was not known how many individual raptors hunted in the area although there were likely to be several Sparrowhawks given the potentially large overlap in their winter home ranges (Marquiss & Newton 1982).

Although it is generally well established that juvenile waders suffer higher annual mortality rates than adults (e.g. Boyd 1962; Goss-Custard 1980) there has been surprisingly little empirical evidence of factors which may contribute to such differences. Clark (1982b) has shown that in severe weather juvenile Redshanks may die in greater numbers than adults. Kus et al . (1984) have identified raptor predation as playing a role in creating such age-related differences in mortality in a Californian wintering population of Dunlin. In this paper I have shown that, in several wader species, the number of juveniles eaten by raptors was higher than would be expected from their representation in the population, although the results for the Dunlin and Ringed Plover must be regarded with some caution because of the uncertain accuracy in ageing these species in the field.

There were many age-related differences in behaviour which may have made juvenile waders more vulnerable to predation than adults. At Scoughall juvenile Redshanks and Turnstones were found feeding more often than adults on the strand line, where waders were more likely to be attacked by Sparrowhawks. Juvenile Turnstones also tended to be positioned on the periphery of flocks where they may be more susceptible to predation (e.g. Hamilton 1971; Jennings & Evans 1980; Inglis & Lazarus 1981). Juveniles may have been forced into such areas of increased predation risk because of competition with adults. Both adult and juvenile Turnstones and Redshanks responded to the appearance of a Sparrowhawk by flying out to sea, but juveniles were slower to do so. This may have made them more likely to have been captured since on the few occasions when I could be certain of the position of a wader when it was captured by a Sparrowhawk, those individuals which did not fly out to sea were taken more often than those that did.

The increased wader mortality in mid-winter is not due to predators simply eating more prey on the study site at this time of the year (Fig. 6). Since Sparrowhawks were probably the major predators at the study site one interpretation of the heavier mortality of waders in December and January invokes seasonal changes in the predatory response of hawks to the availability and vulnerability of potential prey, as has been shown to occur in breeding hawks (Newton & Marquiss 1982).Waders at Scoughall spend a greater proportion of daylight hours feeding in mid-winter than in autumn or spring (Baker 1981; Marshall 1981; Whitfield unpubl. data). This results in an increase in the amount of time in mid-winter spent feeding on the strand line at high tide, where waders are more vulnerable to Sparrowhawk attack. In addition, waders are probably under the greatest pressure to feed in mid-winter (e.g. Goss-Custard et al. 1977), so at this time of the year they may be less likely to detect approaching predators.

I would like to thank Pat Davison and Andy Evans for their help in searching for some kills and Alistair Clunas for interesting discussion and the supply of raptor sightings and peak wader counts at Tyninghame; the latter being carried out by himself and M.& E. Leven. I am also grateful to Pat Davison, John Goss-Custard, Alan Heavisides, Ron Summers, two anonymous referees and, particularly, Philip Ashmole and Mick Marquiss for their comments and help with earlier versions of this paper. Tom Dale generously allowed free access around Scoughall and Pat Davison typed the manuscript. The study was carried out whilst I was in receipt of an SERC Studentship.

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FIGURE 1

The study site: searches for remains were made in the black area (1982-83, 1983-84) and shaded area (1983-84).

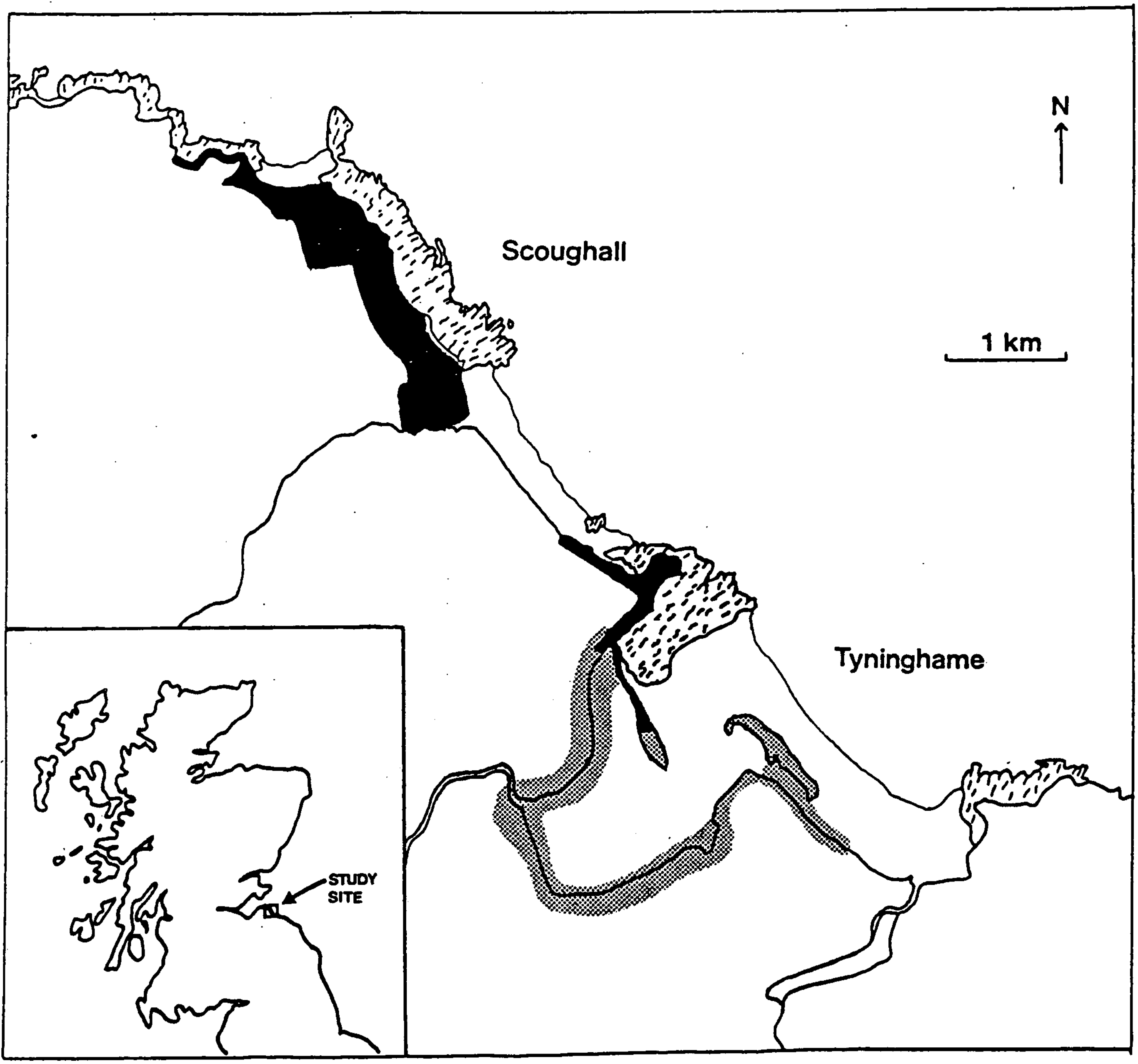
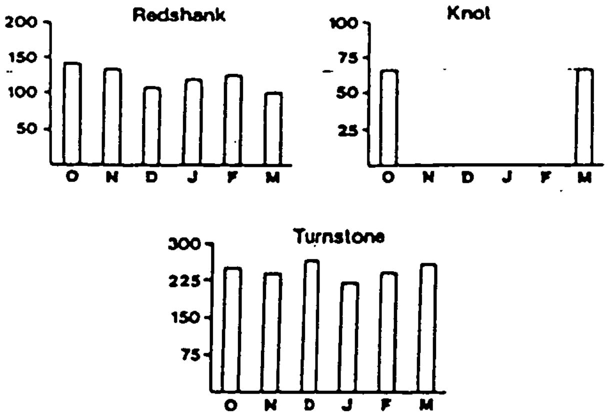

Scoughall
Tyninghame
N
1 km
STUDY SITE

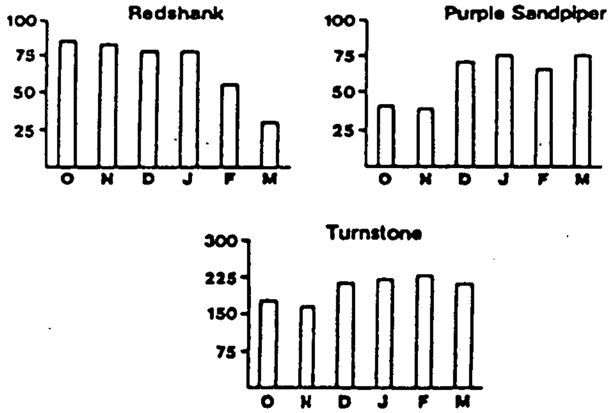
FIGURE 2

Peak wader counts for those species which were eaten by predators: (a) Scoughall 1982-83; (b) Scoughall 1983-84; (c) Tyninghame 1983-84.

Scoughall '82-83



Scoughall '83-84



(c) Tyninghame '83-84

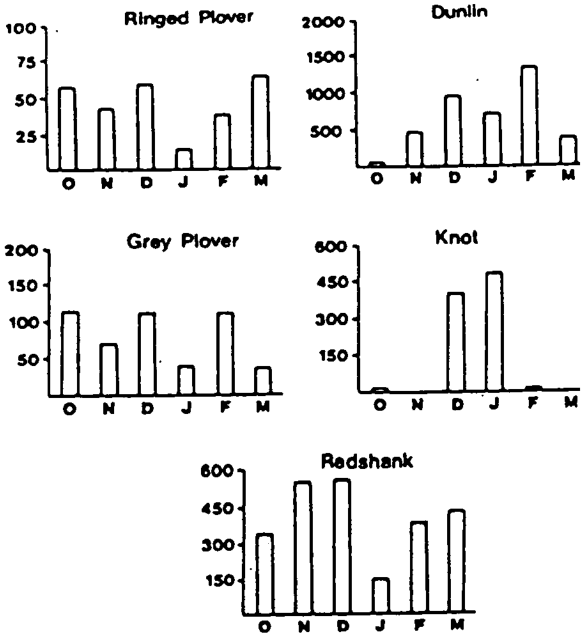
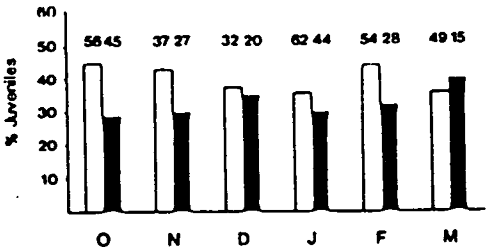


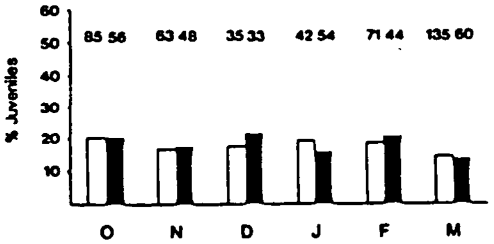
FIGURE 3

Estimates of the proportion of juveniles in wader populations. (a) Scoughall Redshank: open columns 1982-83, black columns 1983-84. (b) Scoughall Turnstone: open columns 1982-83, black columns 1983-84. (c) Tyninghame Redshank 1983-84. (d) Tyninghame Ringed Plover 1983-84. (e) Tyninghame Dunlin 1983-84. Numbers above columns refer to the number of birds aged.

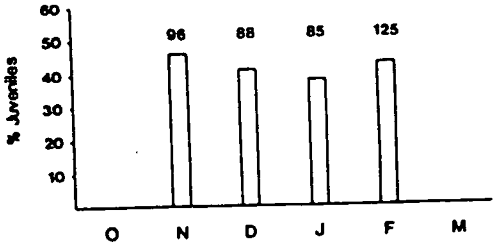
(a)


% Juveniles
60
50
40
30
20
10
56 45
37 27
32 20
62 44
54 28
49 15
O
N
D
J
F
M

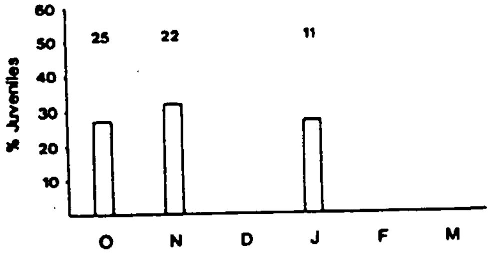
(b)


% Juveniles
60
50
40
30
20
10
85 56
63 48
35 33
42 54
71 44
135 60
O
N
D
J
F
M

(c)


% Juveniles
60
50
40
30
20
10
96
88
85
125
O
N
D
J
F
M

(d)


% Juveniles
60
50
40
30
20
10
25
22
11
O
N
D
J
F
M

(e)

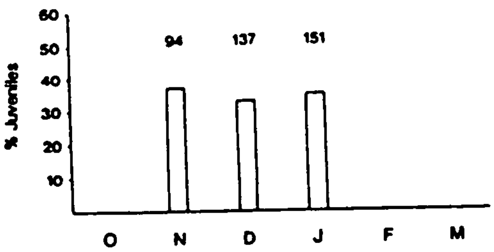
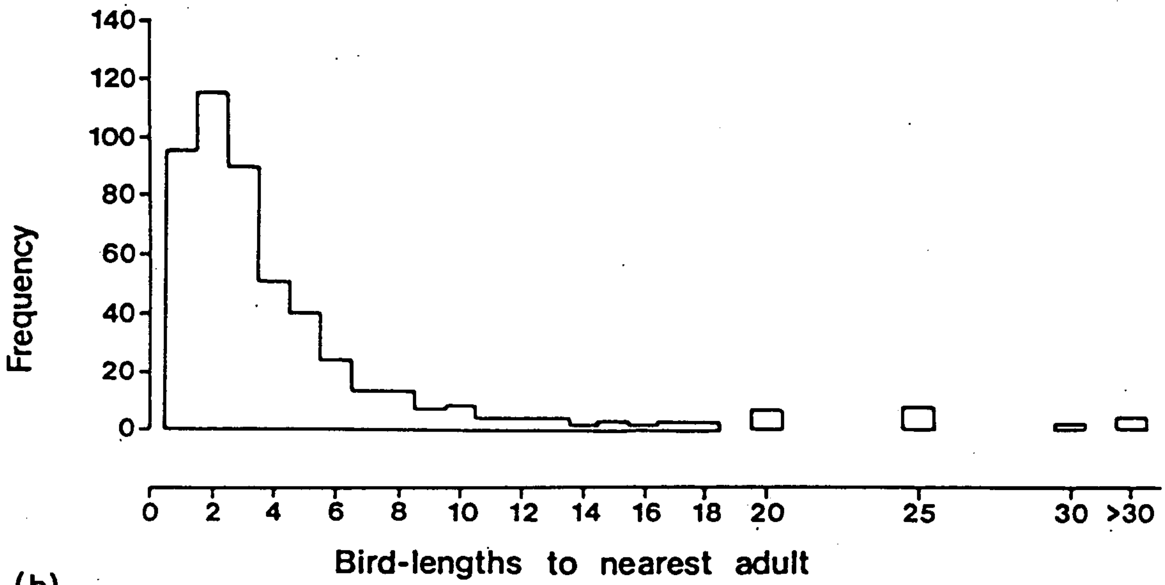

% Juveniles
60
50
40
30
20
10
94
137
151
O
N
D
J
F
M

FIGURE 4

Frequency distribution of distance between (a) adult and (b) juvenile Turnstone to the nearest adult Turnstone, measured in bird-lengths, in high tide feeding flocks at Scoughall.

(a)


140
120
100
80
60
40
20
0
Frequency
0
2
4
6
8
10
12
14
16
18
20
25
30
>30
Bird-lengths to nearest adult

(b)

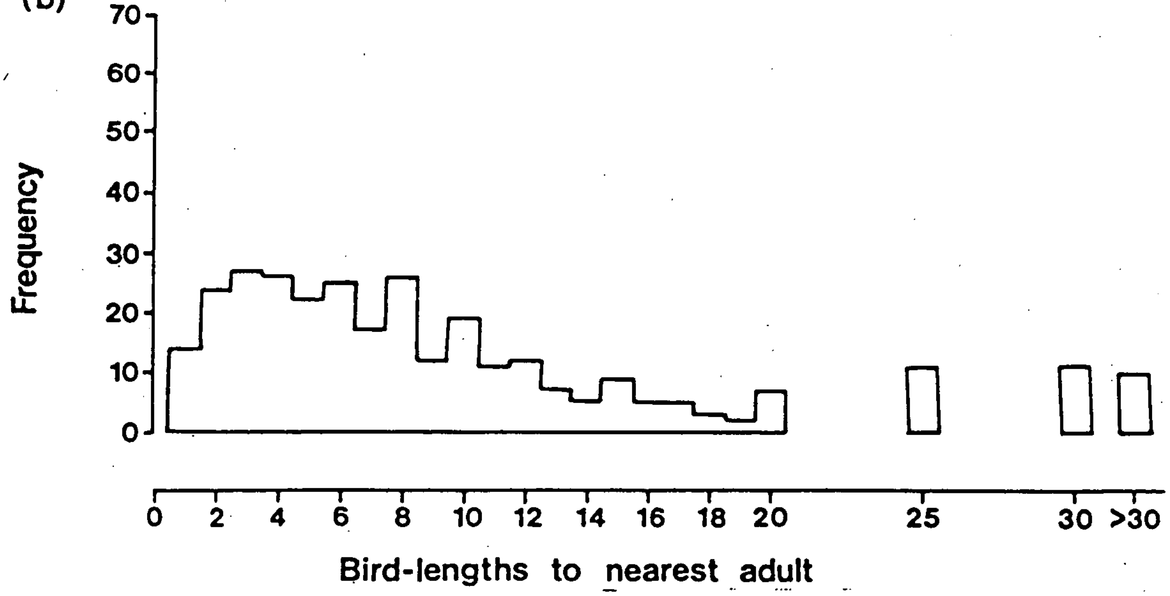
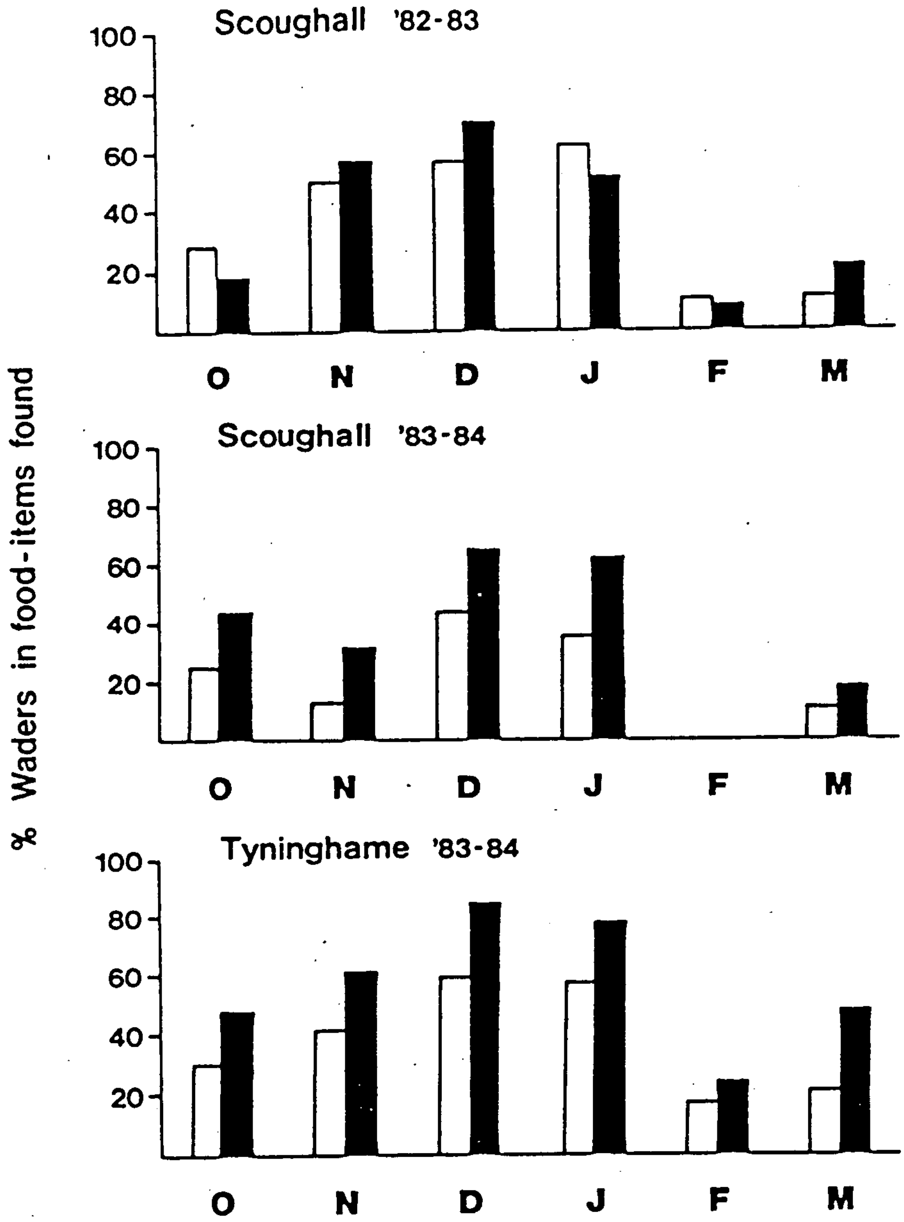

70
60
50
40
30
20
10
0
Frequency
0
2
4
6
8
10
12
14
16
18
20
25
30
>30
Bird-lengths to nearest adult

FIGURE 5

Seasonal variation in the occurrence of waders in the diet of predators as estimated by numbers (open columns) and by weight (black columns).



Scoughall '82-83

Scoughall '83-84

Tyninghame '83-84

FIGURE 6

Seasonal variation in the estimated total weight of prey eaten by predators on the study site.

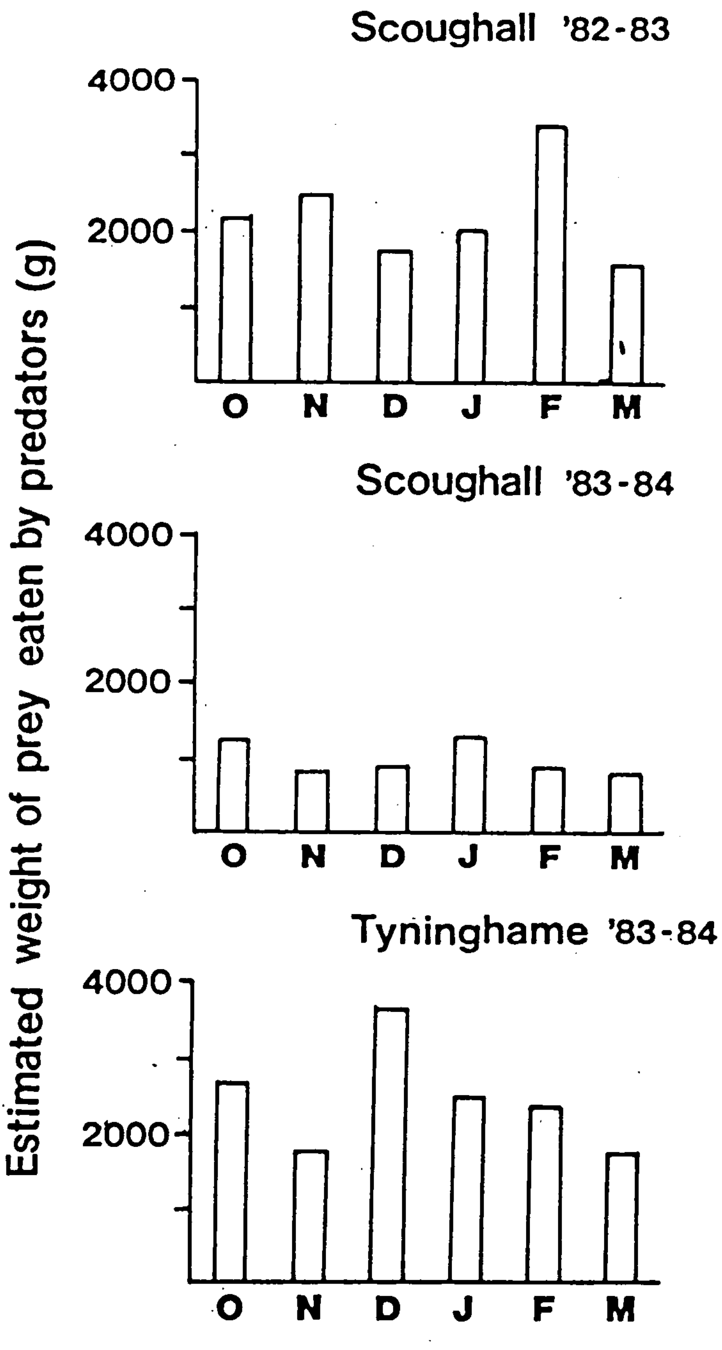

Estimated weight of prey eaten by predators (g)
Scoughall '82-83
4000
2000
O
N
D
J
F
M
Scoughall '83-84
4000
2000
O
N
D
J
F
M
Tyninghame '83-84
4000
2000
O
N
D
J
F
M

TABLE 1

Numbers (%) of predators seen at Scoughall and Tyninghame. Data for Tyninghame kindly supplied by A.Clunas.

	Scoughall		Tyninghame	
	82-83	83-84	82-83	83-84
Number of raptors seen	93	41	28	31
Sparrowhawk *Accipiter nisus* unsexed	14(15)	5(12)	15(54)*	15(48)*
Sparrowhawk *Accipiter nisus* male	10(11)	18(44)	-	-
Sparrowhawk *Accipiter nisus* female	54(58)	9(22)	-	-
Kestrel *Falco tinnunculus*	6(7)	4(10)	6(21)	6(19)
Merlin *Falco columbarius*	0	0	1(4)	3(10)
Peregrine *Falco peregrinus*	1(1)	0	6(21)	7(23)
Short-eared Owl *Asio flammeus*	2(2)	0	-	-
Tawny Owl *Strix aluco*	6(7)	5(12)	-	-
Number of mammalian predators seen	21	18	No data available, but fox & stoat faeces found frequently.	
Stoat *Mustela erminea*	17(81)	15(83)		
Weasel *Mustela nivalis*	1(5)	1(6)		
Fox *Vulpes vulpes*	3(14)	2(11)		

* Probably mainly females (A. Clunas pers. comm.)

TABLE 2

Avian prey found after being eaten by predators at Scoughall and Tyninghame during the "winters" of 1982-83 and 1983-84.

			% of predator diet by:	
		N	no.	wgt.
Starling	*Sturnus vulgaris*	49	12.6	9.2
Tree Sparrow	*Passer montanus*	5	1.3	0.2
House Sparrow	*Passer domesticus*	1	0.3	0.1
Twite	*Carduelis flavirostris*	2	0.5	0.1
Linnet	*Carduelis cannabina*	31	7.9	1.4
Goldfinch	*Carduelis carduelis*	3	0.8	0.1
Greenfinch	*Carduelis chloris*	7	1.8	0.5
Bullfinch	*Pyrrhula pyrrhula*	1	0.3	0.1
Brambling	*Fringilla montifringilla*	2	0.5	0.1
Chaffinch	*Fringilla coelebs*	15	3.8	0.8
Reed Bunting	*Emberiza schoeniclus*	1	0.3	<0.1
Yellowhammer	*Emberiza citrinella*	1	0.3	0.1
Blue Tit	*Parus caeruleus*	11	2.8	0.3
Great Tit	*Parus major*	2	0.5	0.1
Coal Tit	*Parus ater*	1	0.3	<0.1
Blackbird	*Turdus merula*	28	7.2	6.3
Song Thrush	*Turdus philomelos*	24	6.2	4.7
Redwing	*Turdus iliacus*	7	1.8	1.2
Fieldfare	*Turdus pilaris*	12	3.1	3.3
Robin	*Erithacus rubecula*	9	2.3	0.4
Goldcrest	*Regulus regulus*	1	0.3	<0.1
Dunnock	*Prunella modularis*	12	3.1	0.5
Skylark	*Alauda arvensis*	2	0.5	0.2
Collared Dove	*Streptopelia decaocto*	9	2.3	4.4
Domestic Pigeon	*Columba livia*	2	0.5	2.1
Wood Pigeon	*Columba palumbus*	11	2.8	12.9
Teal	*Anas crecca*	1	0.3	0.6
Wigeon	*Anas penelope*	1	0.3	1.7
Black-headed Gull	*Larus ridibundus*	2	0.5	1.3
Knot	*Calidris canutus*	4	1.0	1.2
Dunlin	*Calidris alpina*	14	3.6	1.9
Purple Sandpiper	*Calidris maritima*	1	0.3	0.2
Grey Plover	*Pluvialis squatarola*	2	0.5	1.2
Ringed Plover	*Charadrius hiaticula*	5	1.3	0.8
Turnstone	*Arenaria interpres*	20	5.1	5.8
Redshank	*Tringa totanus*	91	23.3	36.3

TABLE 3

Numbers(%) of pluckings and remains of dead waders placed in categories based on their appearance and position. See text for descriptions of categories.

	Scoughall					Tyninghame				
Category	A	B	C	D	G	A	B	C	D	G
N	46(72)	0	2(3)	8(12)	8(12)	60(62)	15(15)	4(4)	2(2)	16(17)
Redshank	33(83)	0	0	6(15)	1(2)	48(83)	2(3)	0	2(3)	6(10)
Turnstone	13(86)	0	1(7)	1(7)	0	4(80)	1(20)	0	0	0
Purple Sandpiper	0	0	0	1(100)	0	-	-	-	-	-
Dunlin	-	-	-	-	-	3(21)	7(50)	4(29)	0	0
Knot	0	0	1(100)	0	0	2(67)	1(33)	0	0	0
Ringed Plover	-	-	-	-	-	3(60)	2(40)	0	0	0
Grey Plover	-	-	-	-	-	0	2(50)	0	0	2(50)
Curlew	0	0	0	0	2(100)	0	0	0	0	2(100)
Oystercatcher	0	0	0	0	5(100)	0	0	0	0	6(100)

TABLE 4

Estimates of wader winter mortality rates (%) due to predation.

	Scoughall		Tyninghame
	1982-83	1983-84	1983-84
Redshank	20	16	15
Turnstone	4	5	-
Purple Sandpiper	0	1.5	-
Knot	1.5	-	0.5
Dunlin	-	-	4
Ringed Plover	-	-	19
Grey Plover	-	-	2

TABLE 5

(a) Numbers of aged individual waders found eaten by predators. (b) Probability levels that juveniles were eaten in direct proportion to the mean age-composition of the relevant wader population. * Fisher's Exact Probability Test, ** Chi-squared Test.

(a)

	Scoughall						Tyninghame		
	1982-83			1983-84			1983-84		
	Ad	Juv	?	Ad	Juv	?	Ad	Juv	?
Redshank	4	23	1	3	8	0	7	40	0
Turnstone	3	6	0	5	5	0	-	-	-
Ringed Plover	-	-	-	-	-	-	0	5	0
Dunlin	-	-	-	-	-	-	3	8	1

(b)

	1982-83	1983-84	1983-84
Redshank	$p<0.001$**	$p=0.026$*	$p<0.001$**
Turnstone	$p=0.004$*	$p=0.028$*	-
Ringed Plover	-	-	$p=0.008$*
Dunlin	-	-	$p=0.001$*

TABLE 6

The age of individual (a) Redshank and (b) Turnstone on the strand line before and after the appearance or attack (*) of a Sparrowhawk.

(a) Redshank

Before			After		
Flock size	Juv	Ad	Flock size	Juv	Ad
12	8	4	*4	4	0
49	20	29	*20	15	5
51	15	36	28	15	13
34	11	23	19	9	10
30	9	21	7	6	1

(b) Turnstone

Before			After		
Flock size	Juv	Ad	Flock size	Juv	Ad
52	10	42	*4	4	0
40	9	31	6	6	0
38	9	29	18	9	9
28	5	23	*5	5	0

Appendix 2.

PLUMAGE VARIABILITY AND TERRITORIALITY IN BREEDING TURNSTONE ARENARIA INTERPRES: STATUS SIGNALLING OR INDIVIDUAL RECOGNITION?

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Running title: WHITFIELD PLUMAGE VARIABILITY IN TURNSTONE

Abstract. The turnstone _Arenaria interpres_ has marked plumage variability in comparison with many other waders (shorebirds). Two hypotheses were tested in an attempt to explain plumage variability in breeding turnstone. The first, the status signalling hypothesis (SSH), suggests that plumage type signals status, and the second, the individual recognition hypothesis (IRH), suggests that plumage differences enable territorial birds to be recognised by their neighbours. The SSH was rejected by two tests: a) there was no correlation between plumage phenotype of males and the quality of the territories they occupied; b) there was no correlation between the the plumage phenotype of males and females paired to each other (assuming assortative mating according to rank). The IRH was supported by a test which showed that males could discriminate between neighbours and strangers on plumage differences alone: fibre glass models mimicking neighbours were effectively ignored whilst models mimicking strangers elicited an aggressive response. It is stressed that this result does not demonstrate that plumage variability in breeding turnstone evolved to facilitate recognition by neighbours, and the potential of the IRH as an explanation of breeding plumage variability in waders is discussed.

Several species of birds have continuously variable plumage which does not appear to be due to sexual selection, mimicry, camouflage or physiological efficiency (Rohwer 1975). In the past decade considerable attention has been paid to the possibility that such continuous intraspecific plumage variability is related to selection for birds to signal their fighting ability (Rohwer 1975, 1977, 1978; Baker & Fox 1978; Rohwer & Rohwer 1978; Balph et al. 1979; Ketterson 1979; Parsons & Baptista 1980; Rohwer & Ewald 1981; Edwards 1982; Maynard Smith 1982; Fugle et al. 1984; Jarvi & Bakken 1984; Watt et al. 1984). Most of these studies have focussed on birds within winter flocks and two hypotheses have been invoked as functional explanations for plumage variability.

The first hypothesis, initially proposed by Rohwer (1975), suggests that plumage type signals social status. The number of costly escalated agonistic disputes a bird is involved in will thereby be reduced, because the bird´s status and, therefore, fighting ability can be recognised by other individuals. The second hypothesis (Collias 1943) suggests that the function is to allow individual recognition; if a bird can be recognised individually then other individuals can remember its fighting ability, so the bird is involved in fewer costly escalated contests. Although not mutually exclusive, these two hypotheses are potential competitors as explanations of plumage variability (Shields 1977), but most studies have investigated only status signalling (although see Jarvi & Bakken 1984).

The turnstone Arenaria interpres is a wader with a circumpolar breeding range extending from the high arctic to the subarctic, and observations in N.E.Greenland have shown that the plumage of breeding turnstone is highly variable (Ferns 1978). Ferns suggested that turnstone have unique head and neck patterns to allow neighbouring territory holders to recognise each other visually. There is evidence that territorial neighbour recognition via vocal communication functions in some birds to reduce wasteful energy expenditure in territorial defence against neighbouring territory holders who are unlikely to usurp the territory (e.g. Brooks & Falls 1975). Turnstone have no song and Ferns postulated that they defend their territories by visual ground displays rather than the elaborate aerial song flights of many other waders because of the relative compactness of their territories, which results from their breeding habitat preferences. Turnstone therefore recognise neighbours visually by individual plumage differences rather than by individual song differences as do waders with larger territories, in accordance with Marler´s (1957) argument that visual communication is more efficient than vocal communication for individuals in close proximity to one another.

Another possible explanation of plumage variability in breeding turnstone is a status signalling hypothesis (SSH). Edwards (1982) found that in another breeding wader, the golden plover Pluvialis apricaria, those males with the blackest breasts were the highest ranking and held the best territories. It is possible therefore that plumage variability in the turnstone functions to signal status. This paper describes experimental and observational attempts to test the individual recognition hypothesis (IRH) and the SSH in breeding turnstone.

The SSH leads to one firm prediction that could be tested in the present study, namely that there should be a correlation between status and plumage phenotype in turnstone (after Rohwer 1975) (prediction 1). One subsidiary hypothesis suggested by Edwards (1982) to be implied by the SSH was also tested, namely that high ranking males might tend to be mated to high ranking females so that male turnstone should be mated to females who have equivalent plumage characteristics (prediction 2). This prediction assumes there is assortative mating by rank in monogamous birds, which may not always be true. Even if assortative mating according to rank is expected, it may not occur because availability of potential partners may be limited at any one time, especially in long lived species which show strong mate fidelity (such as many waders). These two predictions are exclusive to the SSH in the sense that they can not be derived from the IRH. I also tested a prediction of the IRH, namely that a territory holder should be able to discriminate between a neighbour and a non-neighbour on plumage differences alone.

The Study Site

The study was carried out in the summer of 1983 on the archipelago of Valassaaret, Finland ($63^o25'$N, $21^o04'$E), which is situated in the centre of the Quark, the narrowest portion of the Gulf of Bothnia. Valassaaret consists of seven relatively large, partly wooded central islands and about 60 small treeless islets. The islands are low, made up primarily of cobble or boulders, with varying amounts of vegetation and sand or gravel. Sheltered coves in the central islands, by virtue of their mud ooze bottoms, serve as breeding areas for considerable chironomid (Diptera: Chironomidae) populations (Paasivirta 1972). A detailed description of the archipelago is provided by Hilden (1964). The vast majority of the approximately

170 pairs of turnstone which breed on Valassaaret set up breeding territories on the islets (Hilden 1966; Hilden et al. 1978) and as a study area I chose the westerly islets of Ovre Oxgrynnan (O), Yttre Oxgrynnan (Y), Norra Karingbaden (NKb), and Tuorelarevet (T), and the northerly islet of Langgrynnan (L).

Testing the Status Signalling Hypothesis (SSH)

Methods and Experimental Rationale

Measuring plumage variability. Turnstone were nest trapped whilst they were incubating their eggs and on capture each individual was photographed with slide film against a neutral grey background from three angles: lateral view, dorsal view, and ventral view (Figs.1-3). A "standard outline" was then constructed on a large sheet of paper for each of the three views and a slide of each bird was projected onto the appropriate standard outline. The boundaries of the various plumage markings were then drawn in pencil around the projected image within the standard outline. Measuring the area encompassed by the pencil boundaries gave an index of each plumage variable, in cm^2, within the standard outline. This method of quantifying plumage variability is useful because any effect of the differing sizes of birds can be cancelled out simply by moving the slide projector backwards or forwards until the image fits into the standard outline. Feathers put out of position during handling also had little effect on the final indices: tests using the same method with wintering turnstone showed around 95% consistency regardless of the extent of feather disorder, stretching of the neck, etc. (unpublished data). In addition to the photographs of birds in the hand, I also obtained many close-up photographs of free-living birds which were useful in calculating the ratio of old retained winter wing coverts to new summer wing coverts; variability between birds in this respect may reflect differences in an ability to acquire food during the prenuptial moulting period. Indices were calculated for eight plumage variables which seemed candidates for badges of status: (1) black breast; (2) white throat (3) ginger mantle patch; (4) ginger scapular patches; (5) ginger on "back" (3+4); (6) crown patch; (7) white nape patch; (8) old:new wing coverts ratio.

The aggressive display of the turnstone is similar to many other waders. The aggressor crouches, ruffles the back feathers, and spreads and depresses the tail whilst facing its opponent. More escalated displays involve both birds facing each other and stretching their necks skywards, each bird displaying its black breast and white throat (further details in Bergman 1946; Groves 1978; Marshall 1981; Cramp & Simmons 1983). Given these displays and other work on status signalling, the white throat and particularly the prominent black breast seem to be the most likely candidates for possible badges of status in the turnstone.

Prediction 1. To date most investigations of status signalling have involved attempts to discover a relationship between dominance status and plumage phenotype in flocking birds in winter. Due to site-related and ownership asymmetries in contests between territory holders (e.g. Maynard Smith 1982) assessment of rank by results of dyadic agonistic interactions is unrealistic in territorial individuals, so direct testing for the presence of a correlation between status and plumage is not feasible. Even if ranking of territorial individuals were possible using the outcome of territorial border disputes, because of the high site fidelity of territory holders most birds will interact with very few conspecifics. Consequently it is difficult to obtain a reasonably sized sample of dyadic interactions. However, it is reasonable to assume that the higher ranking birds should have the greater resource holding potential (Parker 1974), and thus should hold the best quality territories. The problem is then how to measure territory quality.

In testing for a correlation between territory quality and plumage phenotype I only considered male plumage because males set up territories and perform almost all territorial defence (Nettleship 1973; Whitfield in prep.). The reproductive success of males during a single breeding season is unlikely to give a reliable measure of male quality because the turnstone is a comparatively long-lived bird and often breeds under unpredictable conditions (Cramp & Simmons 1983). Territory quality is therefore likely to give a more reliable index.

I considered two factors as being likely determinants of territory quality: food supply and protection against predators. I did not consider nest site availability to have any effect on territory quality because potential nest sites appeared to be limitless on every territory and the high variability in the choice of nest site suggested that turnstone were not limited by any particular feature of the environment in this respect.

The turnstone is an aggressive species, so territorial borders were very easily plotted on maps of the islets by noting areas defended against intruders and "guard rocks" used as look out points by territorial males and the position of border disputes and "head bob" displays (Cramp & Simmons 1983; Brearey 1983; Whitfield in prep.) between neighbouring birds. Having plotted the boundaries, the size of territories could easily be calculated from the maps of the five islets.

After the breakdown of territorial behaviour, arctic breeding turnstones move their chicks away from the territories into communal feeding areas and females tend to leave the breeding ground soon after the hatching of chicks (Nettleship 1973). In contrast, at Valassaaret turnstone chicks remain and feed on the territories which males continue to defend, and females stay with the males and young until fledging (Brearey 1983; Whitfield in prep.). The greatest strain on the food resources of a turnstone territory at Valassaaret therefore occurs at the time when the chicks are a few days old. At this time the territory must contain sufficient food to maintain the two parents and up to four chicks whose foraging abilities are limited by virtue of their inexperience and morphology. For this reason I chose to sample the food of all the territories on 3 July, a time when most pairs of turnstones which had successfully hatched eggs had young under one week old.

Several lines of evidence indicated that chironomids were the main food of adult and young turnstone during the incubation and chick rearing phases of the breeding cycle: (a) pellets coughed up by adults contained mainly the hard parts of chironomid remains; (b) direct observations of feeding birds of all ages showed that chironomids were the predominant food items; (c) chironomids were by far the most abundant potential prey; (d) the peak hatching period of turnstone eggs coincided with the peak in chironomid abundance (Whitfield in prep.). Therefore I sampled chironomids to gain a measure of territory quality in terms of food abundance. To take into account the heterogeneous nature of the habitat which turnstone territories encompassed I mapped out the vegetation of each territory into the following microhabitats: tall vegetation (TV); grass and/or short vegetation (GSV); grass and/or short vegetation and boulders (GSVB); tall grass (TG); boulders (B). Within each territory I took two randomly placed samples from every microhabitat which was present. Each sample involved twenty sweeps of a 35cm diameter net with 0.25mm mesh in an area of 0.25m^2. The number of chironomids from each sample was counted, thereby giving a known number of chironomids (n) from 0.25m^2 of microhabitat. An estimate of the total number of chironomids in each microhabitat was therefore:

$$n \times \frac{1}{0.25} \times \text{total area}(\text{m}^2) \text{ of microhabitat within territory}$$

and the total number of chironomids within each territory was estimated by summing the totals for each microhabitat. Chironomid density was calculated by dividing the total chironomid number by territory size. I excluded the TG chironomid estimates from all calculations as turnstone never fed in this microhabitat, probably because of the inpenetrability of tall grass and its low chironomid densities (Whitfield in prep.). The chironomid abundance of Langgrynnan territories could not be compared with other islets because Langgrynnan samples were not taken until 4 July, under different weather conditions, and the weather (particularly windspeed) can drastically affect chironomid abundance (Whitfield in prep.).

Turnstone at Valassaaret only breed where larids also breed and this does not appear to be due to similar nest site requirements, but rather larids seem to be a cue for habitat selection by turnstone. It is likely that larids provide turnstone with protection against nest predators (Hilden & Brearey in prep.). Since there is a possibility that a greater number of larids in a turnstone territory provides better protection for the turnstone's nest, the number or density of larids may provide an indication of territory quality. Therefore I counted all the nests of arctic terns _Sterna paradisaea_ , common terns _S.hirundo_ and gulls _Larus_ spp. (principally common gulls _L.canus_) in each turnstone territory to provide a measure of the number and density of larids.

The procedures described above allowed estimates of eight measures of territory quality to be made: (1) total number of chironomids on territory; (2) density of chironomids on territory; (3) number of gulls _Larus_ spp. breeding on territory; (4) density of gulls _Larus_ spp. on territory; (5) number of terns _Sterna_ spp. breeding on territory; (6) density of terns _Sterna_ spp. on territory; (7) total number of larids breeding on territory (3+5); (8) overall density of larids breeding on territory (4+6).

Prediction 2. In a monogamous species such as the turnstone, birds might tend to mate with members of the opposite sex whose dominance status is equivalent to their own (Edwards 1982). Taking into account the slight sexual dimorphism of breeding turnstone, there should therefore be a positive relationship between the plumage badges of males and females in mated pairs if the SSH is to be supported. To test if such a relationship exists I trapped and photographed several pairs of turnstone and measured their plumage markings as described earlier.

Results and Discussion

Prediction 1. A consistent pattern emerged when the territories were ranked according to the measures of territory quality: territories on Yttre tended to be of higher quality than those on Ovre, Karingbadan and Tuorelarevet (Table 1). This is confirmed by the finding that the number of intruders onto territories was greater on Yttre than on the other three islets (Fig. 4). Chironomid density was the only territorial variable which was significantly correlated with territory size: chironomid density was inversely related to territory size so that smaller territories tended to have higher densities of chironomids ($df=17$, $r = -0.587$, $P<0.01$). The highest turnstone density was on Yttre and this islet also tended to have the highest chironomid densities in every microhabitat (Fig.5). Whilst caution must be exercised in interpreting simple correlations, the present data suggest that food density controls territory size in breeding turnstone at Valassaaret, either directly (e.g. Holmes 1970), or indirectly (e.g. Myers et al 1979) through the intermediate effect of intrusion pressure and, of those variables tested, chironomid density provides the best measure of territory quality. Mean territory size at Valassaaret was 2937m^{2} $^{+}$ 390 SE (N=25).

Although larids are probably an essential feature of a turnstone territory at Valassaaret, it is doubtful whether larger numbers of larids provide better protection against nest predators (Lemmetyinen 1971). The high densities of both larids and turnstone on Yttre was probably coincidental; on other islets in the east of the archipelago only one or two pairs of turnstone were associated with large larid colonies and my subjective impressions were that these islets held low chironomid densities.

Prediction 1 of the SSH states that there should be a correlation between dominance status (=territory quality) and plumage type of territorial males. However there was no correlation between any of the measures of territory quality and any measure of plumage variability: most importantly there was no relationship between chironomid density and the black breast index (Table II). Therefore the data do not support prediction 1 of the SSH.

Prediction 2. According to this prediction of the SSH turnstone should be mated to conspecifics who have similar status, and therefore similar plumage markings, but since there were no correlations between the plumage of male turnstone and their mates, prediction 2 is not upheld (Table III).

None of the tests supported the two predictions of the SSH. In addition, wintering turnstone also have variable plumage and form stable dominance hierarchies, but the dominance rank of individuals can not be predicted by plumage type so there is no correlation between status and plumage type (Whitfield unpubl. data). In other words, there is reasonable evidence against the SSH as a functional explanation of plumage variability in turnstone. In breeding golden plovers, Edwards (1982) invoked the SSH as an explanation of plumage variability. Edwards found that the darker males occupied the best central territories, with the lighter males on the poorer peripheral territories, yet in S.Norway the reverse situation can occur (Byrkjedal pers. comm.). Plumage variability in golden plovers, unlike the turnstone, is primarily due to differential retention of non-breeding plumage and there is a latitudinal cline in this characteristic (Wynne-Edwards 1957; Ratcliffe 1976; see General Discussion), so the situation may be more complex than is suggested by Edwards´ results.

Testing the Individual Recognition Hypothesis (IRH)

Methods and Experimental Rationale

A prediction of the IRH is that territorial ´reactor´ male turnstone can visually discriminate between an ´intruder´ male and a ´neighbour´ male. My aim was to test this prediction by observing the response of a reactor male to both a fibre-glass model mimicking a male from another islet (intruder model) and a model mimicking a neighbouring male (neighbour model) when the said neighbour was substituted by the models. The models were carved from a solid foam polymer, coated with fibre glass, and painted with poster paints, white emulsion paint and black indian ink. The bill was carved from wood and stuck onto the fibre glass with araldite glue, and the legs were made from heavy duty wire which were embedded and glued into the foam through the fibre glass. Each model was held on a rock by means of grey plasticine around the tips of the ´legs´. I either temporarily removed the neighbour (N=6) or waited until the neighbour temporarily vacated his territory (N=4) , and then placed a model on a guard rock in the neighbour´s territory within 10m of the boundary with the reactor male´s territory. The models were used sequentially on the same guard rock in ten paired-test experiments. On five occasions the intruder model was used first and in five tests the neighbour model was used first: this controlled for any effects of novelty or habituation on the reactor´s part. I observed the response of the reactor male to a model in the fifteen minutes after the reactor was in a position where he could see the model. The following responses of the reactor were noted: number of attacks on model; time spent displaying aggressively at model; nearest approach to model; time spent less than 10m away from the border with the neighbour´s territory; time spent attending to (=appearing to look at) model. Considerable time was spent prior to each experiment making sure I had painted the model to resemble the neighbour as accurately as possible. In the ten experiments I tested ten different reactors using models mimicking eight different neighbours and eight different intruders. The experiments were conducted mainly during the incubation phase of the turnstone population, between 8 June and 26 June. Between 30 May and 5 July I also took incidental field observations of all encounters between neighbouring territory holders and between territory holders and intruders.

Results and Discussion

There were marked differences in the response of reactor males to the intruder models compared to their response to the neighbour models (Table IV). Reactors tended to spend more time displaying aggressively at the intruder model (sign test: P=0.002), approached nearer to the intruder model (sign test: P=0.002), spent more time within 10m of the territorial boundary when the model was an intruder (sign test: P=0.002), and spent more time attending to the intruder model (sign test: P=0.022). In three tests the intruder model was attacked and in one test the reactor spent 26s head bobbing at the neighbour model.

Since the reactors showed considerably more aggressive behaviour towards intruder models and often appeared to ignore the neighbour models, the results support the IRH as male turnstone clearly demonstrated an ability to discriminate between neighbouring males and strange males on a purely visual basis. This finding reflected field observations of differences in the behaviour of territory holders towards neighbours and strangers (Fig. 6). Since the initial recognition process in these interactions usually seemed to be visual (the head bob display is silent throughout) the observations provide further anecdotal evidence for the IRH.

The differential response of reactor male turnstone may be viewed as evidence that the resident reactor could not only discriminate between a stranger and a neighbour but recognised the stranger as a threat to his territory, and accordingly showed an aggressive response. The neighbour appeared to be recognised as an established individual who represented little threat and the response was therefore minimal.

This experiment also provided further evidence against the SSH. According to Edwards (1982) the SSH predicts that a territory holder should react less aggressively to birds of higher status who attempt to enter its territory. In the pairwise tests the reactors should always respond more aggressively to models with a badge of lower status than themselves and less aggressively to models with a badge of higher status, irrespective of whether the model was of a neighbour or intruder. However, there was no difference in the aggressive response of reactors relative to the size of any plumage variable of the models (Mann Whitney U test, $P>0.05$ for each plumage variable). Reactor males clearly responded more to whether the model resembled a familiar or unfamiliar bird, rather than to plumage phenotype per se.

General Discussion

It can be argued that in long-lived birds with strong year to year site fidelity few breeding territories become available each breeding season, so males should settle on any territory which becomes available provided it is above a certain quality threshold. Status should therefore be correlated with possession or non-possession of a territory and not with the relative quality of a territory (e.g. Rohwer 1975, page 594). This argument implies that territories are acquired only when owners die and that competition for territories is equal in all suitable habitats. Several observations of turnstone at Valassaaret, however, contradict this ´have or have not´ argument (Brearey 1983; Whitfield in prep.): (a) males probably often acquire territories by establishing themselves between or on existing territories; (b) territory holders may be usurped; (c) there is more intense competition for territories on high quality sites (Fig. 4). In addition, in five cases where a male was beaten in a fight on his own territory by a known male, the winner always came from a higher quality territory (victory was not always as predicted by plumage phenotype, however). These observations suggest that birds which hold territories on high quality sites will be of a higher status than those on poor quality sites. Since territory quality and status should be more or less matched it seems reasonable to assume that a territorial status signal which displays information concerning the wearer´s status should evolve if it confers an advantage of reduced involvement in escalated agonistic interactions to the wearer (Rohwer 1975, page 606; Edwards 1982). Consequently, the SSH probably predicts that the advantage of badges of status should increase with increasing variation in territory quality. Nevertheless, the SSH does not appear to be an adequate functional explanation of plumage variability in breeding turnstone.

Whilst the results of this study support a prediction of the IRH they do not demonstrate that plumage variability evolved to "allow" territory holders to be recognised by their neighbours. It is plausible that plumage variability could evolve as suggested by the IRH: in an ancestral monomorphic population individual differences in plumage could evolve via frequency dependent selection due to the individual benefits of being individually recognisable. The IRH is essentially a fine-grained version of the SSH and makes similar assumptions about concomitant selection for the ability to discriminate between individuals or ´types´, and also assumes that variability incurs costs which must be outweighed by the benefits of variability for individual plumage differences to persist. Although the IRH seems to be the most attractive adaptive explanation for the evolution of plumage variability in the turnstone, further tests are needed. For instance, according to the IRH there should be a negative correlation across species between territory size and the extent of plumage variability, since large territories should lead to increasing emphasis on vocal communication between neighbours. This test of the IRH using interspecific comparisons is currently in progress, and it appears that as well as the general problems of the comparative approach (Harvey & Mace 1982; Jarman 1982; Clutton-Brock & Harvey 1984) there are several confounding variables which may produce difficulties in testing the general applicability of the IRH.

Plumage variability per se could be selectively neutral. In several waders territory size increases with increasing latitude (e.g. Holmes 1970; Pienkowski 1983) and breeding populations at lower latitudes often retain a larger proportion of non-breeding winter plumage (e.g. Byrkjedal 1978; Greenwood 1979). A mixture of retained winter and new summer feathers gives the plumage a "patchy" appearance. In all populations there is individual variation in the position and number of retained feathers but since lower latitude birds tend to retain more winter feathers there is greater variability in such low latitude populations. Consequently there is greater variability in the appearance of southern birds as a result of increased variability in plumage "patchiness". An IRH interpretation of these observations would be that decreasing territory size leads to selection for increased plumage differences to facilitate neighbour recognition. Enhanced plumage variability is achieved by different individual patterns of winter feather retention. On the other hand Hale (1971) views polymorphism due to differential non-breeding plumage retention as an indication of a hybrid swarm derived from sub-specific hybridisation, and Byrkjedal (1978) comes to a similar conclusion. There are several arguments against this interpretation however (e.g. Parr 1980; Cramp & Simmons 1983: page 540), notably the widespread occurrence of such variation in situations where distinct sub-species do not exist. Perhaps the most plausible explanation of geographical variation in prenuptial moult has been proposed by Fjeldsa (in Byrkjedal 1978). Wader populations at lower latitudes breed earlier (e.g. Vaisanen 1977) and Fjeldsa regards the retention of a greater proportion of winter feathers in southern populations as an adaptation relating to the energy budget under circumstances where early breeding threatens to overlap with the moulting process.

There may in some cases be counter-selection against being individually recognisable. For instance, the buff-breased sandpiper Tringites subrufficollis is a polygynous lekking wader, and because the lek territories are comparatively small, compared with several other waders, the IRH would predict marked plumage variability in males. Yet the plumage of males resembles that of females, unlike most polygynous species, and shows little variability (Myers 1979, pers. comm.). Myers has proposed that the male's similarity to the female may be related to a 'sneaky male' mating strategy, allowing males to steal and/or disrupt other males' copulations. If this is the case, then it will not be advantageous for a resident male to be easily recognised as such by a neighbouring male, and there will be selection against individual plumage differences.

There may also be evolutionary constraints and predispositions involved in plumage variability. Gould & Lewontin (1979) have stressed that there may often be explanations such as developmental and phyletic history and random fixation of alleles which may be at least as important as adaptation in accounting for observed 'traits'. The IRH, as an adaptive hypothesis, may be inadequate as an explanation of all inter-species differences in the extent of plumage variability in breeding waders. According to Cott (1966) distinct colour markings in waders may have a disruptive colouration function during incubation. This was supported by Graul (1973) who found a correlation between the presence of breast bands in plovers (Charadriinae) and a discontinuous nest substrate. Intricate head and breast markings, possibly selected initially for their disruptive qualities, provide greater potential for individual differences than does uniform plumage. There may therefore be an inherent bias towards visual communication between territorial neighbours in species with complex plumage and a tendency towards vocal communication in species with uniform plumage, but both communication systems may be equally ´efficient´ given the constraints imposed by different evolutionary backgrounds.

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FIGURE LEGENDS

Figure 1. Lateral views of head and neck plumage variability in breeding turnstone at Valassaaret.

Figure 2. Dorsal views of crown, nape and back plumage variability in breeding male turnstone at Valassaaret.

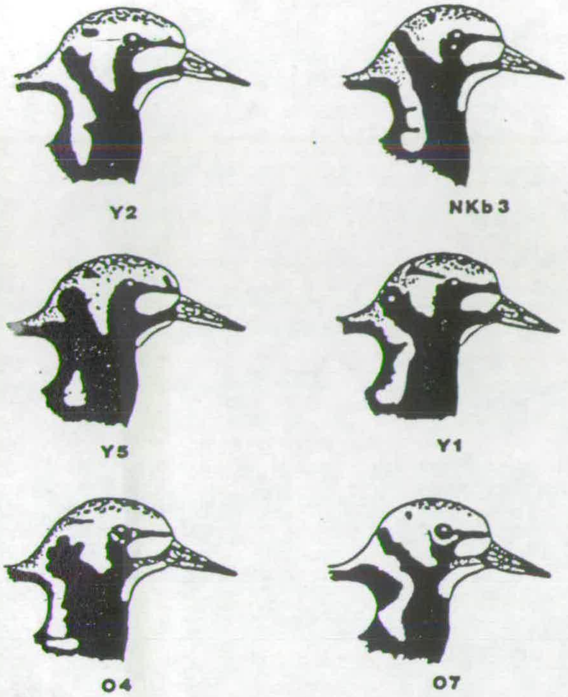
Figure 3. Ventral views of throat and breast plumage variability in breeding turnstone at Valassaaret.

Figure 4. Comparison of turnstone intrusion rates on four different islets at Valassaaret. Each point represents one observation session, and each session lasted between one and seven hours. There was a significantly higher intrusion pressure on Yttre compared with every other islet (Mann Whitney U tests, $P<0.002$ for each comparison).

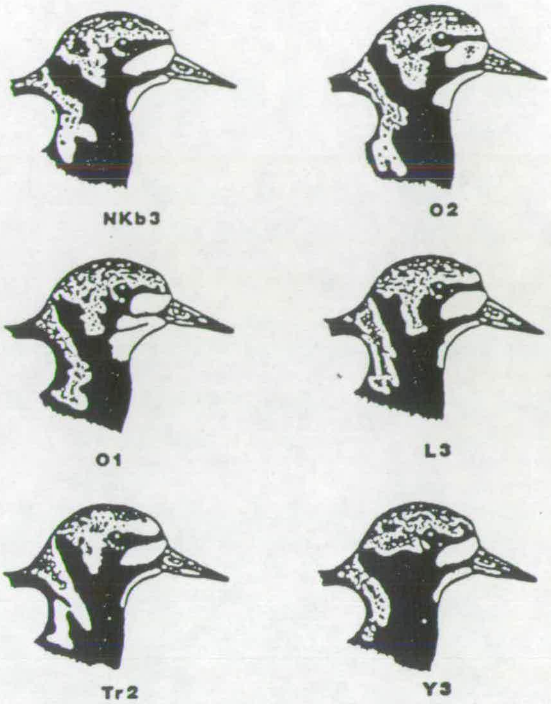
Figure 5. Comparison of chironomid densities on four different islets in three microhabitats. Chironomid densities were significantly higher on Yttre in microhabitats TV and GSV (Mann Whitney U tests, $P<0.002$ for each comparison). In other microhabitats the tendency for higher chironomid densities on Yttre was not significant.

Figure 6. Summary of interactions between territory holders and intruders, and between neighbouring territory holders. Observations

are summarised into a generalised situation of two neighbouring territories, A and B.



Males



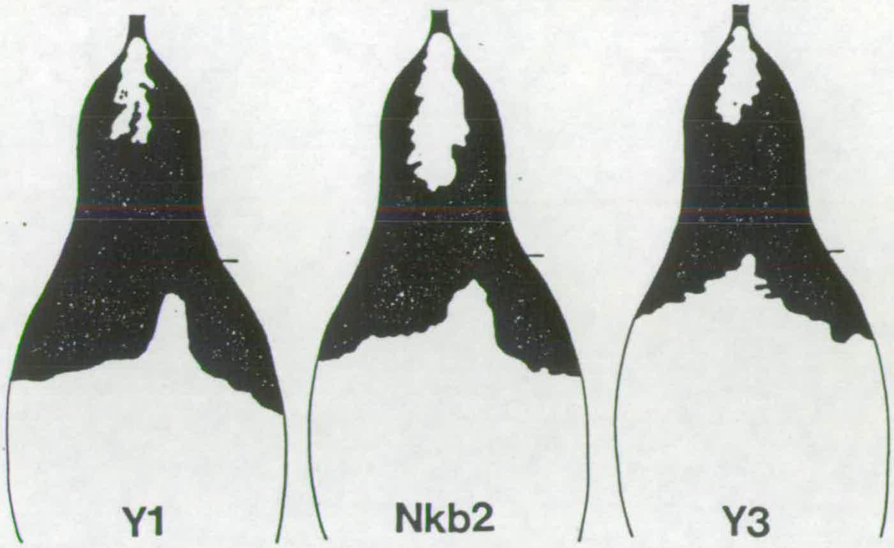
Females

T1

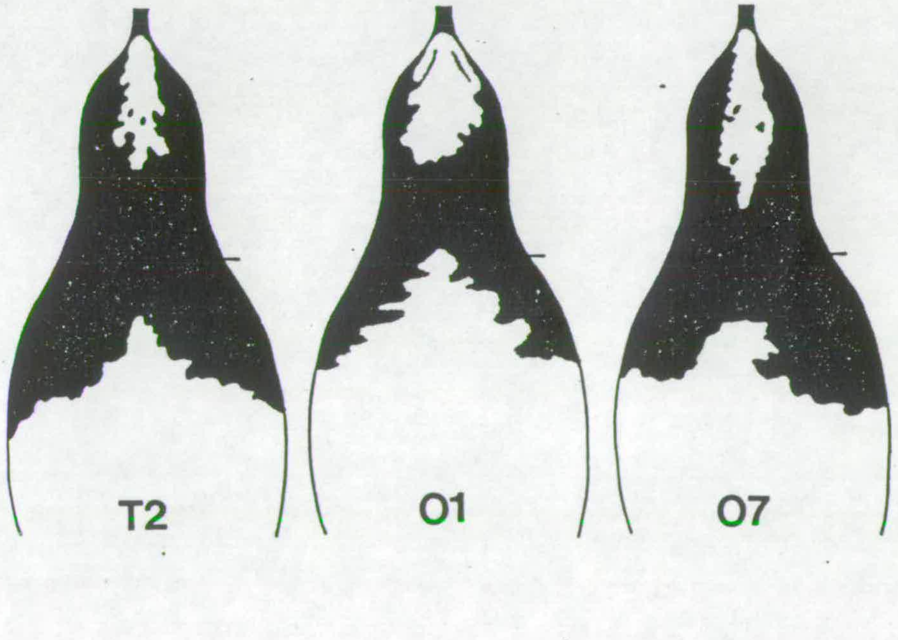
Nkb1

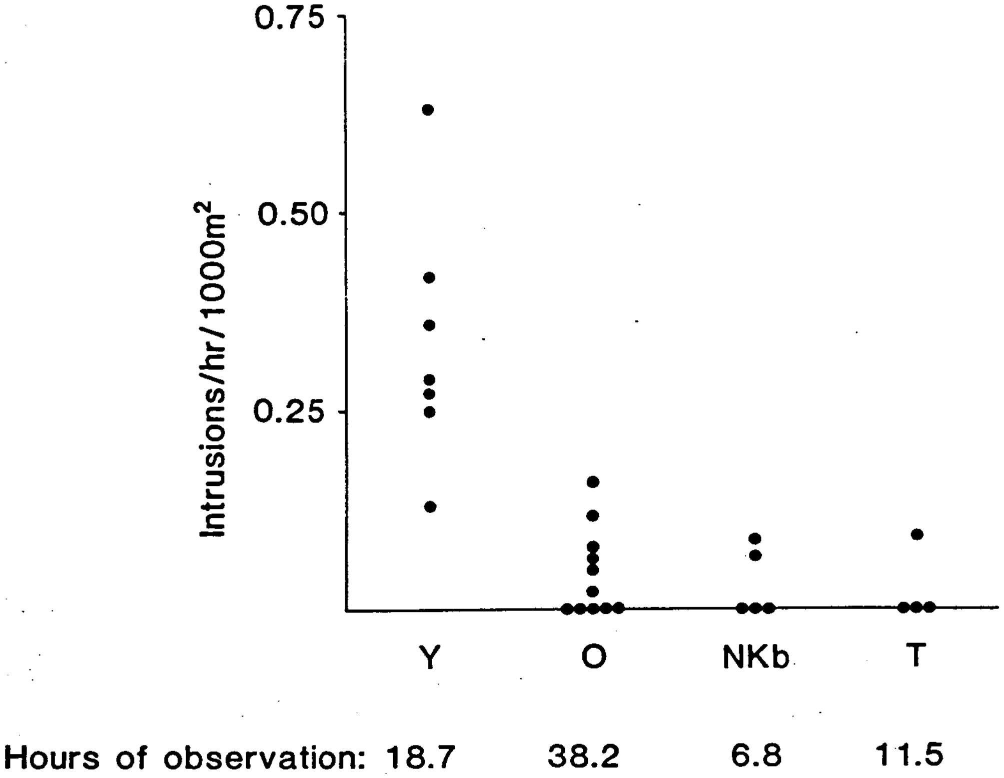
O5

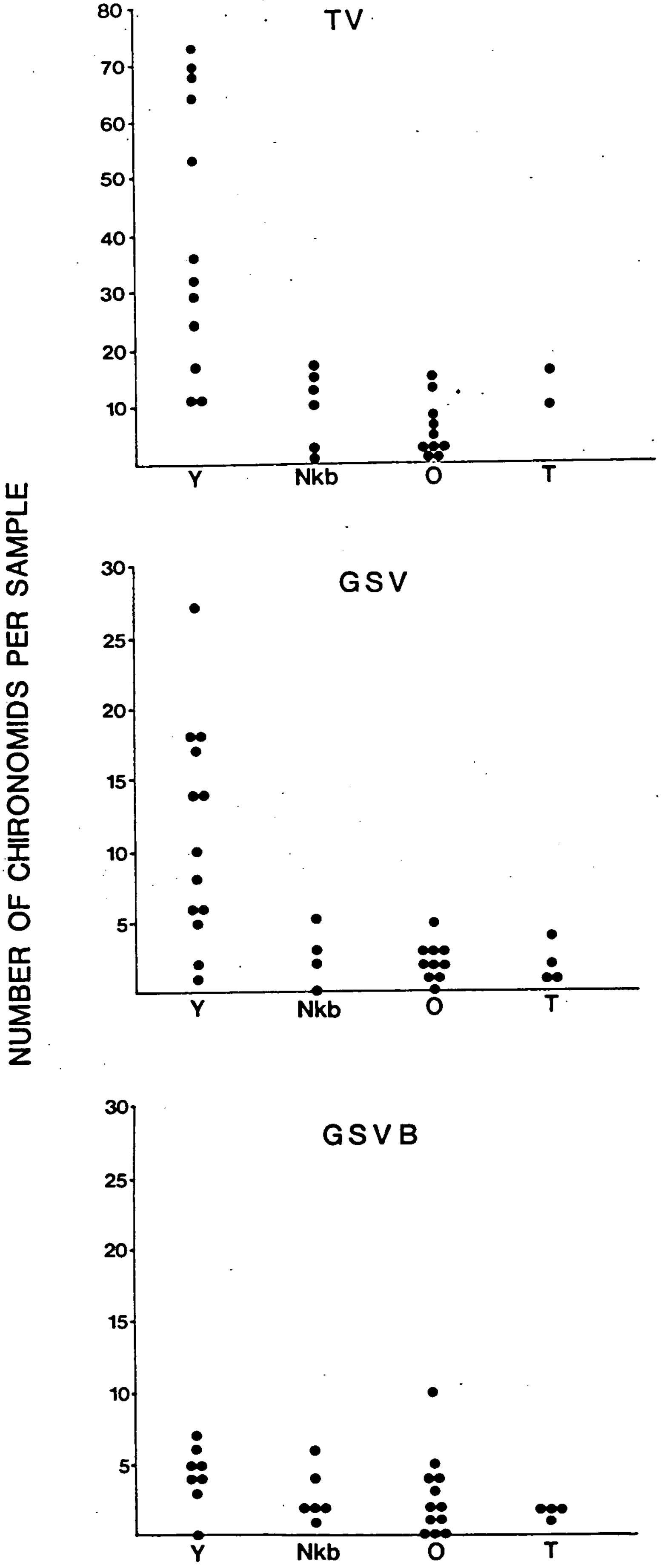
Males



Females




0.75
0.50
0.25
Intrusions/hr/1000m^2
Y
O
NKb
T
Hours of observation: 18.7 38.2 6.8 11.5


NUMBER OF CHIRONOMIDS PER SAMPLE
TV
80
70
60
50
40
30
20
10
Y
Nkb
O
T
GSV
30
25
20
15
10
5
Y
Nkb
O
T
GSVB
30
25
20
15
10
5
Y
Nkb
O
T

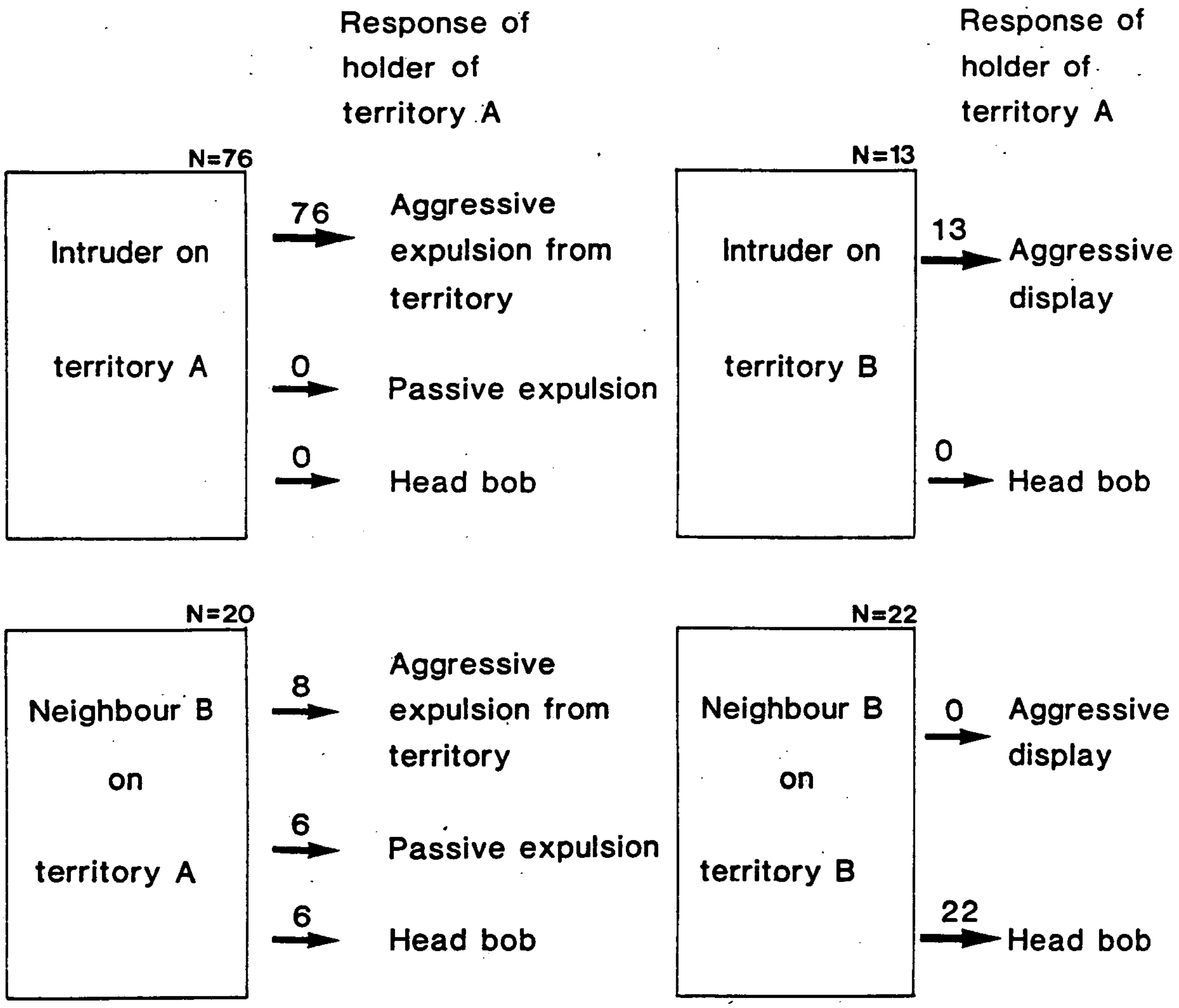

Response of holder of territory A
Response of holder of territory A
N=76
Intruder on territory A
76
Aggressive expulsion from territory
0
Passive expulsion
0
Head bob
N=13
Intruder on territory B
13
Aggressive display
0
Head bob
N=20
Neighbour B on territory A
8
Aggressive expulsion from territory
6
Passive expulsion
6
Head bob
N=22
Neighbour B on territory B
0
Aggressive display
22
Head bob

Table I. Ranking of territories using several measures of territory quality. The rankings are essentially the same by Kendall´s coefficient of concordance, W=0.698, $X^2=62.82$, df=18, P<0.001.

Chironomid no.	Chironomid density	*Larus* density	*Sterna* density	Larid density
N1	Y2	Y4	Y1	Y4
Y5	Y3	Y2	Y4	Y1
Y1	Y1	Y3	Y3	Y3
Y4	Y5	Y5	Y6	Y2
Y3	Y4	Y6	Y5	Y5
Y6	Y6	O6	O1	Y6
Y2	O2	O3	T2	O1
O2	N1	O4	T1	T2
O5	O5	O7	Y2	O4
T1	N2	Y1	O4	T1
N2	O6	N1	N1	O6
O6	T1	O1	N3	O3
O3	Y7	N3	O2	N1
T2	O7	O2	O5	O7
O4	O3	O5	N2	N3
N3	O1	T1	O6	O2
O7	T2	N2	O3	O5
O1	O4	T2	O7	N2
Y7	N3	Y7	Y7	Y7

Table II. Matrix of correlation coefficients (r) for relationships between measures of territory quality and plumage variables. Critical value of r at P=0.05 is $^{+}$0.553 (df=11). CN = chironomid no.; CD = chironomid density; LN = *Larus* no.; LD = *Larus* density; SN = *Sterna* no.; SD = *Sterna* density; LDN = larid no.; LDD = larid density. None of the correlations are significant.

	CN	CD	LN	LD	SN	SD	LDN	LDD
Black breast	-0.103	0.230	-0.143	0.225	-0.170	-0.049	-0.199	0.320
White throat	-0.338	-0.179	-0.529	-0.155	-0.209	-0.450	-0.415	-0.282
Crown patch	-0.043	-0.060	0.153	0.120	-0.097	-0.116	0.000	0.123
Nape patch	-0.119	-0.360	-0.417	-0.411	-0.157	-0.458	-0.321	-0.440
Mantle patch	0.386	0.269	0.393	0.377	-0.088	-0.122	0.123	0.224
Scapular patch	-0.023	0.139	-0.047	-0.014	-0.008	0.070	-0.029	0.017
Ginger on back	0.186	0.257	0.170	0.189	-0.053	-0.007	0.042	0.133
% old coverts	0.108	-0.240	0.264	0.015	-0.123	-0.181	0.034	-0.225

Table III. Correlation coefficients (r) for relationships between plumage variables of male and female turnstone which are paired to each other. Critical value of r at P=0.05 is $^{+}0.707$ (df=6). *Critical value of r at P=0.05 is $^{+}0.532$ (df=12).

	r	Significance level
Crown patch	0.121	NS
Nape patch	-0.231	NS
Mantle patch	0.108	NS
Scapular patch	0.359	NS
Ginger on back	0.507	NS
Black breast	0.315	NS
White throat	0.053	NS
% old coverts*	-0.468	NS

Table IV. The responses of ten reactor male turnstone to models mimicking an intruder and a neighbour when the models were placed in the neighbour´s territory.

"Identity" of model N=Neighbour I=Intruder		Time spent in aggression display (s)	Nearest approach to model (m)	Time spent <10m from territory border (s)	Time spent attending to model (s)
1	N	0	35	0	23
	I	21	10	168	224
2	N	0	5	240	240
	I	323	0	797	891
3	N	0	20	0	144
	I	13	0.5	31	120
4	N	0	30	0	148
	I	28	10	32	900
5	N	0	10	210	242
	I	35	5	309	475
6	N	0	10	12	17
	I	104	0	317	317
7	N	5	20	0	42
	I	13	20	0	233
8	N	0	20	0	64
	I	27	15	467	589
9	N	0	20	0	64
	I	54	10	376	401
10	N	0	10	98	98
	I	60	0	366	366

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APPENDIX 3: PLUMAGE ALTERATIONS MADE TO CAPTIVE BIRDS (TESTING IRH)

1. Lores whited, black neck stripe enlarged.
2. Black breast enlarged, neck stripe enlarged & black marking put in from neck stripe towards eye.
3. White throat blacked in, white markings around base of bill & around eye blacked in.
4. Lores blacked, white/brown neck-to-breast marking blacked near breast, blacked from lores to black neck stripe.
5. Black breast reduced, white/brown neck-to-breast marking enlarged, black neck stripe reduced.
6. White throat enlarged, black breast enlarged, lores touched with white.
7. Black breast enlarged, white throat reduced, white/brown neck-to-breast marking blacked near breast.
8. Black breast reduced, white throat enlarged, black neck stripe enlarged.
9. White/brown neck-to-breast marking enlarged, lores blacked, black neck stripe enlarged.
10. Black breast enlarged, lores whited, black neck stripe enlarged.

APPENDIX 4: MEMBERSHIP OF INTERTIDAL AREA 'FLOCKS'

Scoughall: YOBN YNLG YWOB YNNG YLLB YLGR YWWL YWNR YLBG YOWL BWRY YWWR YWLR YWGN YGRW YWWB BWLW (YWWG)

Field Space: BWWL YWNL YBWL YLNW YONO YLNO YWWO YWGW YOWO YOOW BWYO YNNW YWLO YGLG YROL BGYW BGYG

Coastguard : YRM YLWN YWNW YNBG YNWO YLWL YWBW YRWR YBOL YLBG YLOL YLON YOWL YWGB YWNB YNGB BWWO YORW YNOR YNWN YOBL YRLG YLLG YLGN BWWR BWYL BWOG BGWL BGOY (BWLY)

Car Rocks: YNBR YBOR YNOL YLOW YWNG YBGO YOGN YNGR YNLW YRGN YRRW YBNR YWRG YLRN BWYN YLBR YRNW YBWB YLLW YLNR YRGL YGOW YWOL YOBR YOGW YRLW YRNG YRON YRWL YWOR YRBN YLOG YNRG YNLR YLBW YNRW YBLR YRNL YOWG BGWN YRNB YOLN YRBW YLWR BWWY BWYG BGYR BGYO BGOL BGOG YLNB YLNG YGOL