THE FLOCKING BEHAVIOUR OF WINTERING TURNSTONES <u>ARENARIA</u> <u>INTERPRES</u>

AND PURPLE SANDPIPERS <u>CALIDRIS</u> <u>MARITIMA</u>

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Presented in candidature for the degree of Doctor of Philosophy

to the Faculty of Science, University of Glasgow

December 1984.

ProQuest Number: 10391245

ProQuest 10391245

ACKNOWLEDGEMENTS

I declare that the work contained within this thesis is my own.

SUMMARY

The aims of this project were to investigate the extent of social organisation, and the adaptive significance of mixed-species flocking, in two species of waders wintering on rocky shores. The approach adopted was to study firstly the stability of the populations, through monitoring of the movements of marked individuals and the population as a whole. This was followed by more detailed analyses of the associations between individual birds. Several major costs and benefits of flocking were then investigated, with emphasis on how these varied according to the composition and density of the flock, the identity of the individual, the environment and the time of year. The observed flocking dynamics of the two species were then compared to those predicted on the basis of the cost/benefit analyses of flocking, and the mechanisms of these flocking tendencies investigated.

The results showed that turnstones _Arenaria interpres_ and purple sandpipers _Calidris maritima_ formed very stable communities, with very limited population turnover during the course of a winter, high survival rates and a high degree of site faithfulness by individual birds between years. Analyses of turnstone movements revealed that birds maintained small home ranges, and so came in contact with only a limited number of other conspecifics. This enabled the formation of a dominance hierarchy, presumably based on individual recognition; dominant turnstones stole food from more subordinate birds whenever possible, leading to high rates of aggression in high density flocks and avoidance of dominants by subordinates. Aggression and interference in feeding constituted a cost of flocking to at least the majority of birds of both species, especially at high densities of conspecifics; major benefits of flocking were concerned with vigilance and the avoidance of

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predation. Birds gained from increased corporate vigilance at a reduced time cost to the individual when feeding in flocks; the extent of this gain was, however, affected by the species composition and density of the flock, the visibility of the habitat, and the bird's food intake requirement.

Thus the optimal flock composition and density was predicted to vary according to the individual's species and dominance status, the risk of kleptoparasitism (which varied between habitats) and the visibility of the habitat. Observed patterns of flocking generally corresponded well with these predictions: birds maintained intermediate flock densities (which were modified by habitat visibility), and reduced their rates of interference with conspecifics by flocking preferentially with those other species with which they shared vigilance. Removal of these other species led to greater aggregation by conspecifics; these aggregations were maintained by birds modifying their foraging search paths so as to remain within flocks, especially when the selective pressures for the maintainance of high conspecific densities were predicted to be greatest. However, there was evidence for variation in flocking behaviour between birds of different dominance status within this general pattern.

These findings are discussed in relation to how such details of flocking and social behaviour could affect other aspects of an animal's biology, with particular reference to their implications for the movements and survival of individuals, and hence the population dynamics of the species.

CHAPTER ONE -- INTRODUCTION AND GENERAL METHODS

For any animal, the distribution and abundance of its contemporaries rank among the most important influences upon its lifestyle. Conspcifics in particular may constitute a reference point in the environment, by which the animal may be attracted, as in social species, or repelled, as in solitary species. Since population dynamics are in part a consequence of this kind of behaviour, it is impossible to fully understand the dynamics of a population without some knowledge of the behaviour of the individuals of which it is composed. Furthermore, for vertebrates in particular, the population cannot be assumed to be made up of identical units, and individual differences in behaviour must be taken into account. There are exceedingly few higher animals which do not interact with conspcifics over and above the behaviours necessary for breeding. Whether these interactions are positive (leading to group formation) or negative (leading to avoidance and spacing), they may act as constraints on movement thus affecting both dispersal and dispersion, and will often influence breeding performance, foraging efficiency and predation risk, and hence survival.

There are many situations where we do not have a clear picture of the dynamics of an ecological community, or the adaptive significance of behaviour, due to a failure to study the interactions between the individual and the population. This thesis represents an attempt to bring together studies of the social behaviour of individual animals with the effects this behaviour has on their distribution within a particular habitat, and on the ecology of the population. This has been done through a detailed study of wader groups composed of more than one species, and of individual differences in the behaviour of the birds which comprised these

groups.

1.1 Why Study Groups?

Animals may form groups for various reasons; the potential costs and benefits of living in groups will be discussed in detail in the final chapter. However, an important point to be considered here is that groups also vary in the stability of their composition. In some cases the division appears to be clear. For example, gorillas _Gorilla gorilla_ live in the same small troop throughout most, if not all, of their adult life, with many of the female troop-members being closely related to one another (Wilson 1975). In constrast, starlings _Sturnus vulgarus_ forage in groups ranging in size from 1-100 birds, and spend the night in roosts of up to 2 million (Hamilton & Gilbert 1969). The assumption has usually been made that, in the latter case, the foraging groups are aggregations of anonymous individuals drawn at random from the population. However, this has largely remained untested. There is a rather grey area in the putative range of stability of groups, from those cases where groups are of constant composition ('closed' groups), to those where the individual membership is constantly changing ('open' groups). It is possible, for instance, for individuals to move between groups opportunistically yet have a restricted range of fellow group-members, due to their always moving within a small home range. This, in fact, is equivalent to a closed group (composed of all the animals that live in the one area) divided into a fluctuating pattern of subgroups. The distinction between open and closed groups is important, as the latter can lead to far subtler interactions between individuals than can open groups, and the individual's identity assumes a far greater importance.

There has been a tendency to ignore individual identity and

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variation in studies of these types of group. Whereas this variation has almost been taken for granted in species which have territorial or family-group dispersion, those that form fluctuating groups have often been treated as if all members of a group are identical. This is true even of some recent quantitative optimality approaches to the costs and benefits of group living (examples being Krebs 1974, Caraco & Wolf 1975, Davies 1976 and Stinson 1980). Notable exceptions are the theoretical developments of Gauthreaux (1978), Rubenstein (1978) and Pulliam & Caraco (1984), and the combined theoretical and empirical studies of Fretwell (1969), Caraco (1979a,b), Baker et al. (1981), Rohwer & Ewald (1981) and Barnard & Sibly (1981). All of these acknowledge that the costs and benefits of being in a group may be altered by the quality of the individual. Thus dominant or aggressive animals may either exploit the food-finding abilities of other group members (Baker et al. 1981, Barnard & Sibly 1981, Rohwer & Ewald 1981), or attempt to drive them out of the group (Caraco 1979a), depending on the distribution and form of the food supply. As a consequence, subordinates may be better off leaving the group as the level of competition increases (Gauthreaux 1978, Rubenstein 1978).

Therefore there is a need to regard grouping behaviour from the point of view of each individual, even in those species that appear to form random groups. This is because there is unlikely to be a simple single solution to the questions of whether a species should form groups or not, or of how large such groups should be: the answer may be different for different individuals.

It is also important to consider the fluidity in the individual composition of groups, and to determine the stability of their membership. It may be the case that individual associations are far more stable than might appear from cursory examination of flocking

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dynamics. Conversely, it is dangerous to assume on the basis of laboratory studies the existence of complex social structures such as a stable dominace hierarchy in the wild, as it is possible that the population fluidity is too great to allow this to develop.

Why Study Mixed-Species Groups?

Groups are not always composed of a single species. There are many documented cases of fish, birds and mammals forming multi-species groups (reviewed in Morse 1977, see also Morse 1978, Gosling 1980, Sullivan 1984), and it can be presumed that they form for much the same range of reasons as monospecific groups (Morse 1977). However, most of the research on multi-species associations has been purely descriptive, concentrating on tropical bird flocks (Short 1961, Moynihan 1962, Morse 1970, Buskirk 1976, Greig-Smith 1978) and primates (Gartlan & Struhsaker 1972, Gautier-Hion & Gautier 1974, Waser 1980). The main investigative and quantitative studies have tended to be on interspecific kleptoparasitic, rather than mutualistic, associations (see Brockmann & Barnard 1979, also Kushlan 1978, Barnard et al. 1982, Sullivan in press). However, in many cases it is evident that all species may potentially gain from the association (although the trade-offs may not be the same); the position is then analogous to the single-species group except that another factor, the individual's species, is added to the list of parameters (such as age, sex, competitive ability and so on) which may vary between different individuals in the group. Thus although all species present may benefit from grouping per se, they may vary in their optimal group sizes, densities, compositions, and so on, in the same way as may different individuals of the same species.

The multi-species association is thus more complicated than that of the single-species group, although at the same time it provides a

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more convenient situation in which to study the effect of grouping on different classes of individual. This is because the multi-species group can be sub-divided into species more easily than can the single-species group be divided into categories of, for instance, competitive ability. Therefore by studying the interactions and associations that occur between species in mixed-species groups we may get insights into the similar (but less tangible) processes that affect monospecific groups, and which may have such important consequences for the dispersion, dispersal and survival of individual animals, and hence their population dynamics.

Why Waders?

Waders form a convenient group of animals in which to study this form of social behaviour, since outside the breeding season they adopt a wide range of dispersion patterns (even within the same species), from territoriality to flocking (both in single- and multi-species flocks). They have been used as models in a number of other studies of the adaptive significance of different dispersion patterns (e.g. Recher 1966, Goss-Custard 1970, 1976, Myers & Myers 1979, Myers et al. 1979a,b, Blick 1980, Stinson 1980, Vines 1980, Barnard et al. 1982, Townshend et al. 1984). Since they do not have prolonged parental care, generally have separate breeding and wintering ranges, and show no evidence of remaining paired in the wintering areas, there is unlikely to be the complication of non-breeding social behaviour being affected by kin selection considerations; nor is there the problem of winter dispersion being partly determined by the need to obtain and retain breeding territories (as is the case in several Parid species (Hartzler 1970, Ekman 1979). Wintering waders should therefore form a multi-species community of freely-moving individuals, which have been moulded by natural selection into adopting dispersion patterns that maximise the probability of their

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own survival until their next breeding attempt.

Ideally, all species present in the flock should be studied, but given the limited duration of this project, logistic problems of obtaining enough detailed information were too great to allow this approach. Instead I chose to study two species, which live in the same habitat but are of different sizes and feeding techniques, so allowing simultaneous comparisons of two components of the same community. The two species chosen were the turnstone *Arenaria interpres* and the purple sandpiper *Calidris maritima*.

The environment is a further variable which can affect the social behaviour of the individual, through its effect on food supply (e.g. Davies 1976, Caraco 1979a,b) or food dispersion (Myers *et al.* 1979b, Monaghan & Metcalfe in press), or the risk of predation (Willis 1972, Jarman 1974, Caraco *et al.* 1980a). The two study species live outside the breeding season on predominantly rocky shores, which are a far more varied habitat than the sandy beaches and estuaries which hold the major European wader concentrations, and so offer more scope for studies of the effect of environment on social behaviour.

1.2 General Biology of Turnstones and Purple Sandpipers

The breeding range of both of the study species lies almost entirely above the latitude of 60° N, ranging from the limits of the boreal range of southern Scandinavia to the exposed tundra of the high arctic. Turnstones can be divided into several distinct populations on the basis of their breeding distribution. Those birds that breed in Scandinavia may pass through Britain in late summer, but winter in north west Africa. The British wintering population comes from the breeding areas of Axel Heiberg and Ellesmere Islands in northwest Canada, and from Greenland (Branson *et al.*1978, 1979,

Cramp & Simmons 1982). These birds arrive in Britain in late July and August, and leave on spring migration usually in April and May; they may therefore be present in the 'wintering' quarters for over nine months of the year. Less is known about the origins of purple sandpipers that winter in Britain. Those on the east coast of Scotland are predominantly Norwegian breeders (Atkinson et al.1981), but those in the north and west are likely to be mainly from Iceland, Greenland and possibly north-east Canada (Anon. 1984, Morrison 1984, Buxton et al. in press). The majority of the population wintering on the west coast do not arrive until late October each year, and depart in early May; they are thus on the coasts of Britain for around seven months each year. These movements will be examined in more detail in Chapter 2.

Outside of the breeding season both species frequent mainly rocky shores, where their small size and dark or disruptive colouration (the purple sandpiper being a dark speckled grey, while the turnstone is a mixture of black, brown, grey and white) makes them among the most inconspicuous of shorebirds. Both the turnstone and purple sandpiper feed on the exposed, outer rocks of the shoreline as well as in more sheltered sites such as amongst rock pools and musselbeds. Turnstones are rather less restricted in their choice of habitats, feeding in sand and shingle areas especially if these are littered with banks of dead wrack Fucus spp. (Feare 1966, Harris 1979, Cramp & Simmons 1982, McKee 1982). The diet of both species is predominantly one of littoral invertebrates, obtained using a variety of feeding techniques. The following account of the prey types taken on British coasts is mainly based on the review by Cramp & Simmons (1982) and on personal observation. Both species specialise on small molluscs such as periwinkles Littorina littorea,

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L. saxatilis and small dogwhelks Nucella lapillus. These may be taken whole if small, or removed from the shell if larger (Marshall 1981). Small mussels Mytilus edulis may also be taken, and both species may feed on the remains of larger mussels left by other birds such as oystercatchers Haematopus ostralegus. The bill of the turnstone is strong enough to hammer open barnacles Balanus spp. and even to prise limpets Patella vulgata and Patina pellucida off the rock; both species eat small crabs such as the shore crab Carcinus maenas and amphipods (e.g. Gammarus spp.). Turnstones often feed over the high water period on banks of dead wrack, turning over and burrowing into the seaweed with strong pushing and flicking movements of the head to reach the buried eggs and larvae of the kelp fly Coelopa spp.. This same motion is used to overturn stones or fronds of living wrack, exposing the more troglodytic prey species such as the gammarids. Both turnstones and purple sandpipers will also make rapid pecks at small floating pieces of detritus brought in by the tide, and will probe into rock pools, often to a depth that covers the eyes. The purple sandpiper often appears to use its bill as a tactile sense organ, feeling its way under water or into cracks in the rock, whereas the turnstone relies more on sight to detect its prey (McKee 1982).

The two species are often found in close association with each other outside the breeding season (Rees 1969, Cramp & Simmons 1982). Other bird species often found in the same habitats include three larger waders; redshank Tringa totanus, oystercatcher and curlew Numenius arquata, also an inshore seaduck the eider Somateria mollissima, and gull species such as herring, great black-backed and black-headed gulls Larus argentatus, L. marinus and L. ridibundus. Certain predominantly inland birds may also feed in the intertidal zone; these include starlings Sturnus vulgarus, crows Corvus corone

and feral pigeons Columba livia, which feed on the dipteran larvae and amphipods in the sand near the high tide zone.

While there are many other wader species which feed intertidally, they tend to be restricted to the soft-bottomed substrates of sand and mud beaches or estuaries; their contact with turnstones and purple sandpipers is therefore limited.

1.3 The Study Area and Its Habitats

The study area was a six kilometre stretch of coastline in the Firth of Clyde. west Scotland, running from the northern boundary of the town of Ardrossan south to the headland of Stevenston (Fig.1.1). The shoreline is a mosaic of rocky and boulder outcrops interspersed with with musselbeds, stretches of sandy beach, and some man-made breakwaters. In addition to a number of rocky islets lying just off shore, the area also contains one substantial island, Horse Island, used by many of the birds as a high tide roost site. The populated nature of the site results in it suffering from a relatively high level of human disturbance, ranging from people walking dogs to fishermen digging on the beach to collect bait. However, while the coastline is essentially urban, the littoral zone supports a full and diverse biological community, with the only region of low biomass being in the vicinity of the deep water harbour at Ardrossan. The study area was only one section of a coastline of similar habitat that runs from Portencross (7km to the north) to south of Girvan (50km to the south); it did not therefore have distinct natural boundaries. However, as turnstones and purple sandpipers only tend to feed on sandy beaches that are adjacent to their more normal habitat of rocky outcrops, the long stretches of 3km of sand to the south of Stevenston headland and 2km to the north of Ardrossan acted as barriers to the movement of both species, as was shown by a study of

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Fig.1.1. Map of the study area. The sea is indicated by hatching, and the mean spring high water mark by the thick black line on the right hand side. The intertidal zone (between mean spring high and low water marks) is separated into sand (white) and other habitats (black). The positions of the towns of Ardrossan, Saltcoats and Stevenston are marked, as are various regions of the study area mentioned in the text, according to the following key: HI = Horse Island, NB = North Beach, A = Ardrossan harbour, McC = McCrindles, NR = North Rocks, SR = South Rocks, S = Saltcoats, C = Coalruffie.

HI

NB

A

ARDROSSAN

McC

NR

1km

N

SR

SALTCOATS

S

C

STEVENSTO
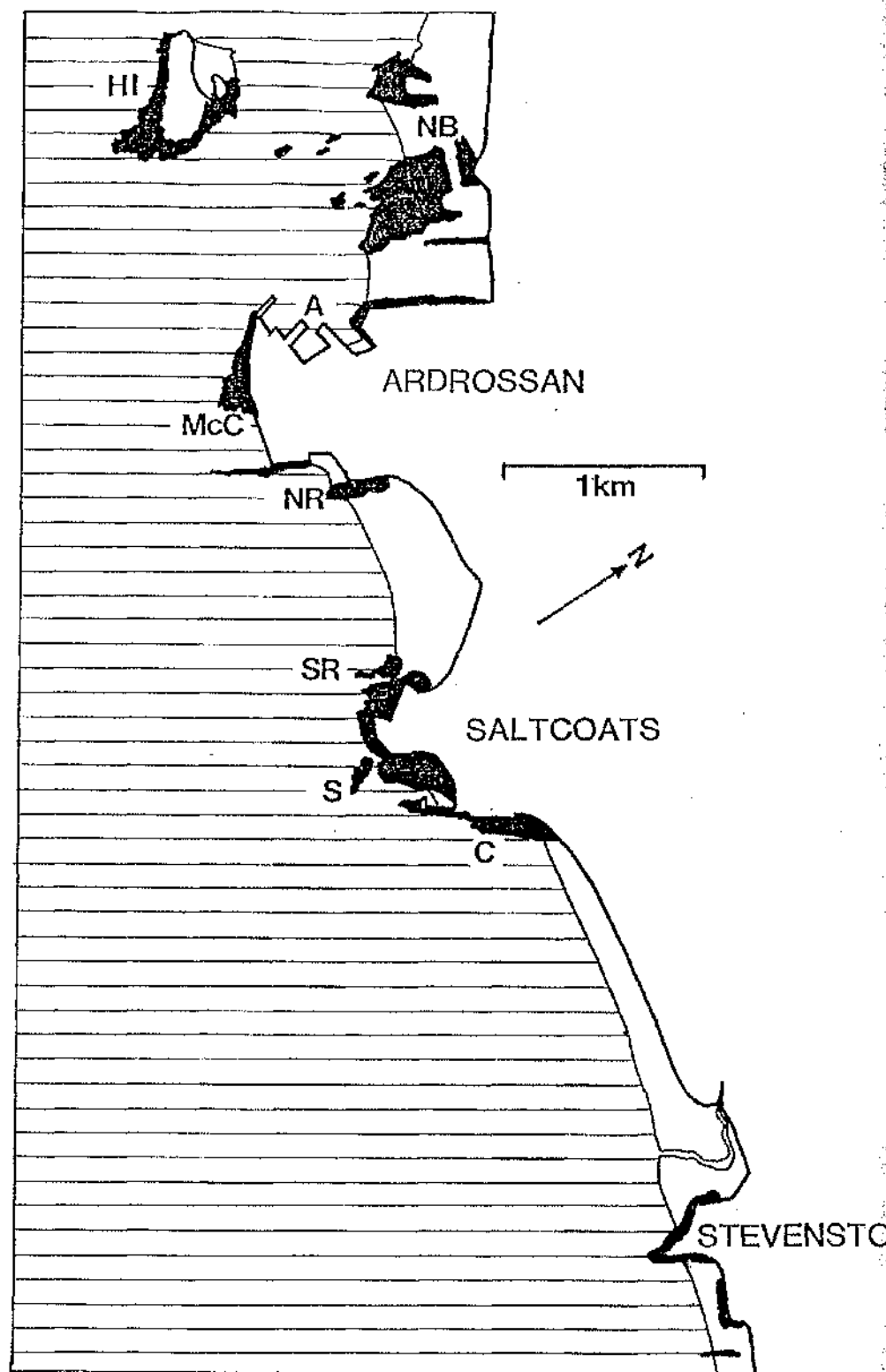
movements of marked birds, described in detail in Chapter 2.

In order to quantify the relative usage by the two species of the various habitats within the study area, a habitat classification was devised which categorised the intertidal zone into eleven distinct types. These are:

1. Rock – all areas of exposed bedrock or large loose rock (c.1m+ in diameter).

2. Boulder – areas of medium-sized rocks (c.0.15-0.75m in diameter), as occurred for instance in some man-made sea walls.

3. Loose Rock – areas of small pieces of rock (less than 0.15m in diameter), lying loose on underlying rocks.

4. Musselbeds – areas where mussels covered at least one third of the available ground space.

5. Pools – Calm patches of water between rocks or musselbeds.

6. Sand – stretches of sandy beach.

7. Shingle – stretches of shingle.

8. Live Wrack – areas where living wrack (predominantly Fucus spp.) covered at least one third of the available ground space.

9. Algae – patches of rock predominantly covered by a mat of the alga Enteromorpha.

10. Dead Wrack – areas of dead, detached wrack left by the tide usually at the high water mark. This was an ephemeral habitat, although it was reasonably predictable in occurrence in some areas.

11. Tideline – this was defined as the thin band of shallow water along the tide edge in which turnstones occasionally foraged by wading: as such it did not have a fixed distribution, but was never more than 0.25m wide.

The availability of these different habitat types was measured by

estimating the extent of each habitat (as a percentage of the total area) in distinct, small sections of the study area. These sections (delimited by natural topographical boundaries) were then marked on large scale (1:2500) maps of regions of the study area, and their areas calculated using a Summagraphics graphic digitiser linked to a Commodore Pet microcomputer. The extent of the study area during the exposure period (defined below) was taken as all intertidal land between the mean spring low water mark and the mean spring high water mark. The area exposed during the high water period was defined as that from 50m below to 25m above the mean spring high water mark, excluding all grassland and man-made structures. The area covered by the dead wrack habitat could not be measured directly, due to its fluctuation in availability. However, it was estimated to cover approximately 1% of the total area of sand exposed during the exposure period, and 10% of it over the high water period. No estimate was made of the extent of the tideline habitat.

1.4 General Study Methods

(a) Methods of Catching and Marking Birds

Birds were caught using cannon nets, which are large (30x15m) nets, fired from a furled position over feeding or roosting birds with the use of projectiles propelled by explosive charges. In principle they are capable of catching many birds at a time, but in this situation the fact that the only major concentrations of birds occurred at the inaccessible roosts on Horse Island limited the size of catches, as attempts were restricted to smaller feeding flocks. Due to the logistic problems of setting up the nets close to the water line, it was easiest to attempt catches over the period of slack water at high tide. However, this resulted in very few purple sandpipers being caught, since they almost all roost over the high

tide period. Attempts on the incoming tide were similarly more successful in catching turnstones than purple sandpipers, as the latter were less predictable in their movements (Chapter 2), and would often remain on the outermost rocks, beyond the reach of the nets.

In total 100 adult and 19 juvenile turnstones and 8 adult purple sandpipers were caught during the first 18 months of the study. Catching was discontinued thereafter, as this was considered an adequate sample of turnstones (given their high site fidelity and survival), and as the likely investment of time required to produce a similar sample of marked purple sandpipers was considered prohibitive. If recaptures are taken into consideration, the total catch breakdown for turnstones was 123 adults : 22 juveniles, indicating that juveniles comprised approximately 15% of the population.

Each captured bird was given a unique combination of four coloured plastic ('darvic') leg rings, to allow it to be identified as an individual in the field, in addition to a numbered metal British Trust for Ornithology ring. Birds were aged as either juveniles (- less than one year old) or adults on the basis of plumage characteristics (Prater et al.1977), weighed using Pesola balances, and their winglength measured (maximum chord) to the nearest millimetre. They were then released, and appeared to suffer little reaction to any stress of capture, resuming feeding within minutes. The rings appeared to have little if any effect on the behaviour of the birds; only one colour ring was lost from a bird during the study, and the bird remained identifiable due to it being the only one in the study area with three colour-rings.

<u>(b) Observation Methods</u>

Although being in such an urban setting was a drawback in terms of the disturbance caused to the birds by people, a major advantage was the excellent vehicular access afforded to many parts of the site. The presence of promenades, coast roads and harbour walls allowed me to approach feeding birds closely in a vehicle, in effect using it as a mobile hide from which observations could be made. As in most of these areas the vehicle was on top of the sea wall, the observation point was generally some 3-5m above the level of the foraging birds. This helped greatly in the locating of birds amongst rocks and in the estimation of distances. In general, observations were made on birds 10-75m from the vehicle, although in conditions of good visibility birds could be seen clearly and their colour-rings identified at distances of over 150m. Those areas which could not be reached by the observation vehicle (i.e. the North Beach of Ardrossan at low water and the McCrindles area) were covered on foot; however, no behavioural observations (such as on vigilance or aggression rates) were made in this way, as it was possible that my presence could have altered their behaviour. Therefore observations in these areas were limited to the recording of colour-ring sightings and flock parameters (see later).

Observations were made with 10x50 binoculars and a 15-60x telescope. In addition a JVC KY-1800E colour video camera with 6.4x zoom lens was used on occasion to make video films for subsequent behavioural analysis, using slow-motion and freeze-frame analysing facilities. Using video film enabled simultaneous monitoring of the behaviour of several birds, which was essential in the measurement of vigilance schedules (Chapter 5) and search paths (Chapter 6).

Flocks of turnstones were located opportunistically within the study area. For both species a flock was defined as being a group of

birds, none of which was more than an estimated 10m from the nearest conspecific. This figure of 10m was chosen after preliminary observations had indicated that the nearest neighbour distances of birds that behaved as a cohesive flock were almost always under 10m. The location of each flock was noted on large scale (50m=1cm) maps of sections of the study area, and the identity of all colour-ringed birds within it recorded.

I tested my ability to judge distances by selecting two adjacent natural features at a distance from my observation point similar to that of typical turnstone flocks, estimating their distance apart (always between three and 12 metres), then walking up to them and measuring the distance accurately with a tape measure. Two more objects were then selected from a new observation point, and so on. Objects were selected that lay in line either approximately parallel to my line of vision, or perpendicular to it. The results showed that my estimation of distance was naturally subject to some error (the mean error for two objects perpendicular to my line of vision, expressed as a percentage of the actual distance $\pm$ S.E., being $16.4 \pm 2.4\%$, n=20; for parallel objects the mean error = $15.8 \pm 2.7\%$, n=20). However, these errors were not biased consistently in any one direction, as the net errors were not significantly different from zero (perpendicular objects: mean net error = $-0.6 \pm 4.5\%$; parallel objects: mean net error = $-1.5 \pm 4.5\%$). Therefore it can be concluded that my method of judging distances was unlikely to be seriously biased towards either under- or over-estimation.

The method of recording the positions of birds resulted in the distribution of turnstones and purple sandpipers being broken up into a number of flocks of conspecifics, which were in fact often feeding amongst birds of other species (predominantly waders). The density of

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each species in a turnstone or purple sandpiper flock was measured, as will be described in Chapter 6. The size of the total mixed-species flock was not recorded, as it was difficult to measure, since some of the other species do not form flocks per se, but adopt an over-dispersed distribution (an example being the oystercatcher (Vines 1980)).

At least one hour was allowed to elapse between separate measurements of flock distribution, composition and density in the same area, to ensure independence of data. In practice, the continual changes in flocking induced by the tidal cycle and my own movements between different sections of the study area prevented any bias arising from repeated observations of the same flocks. The time of each observation was noted as both the circadian time and the tidal time, recorded as minutes since the previous high water.

Distinctions had to be made between flocks feeding over the high tide period and at other times (as the foraging conditions were so different) and between feeding and roosting flocks. The high tide (or high water) period was distinct from the actual point of high tide, and was considered to be the period of the tidal cycle when most of the typically intertidal habitats were covered by water. It was defined as follows. The mean elapsed time between each low and the following high tide was calculated over a lunar (28 day) cycle, using the Admiralty tide tables for Greenock (20km to the north of Ardrossan). The time between high and low tides was also calculated over the same period. The high tide period was then taken as lasting from the point on the rising tide which is 3/4 of the mean time between low and high tide (i.e. 635 minutes after the previous high water), until the corresponding time on the next falling tide, one quarter of the time between the high tide and the next low tide (i.e. 84 mins. after high water). The time outside this high water period,

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Fig.1.2. Diagram of how the tidal cycle was divided into high tide and exposure periods. Dashed lines indicate the times of high and low water, while the numbers refer to the time (in minutes) since the previous high water. See text for explanation.

HW

HIGH TIDE	EXPOSURE PERIOD	HIGH TIDE

LW   HW

0   84   c.337   635   c.734   84
                                              0

from the falling tide through low tide to the next rising tide, is referred to as the exposure period, and was defined as lasting from 85 until 634 minutes after the previous high tide (see Fig.1.2). To simplify analyses, no distinction was made between neap and spring tides.

Flocks were only classified as feeding if at least 75% of the birds were actually feeding (i.e. less than 25% roosting). The great majority of flocks encountered during the exposure period were feeding, whereas many high water flocks were roosting. Earlier studies have also found that both species tend to spend almost all the daylight exposure period feeding, especially during midwinter (Feare 1966, Baker 1981, Marshall 1981). Conversely, neither species has been found to feed at night (Feare 1966, Brearey 1982, Marshall 1981, pers. obs.), unlike many other wader species (e.g. redshank (Goss-Custard 1969), oystercatcher (Hulscher 1976) and grey plover Pluvialus squaterola (Townshend et al.1984)).

Further details of observational methds are given where appropriate under the relevant methods sections of Chapters 2 to 6.

(c) Habitat Use by Turnstones and Purple Sandpipers

Figure 1.3 gives the availability of each habitat type in the study area (expressed as a percentage of the total intertidal area, estimated as $1,508,000m^2$ during the exposure period and $230,000m^2$ over the high water period). Also shown are the observed habitat preferences of the two species (i.e. the proportion of birds seen in each habitat), given by the number of flocks recorded in each habitat multiplied by the number of birds in the flocks. It is clear that both species avoided certain habitats while prefering others. Purple sandpipers were never seen on sand, and turnstones rarely so, despite it covering almost 60% of the intertidal zone. During the exposure

Fig.1.3. A comparison of the availability of each type of habitat (white bars, expressed as a percentage of the total area), and their use by foraging turnstones and purple sandpipers (black bars, expressed as the total number of birds recorded on each habitat as a percentage of the total number seen foraging). Key for habitat types: S = Sand, B = Boulder, R = Rock, M = Musselbed, Lr = Loose rock, P = Pools, Lw = Live wrack, Sh = Shingle, Dw = Dead wrack, A = Algal rock and T = Tideline (the area of which could not be measured).

(a) = turnstones, exposure period.
(b) = purple sandpipers, exposure period.
(c) = turnstones, high water period.
(d) = purple sandpipers, high water period.

(a)

(b)

(c)

(d)
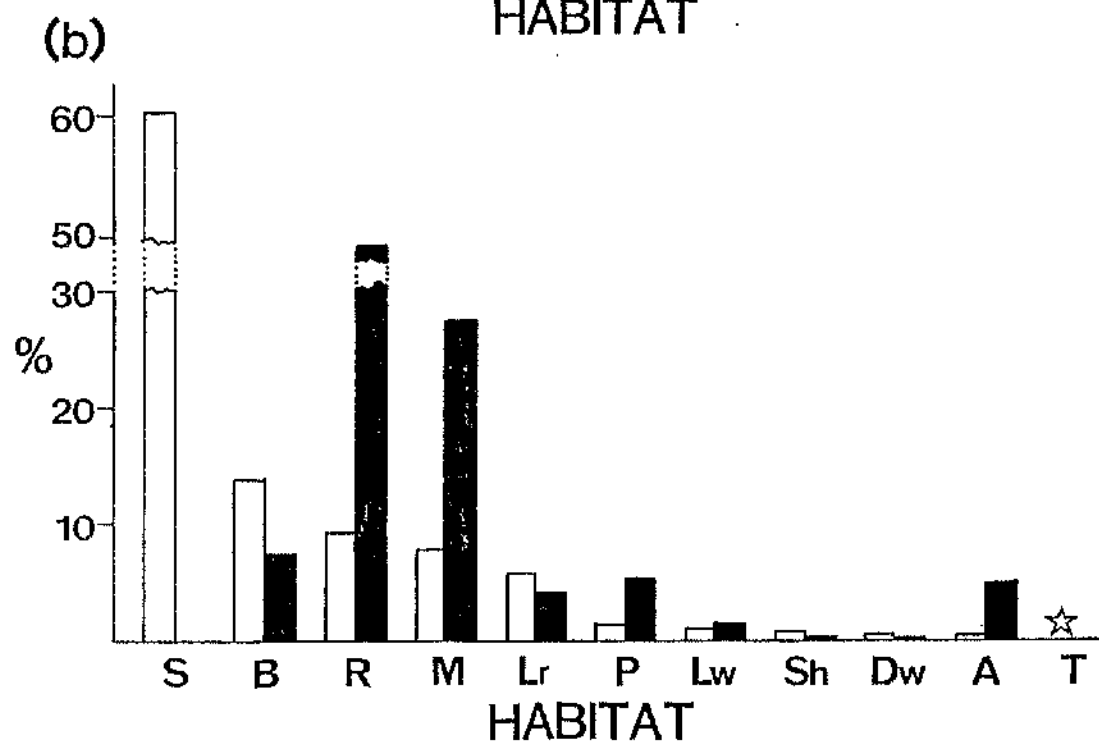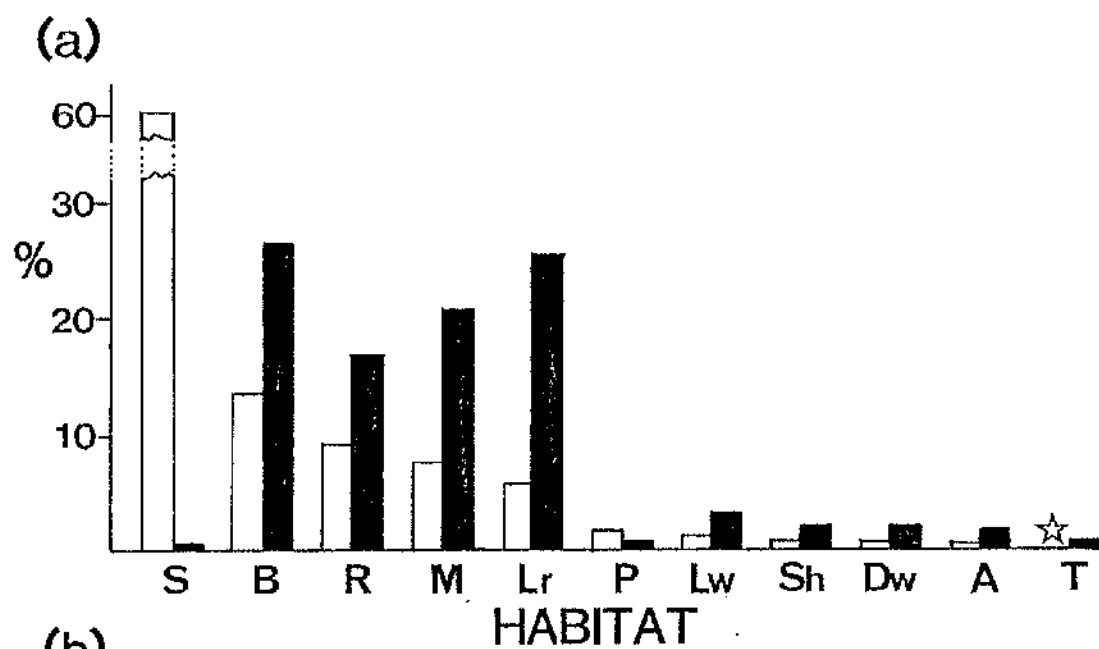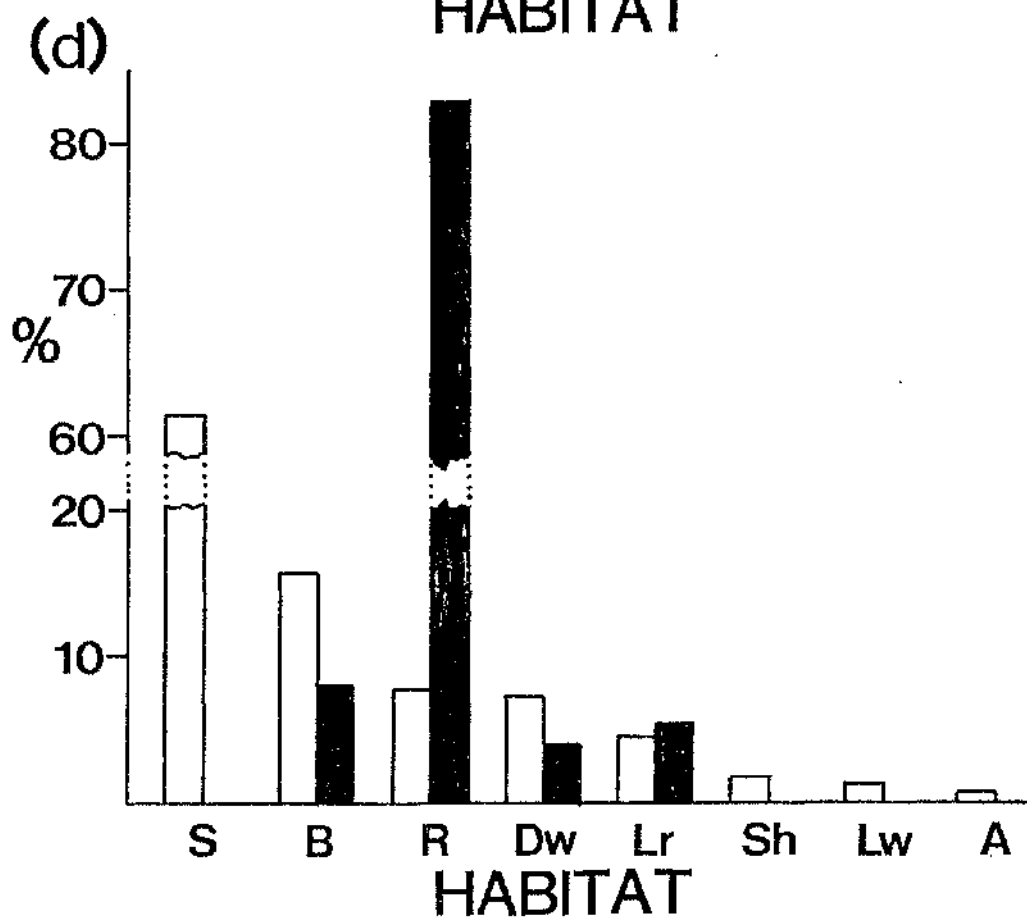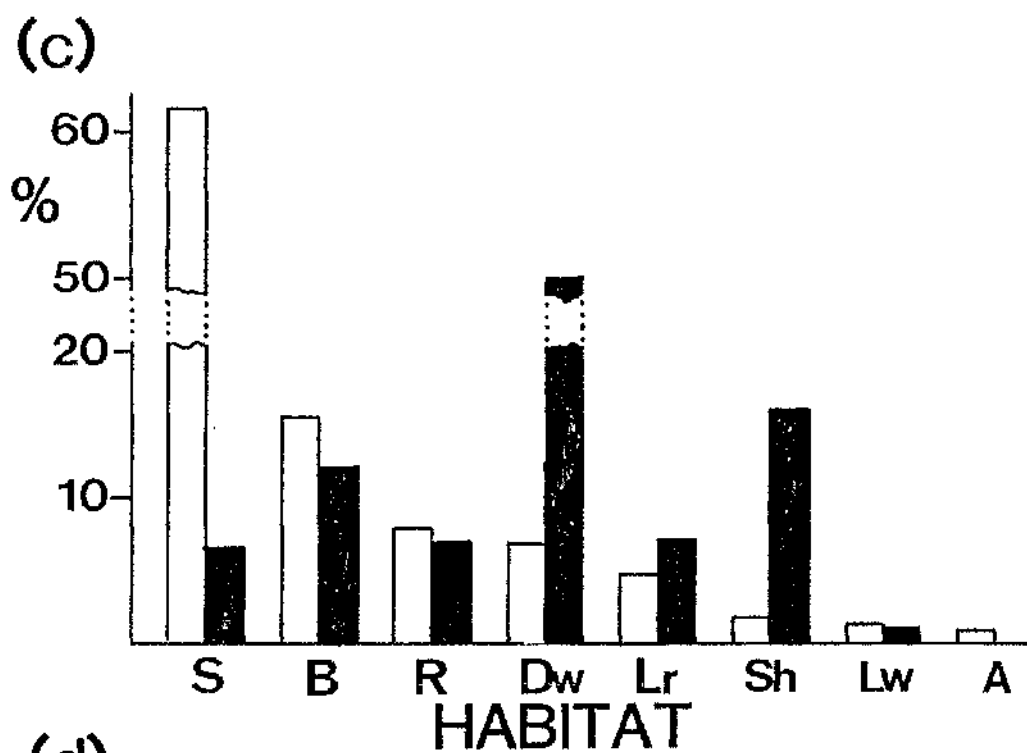
period, turnstones were most frequently seen amongst boulders and on rock, loose rock and musselbeds. They were also seen (although less frequently) on all seven habitats. Over the same period purple sandpipers were most often found on rocks; musselbeds were also frequently used, but many of the other habitats were only used sporadically, if at all. At high water the available choice of habitats was more restricted. Purple sandpipers were only found in four habitats (and showed an even greater preference for rock), while foraging turnstones were predominantly found on dead wrack and shingle, two habitats rarely used at other times. This presumably reflects the reduced availability of littoral invertebrates over the high water period, and the consequent shift in turnstone diets to food present in the debris brought in by the tide and left along the strand line.

(d) Data Analysis

Statistical analyses were carried out (following the procedures and guidelines of Sokal & Rohlf (1981) and Siegel (1956)), using the SPSS, BMDP and MINITAB statistical computer packages (Nie et al. (1975), Dixon (1983) and Ryan et al.(1976) respectively). Data were transformed as appropriate to meet the conditions of particular statistical tests; details of these transformations, and of the methods used to tackle more complex analyses (such as cluster analysis), are described in the relevant sections of the text. All statistical probabilities quoted in the text refer to two-tailed tests of significance.

Any study of the behaviour of animals in groups must take account of constraints which may be imposed by other aspects of a species' socioecology. For instance, adaptations to group living (such as ritualised, non-escalating aggressive encounters, or the sharing of vigilance) would be unlikely to develop if individuals normally moved independently of, or avoided, each other (Monaghan & Metcalfe in press). Even in a gregarious species, the degree of complexity of the social organisation depends partly on the stability and size of its functional units of population. Thus, if individuals are either short-lived or are continually moving between groups, the rapid turnover of group composition will prevent the formation of any subtle inter-individual relationships (such as stable hierarchies based on individual recognition). A similar constraint may apply to very large groups (such as feeding flocks of weaver finches _Quelea quelea_ or migrating wildebeest _Connochaetes taurinus_), unless there is non-random assortative association of individuals within the group.

It thus becomes important in a study of social behaviour to determine not only the extent of aggregation but also the size and stability of the population, so that any constraints on sociality imposed by demographic factors can be evaluated. For instance, the herring gull _Larus argentatus_ and the blue jay _Cyanocitta cristata_ are both gregarious species, but their degrees of population mixing lie at either end of a spectrum that has a great influence on social organisation. Blue jays have small home ranges, maintained from year to year, within which they move in stable groups of around 15 birds. Within each group there is a stable hierarchy, based on individual recognition, so that dominant birds have undisputed prior access to

localised food patches, with subordinates making no attempt to displace those higher in the pecking order (Racine & Thompson 1983). In contrast, individual herring gulls may undergo long migrations (Coulson et al. 1984), travel considerable distances between roosts and feeding sites (Shedden 1983), and often change feeding sites such as rubbish tips from day to day (Monaghan 1980). As roosts may comprise tens of thousands of birds, and as there may be several thousand birds feeding at a tip at any one time, any form of ritualised behaviour based on individual recognition is clearly impossible. Instead, birds contest for food by scramble competition, with frequent aggressive interactions over food items. While females and juveniles tend to lose out in competition with males and adults respectively (Monaghan 1980), these are only generalisations applying to categories of bird, in contrast to the far subtler interactions that occur between individual blue jays.

A second point that arises out of this last example is that subordinate animals may be forced to utilize secondary habitats, which often leads to their dispersing more widely than dominants (Monaghan 1980). This may lead to their suffering higher mortality rates (Fretwell 1969, Watson & Moss 1970, Dittus 1977). Thus social behaviour may in turn be the cause of population turnover, with different components of the population affected in different ways.

Therefore this chapter attempts to determine the stability and size of the populations under study. Stability is assessed by analysis of the survival rates and site faithfulness of birds, and of the timing of movements in and out of the study area. The first stages in this are necessarily to determine what proportion of those birds that were marked were actually part of the resident population, and how adequate were the methods used to census the population.

As much of these analyses utilize data on marked birds, the

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conclusions that can be reached for purple sandpipers are rather limited, as so few birds were ringed. Most of the chapter is therefore concerned solely with the turnstone population. and purple sandpipers are treated separately in section 2.4.

2.1   The Classification of Birds According to their Degree of Residency in the Study Area

2.1.1 Methods

There was great variation in the regularity with which marked birds were seen in the study area. Although the majority were found to have a readily-defined home range within its limits (and were therefore seen frequently), others were only seen occasionally, some disappeared soon after capture and some were never seen at all after they had been released. Therefore birds were categorised according to the frequency with which they were seen, as follows:

Residents: seen at least eight times in the six months following capture (not counting the four months from mid-May to mid-September, when birds were on the breeding grounds), and at a similar rate thereafter.

Visitants: seen less than eight times in six months, but seen on the study site at least four months after capture, and at a similar rate thereafter.

Transients: seen less than eight times, and never seen more than three months after capture.

A fourth category contained the few birds never seen at all after ringing.

2.1.2 Results

Table 2.1 shows the sample of 100 adults and 19 juveniles ringed in this study categorised by the above method.

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Table 2.1 The initial categorisation of all turnstones colour-ringed
in the study, according to their degree of residency

Category	Adults		Juveniles	
	Number	Percentage	Number	Percentage
Resident	73	73	9	47
Visitant	13	13	3	16
Transient	10)		4)	
	)	14	)	37
Never seen	4)		3)	
Total	100		19	

There were very few changes in the frequency with which
individual birds were seen which necessitated their being re-
classified after the initial six months. One bird was seen regularly
during the winter in which it was ringed, then on only five occasions
during the next two years. It was, however, seen during this period
(by a member of the public) at Irvine harbour, 3.5km to the south of
the study area. A second bird, ringed and subsequently seen regularly
in the second winter of the project, was seen at Prestwick (16km to
the south) that April, and then only twice in the study area in the
following winter. Both birds thus appear to have shifted their home
range during the study, to regions outside the main study area. Two
birds were ringed and seen frequently during the first winter, then
not seen at all in the second, only to reappear in the third (one
regularly, in much the same locations as previously, but the other
only sporadically). The first bird has therefore been treated as a
resident that was absent for a year, and the second as a resident
that became a visitant. The final case of a bird changing category is
one that just failed to classify as resident in its first six months
(being seen seven times), but subsequently reached the threshold in
the succeeding period. As there was no evidence of any shift in home
range (the bird always having been seen at Stevenston), the change in

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status of this bird is probably an artefact of the arbitrary division between the categories. Thus if this bird is ignored, there were only three birds (out of 86 adults and 12 juveniles initially classified as resident or visitant) that changed status during the study.

It is likely that many of the birds classified as visitants had home ranges that were partially or wholly outside the study area (and may therefore have been outside their normal range when seen in the study area). This is indicated by:

(a) the intermittent appearance of such birds within the study area, often over long periods;

(b) analogous occasional 'aberrant' movements by resident birds, of up to several kilometres outside their normal home range (chapter 3);

(c) the presence of sizeable populations of turnstones on the contiguous stretches of coastline;

(d) the tendency for visitants to be seen on the periphery of the study area (the 16 visitants were seen a total of 105 times in the first two years of the study (when North Beach was searched extensively); 80.0% of these sightings were either on North Beach (n=53) or at Stevenston (n=31)), and

(e) occasional sightings of visitants away from the study site. Several searches were made (by myself or Dr.R.W. Furness) along the 6km stretch of coast to the north of the study area; the overall proportion of birds colour-ringed in this area was only 2/233, and both of these birds had been categorised as visitants.

It is therefore probable that there was no difference between resident and visitant birds except in the location of their home range (although the visitant category may have included a few birds with exceptionally large home ranges, of which the study area was only a part). In contrast, birds that quickly disappeared or were

never seen after capture must have either died or moved away from the area soon after capture. Proof that some birds may move over long distances outside the breeding season comes from one bird that had been ringed in the study area in mid-February, and had then been seen four times in the following three weeks before disappearing. It was then found freshly dead over a thousand kilometres away in France the next August.

If the two categories of disappearing birds are combined, comparisons with the numbers classified as resident show that a greater proportion of juveniles disappeared than did adults ($X^2 = 4.78$, 1 d.f., P < 0.05). Therefore juveniles must either be more vagile or suffer a higher mortality than adults.

2.2 Tests of the Adequacy of Census Methods

No attempt was made to cover the entire study area evenly, and so it was to be expected that (even amongst residents) some birds would be seen more frequently than others. However, it was useful to have some indication of the likelihood of seeing a particular bird on any one day of observation, as calculations of home ranges, spring departure dates and survival estimates all make the assumption that the birds that are seen on any one day are an unbiased and reasonably substantial proportion of the total present. Therefore two analyses were carried out to examine my ability to locate resident birds: the first being the calculation of an index of the frequency with which individuals were seen, while the second was a test of how long resident birds could go undetected.

2.2.1 Methods

The sighting frequency index was defined as the number of days on which a particular bird was seen, as a percentage of the total number of observation days. This total number was taken as the number

of days of observation from the day of ringing to the final sighting of the bird, discounting days after the last sighting each spring (as the bird was assumed to have departed for the breeding grounds on that date, and so was no longer able to be seen on the study site). This index was not calculated for birds that were classified as transients, as the short period over which the index would have been determined would lead to large errors in any estimates produced. Therefore the minimum time period was four months, and the average was well over a year.

The second test of my ability to locate resident birds was to plot the cumulative total number of individuals seen with increasing number of days of observation since an initial starting date. This would allow estimation of the number of days fieldwork required to see 50%, 75%, 95% and so on of the resident population. The start of the 1982/83 season provided a convenient sequence of observation days for this analysis, as the population already contained a reasonable number of marked birds known to be resident, and the first day of the sequence could be taken as the first day of the season's fieldwork. (This analysis was only conceived after the season was over, so the fieldwork was not unusually orientated towards obtaining a maximum number of sightings.)

2.2.2 Results

Figure 2.1a shows the frequency distribution of the percentage of days on which adults and juveniles were seen, while Figure 2.1b shows the distribution further divided into resident and visitant birds (those that changed category having been omitted). While there is great variation in the percentage of days that a bird was seen when the sample is taken as a whole (the minimum being 3.2%, the maximum 90.9%), resident birds were seen on a minimum of 24% of observation days, and the 'average' resident was seen every other day

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Fig.2.1. (a) Frequency distribution of the number of observation days on which colour-ringed turnstones were seen. Juveniles indicated by speckling. (b) Data as in (a), but split into birds classified as visitants (upper histogram, n=15) and birds classified as residents (lower histogram, n=79).

(a)

No. OF BIRDS

24
16
8
0

0   20   40   60   80   100
PERCENTAGE OF DAYS

(b)

8
0

0   20   40   60   80   100

No. OF BIRDS

24
16
8
0

0   20   40   60   80   100
PERCENTAGE OF DAYS
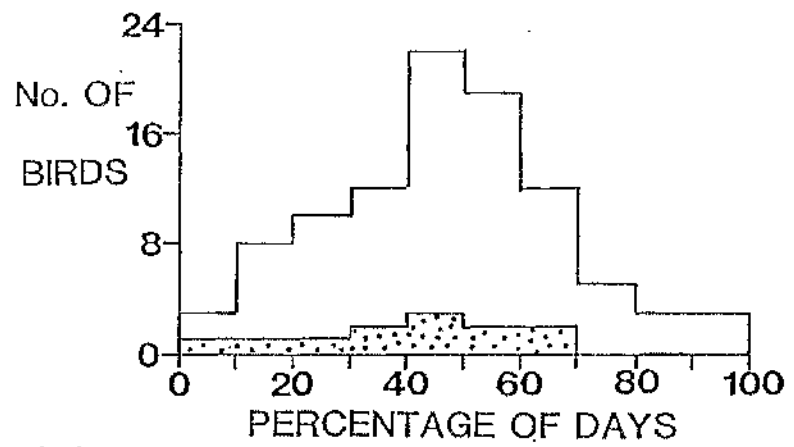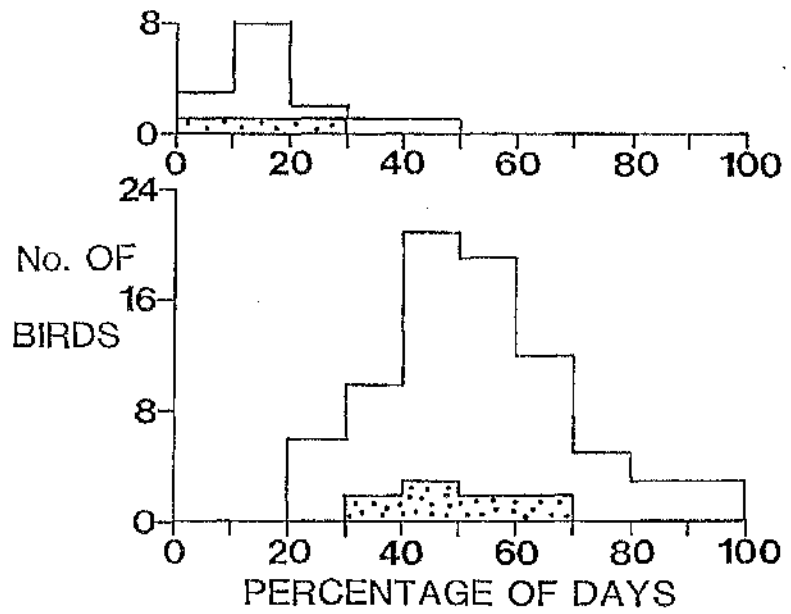
of observation (mean = 51.9 ± 1.8 %, n=79). There was no difference between the regularity of sightings of resident adults and juveniles (Mann-Whitney U test, U=2930, NS).

The cumulative plot of residents seen against days of observation is shown in Figure 2.2. A total of 54 of the birds ringed and categorised as residents in the 1981/82 season were seen to have returned in the 1982/83 season. Adults and juveniles have been combined, as there was no age-related difference in the likelihood of residents being seen. Given the asymptotic nature of the curve, and the fact that no new sightings were made in the 21 visits made in the latter half of the season, it seems likely that all the resident birds present in the study area that year were located. Of this total, over 55% were seen on the first visit, and by the tenth visit (at the end of October) only five percent had still to be seen for the first time. This may have been because they were later than most birds in returning to the study area, or because they were present but had not been seen. The former may have been the case for some birds, as Brearey (1982) found that a small proportion of Teesmouth turnstones did not return in the autumn until October.

As discussed earlier, two resident birds did not reappear until the next season; one was then only seen twice (and so can be considered to have changed to visitant status, and can be ignored in this analysis). The other, having been seen 12 times in the three remaining months following ringing in the first year, was again seen regularly (13 times in four months) in the third year; it thus seems improbable that this bird could have been resident (but remain unseen) in the second year.

The conclusions to be reached are therefore that, while there was variation between individuals in the frequency with which they

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Fig.2.2. Cumulative graph of the number of colour-ringed turnstones, classified as residents in the 1981/82 winter, that were subsequently resighted. Thus thirty had been seen after the first observation day (on 7th September) of the 1982/83 winter, and the last to be seen that winter was on the 16th observation day (on 29/1/83). Two more were seen in the autumn of 1983.

PERCENTAGE OF 1982/83 TOTAL

NUMBER OF DAYS OF OBSERVATION

1983/84

1982/83
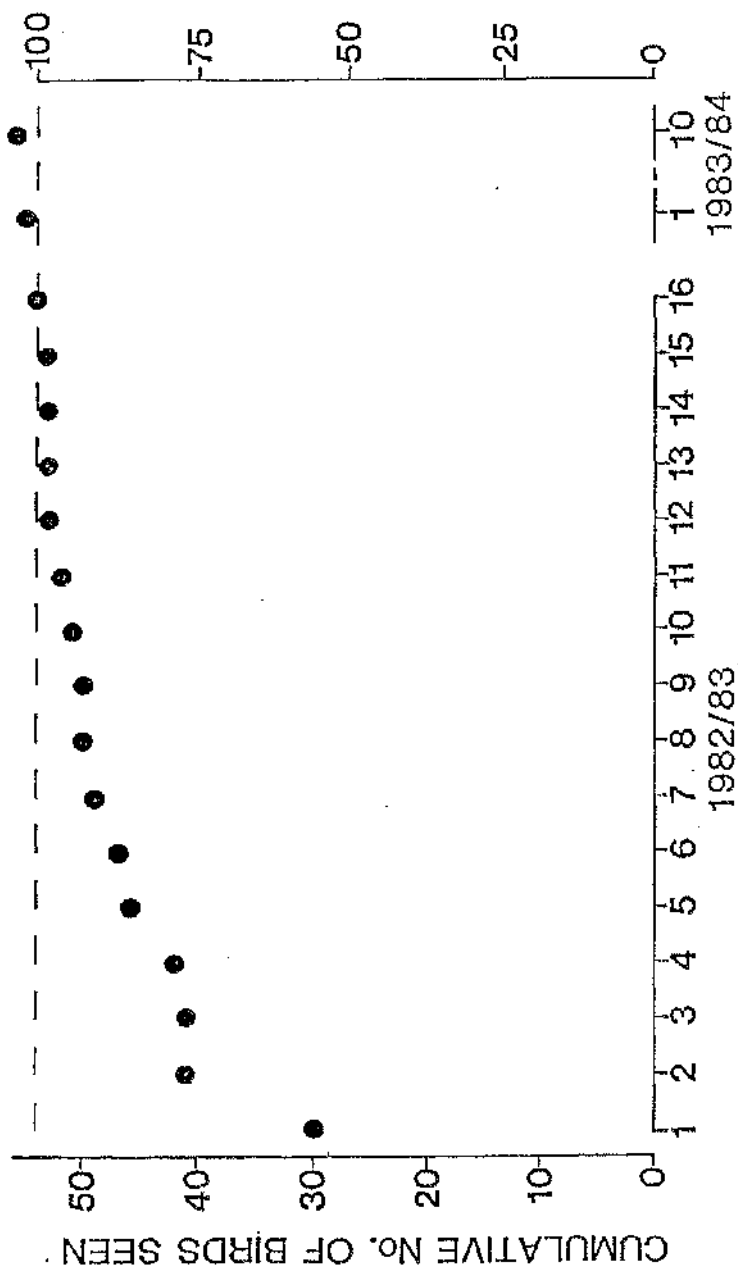
CUMULATIVE No. OF BIRDS SEEN

were seen, on average each resident bird were seen on 50% of observation days, and it was extremely unlikely that colour-ringed residents could have gone undetected for long periods of time.

2.3 The Size of the Population, Survival Rates, and the Timing of Migration

Having established that the majority of birds that were colour-ringed remained within the study area, and that resident birds were unlikely to remain undetected by my censussing techniques, it was now possible to estimate the size of the wintering population, the survival rate and the approximate timing of spring migration. As an assumption in the calculation of the first two parameters is that no emigration was occuring at the time, a logical sequence of analysis is to determine the timing of spring migration first, and then the estimates of survival and population size.

2.3.1 Methods

The study site was visited regularly throughout the spring period (on average approximately every four days in the first two seasons, but only every eight days in the third); a simplifying approximation can therefore be made that birds migrated away from the study area on the day they were last seen. While this gives only a rough indication of the actual time of migration, biased towards a premature estimation of departure date, it is sufficient for comparative purposes, providing there is still sufficient variation in the estimates produced. A distinction has to be made between those disappearances that were assumed to be due to (winter) mortality, and those due to spring migration. The simplest method of separating the two was to decide upon a threshold date in early spring; birds that were last seen before this date were assumed to have died, while those last seen after it were assumed to have migrated. Choice of this date was not entirely arbitrary, as the dates of the last spring

sighting of birds that returned the following autumn could be used to estimate the earliest time of spring migration. After consideration of these departure dates it was decided to adopt the 1st of February as the cut-off point.

The departure dates of individuals could not be compared to changes in total population size, as accurate censuses could not be made in all parts of the study area. Nonetheless, the population at Coalruffie could be counted at most tidal stages with little risk of birds being overlooked. Changes in this subsection of the population have therefore been taken as an indication of changes in the population as a whole. As the group of turnstones that used Coalruffie generally arrived and departed as one flock (Chapter 6), the estimates of population size (if greater than zero) were independent of tidal state.

Immigration into the study area by spring passage birds from elsewhere could be studied by monitoring the proportion of turnstones that were colour-ringed. Therefore the percentages of birds colour-ringed (given by the total number seen to be ringed out of all birds in flocks checked for rings) were compared for different periods of the winter and spring, from the date of last ringing to the end of the study.

As with the estimation of migration times, the occurence of mortality (and hence calculation of survival rates) can only be reliably determined in birds already classified as residents. Therefore the period over which survival was assessed had to commence after the initial classification period of each bird, yet had to terminate before the onset of migration in the final year. Taking the survival assessment period as a complete year would then have restricted the sample size to those birds caught in the first year;

therefore the year was split up into two periods (broadly representing summer and winter) over which survival was independently calculated. Dividing the year into two in this way would also show whether the major mortality occurred in or away from the wintering quarters. The summer period was defined as from February 1st (the onset of spring migration) to October 1st, and winter as from October 1st to February 1st. Thus summer survival was taken as the proportion of all birds, that were known to be alive and that had been classified as resident by February 1st, that were seen on or after the following October 1st. A similar procedure was used to estimate winter (October - February) survival.

Data on the proportion of birds ringed, the proportion of ringed birds that were resident, and the actual number of resident birds present could be combined to produce an estimate of the total size of the population wintering in the study area. However, as the various regions of the study area differed in the number of birds they held, the proportion that were colour-ringed, and the extent to which they had been censussed, separate estimates of population size had to be constructed for each region. The study site was divided into six relatively distinct areas: North Beach, McCrindles/North Rocks, South Rocks, Saltcoats Harbour, Coalruffie, and Stevenston. The period over which all parameters were measured was taken as from 1/10/83 to 28/2/84, as this was well after the time when the last birds had been ringed, and so all transients had disappeared and the proportion that were colour-ringed had stabilised. February is included in this 'winter' period, despite February 1st being taken as the first date of spring migration, as the analysis of departure dates (see later) showed that only 5% of the population had departed by the end of February.

Dividing the study site into these six areas necessitated

estimating the proportion of time each resident had spent in each area (so as to produce a figure for the average number of residents per area). This was done by calculating the proportion of sightings of a bird in each area, compensating for the approximate extent of observer effort in each area by dividing the number of sightings by the number of visits made to the area over the period. Return visits made to an area on the same day were counted separately, provided that at least one hour had elapsed between them.

Thus for a bird seen in T different areas, the proportion of time it was estimated to have spent in area C is given by:

$$Pc = \frac{\frac{Sc}{Vc}}{\sum_{i=1}^{T} \frac{Si}{Vi}} \qquad - (1)$$

where Si = number of sightings of that bird between 1/10/83 and

28/2/84 in area i, and

Vi = number of visits to area i over the same period

The estimated mean number of residents in area C at any one time is then:

$$Nc = \sum_{j=1}^{n} Pjc \qquad - (2)$$

where n = total number of marked resident birds, and

Pjc = proportion of time j'th bird is estimated to have

spent in area C.

It follows that $\sum_{i=1}^{T} Ni = n$, as it has been assumed that residents spent all their time in the six areas.

The total average number of residents present in area C (including unringed birds) could then be estimated as Nc/Rc, where Rc is the proportion of birds that were colour-ringed in area C.

The total number of birds present at any one time (including visitants) can then be obtained by using the ratio of residents : visitants. This can be estimated from the overall proportions present

in samples obtained through cannon-netting. These are not equivalent to the proportions of the total ringed, as in the later catches residents were more likely to have already been marked than were visitants. The overall ratio (taking account of these retraps) was thus 104 : 17. Therefore it is estimated that there were, on average, 0.16 visitants in the study area for each resident. Their distribution can be approximated as equivalent to the distribution of sightings of marked visitants during the first two years of fieldwork.

This method of population estimation makes the following assumptions:

1. Colour-ringed birds are a representative sample of the whole population. There is no reason to suspect that this is not the case, given the relatively high percentage that were ringed and the fact that the sample is composed of birds caught at a variety of locations over a long period.

2. The proportion of birds that are resident is equal over the whole study area. Again, the fact that this estimate is based on a sample of birds caught at eight different locations makes it a reasonable estimate for the population as a whole.

3. The ratio of residents:visitants did not change with time. While there may be periods of increased mobility of birds, especially in early autumn and late spring (Chapter 3), the fact that very few marked birds changed status even over a period of three years indicates that the ratio remains fairly stable.

2.3.2 Results

Timing of Spring Migration

There was no significant difference in the dates of spring departure of adult turnstones in 1982 and 1983, the years in which

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regular visits were made to the study area (Mann-Whitney U test on the dates of last sighting of all residents, taking 1st February as 1, $U = 2895$, $n_1 = 54$, $n_2 = 60$, NS); the median date of last sighting being 30th April in 1982, and 28th April in 1983. Therefore both years have been combined in Figure 2.3, which shows the cumulative percentage of birds that had departed through the spring period. It is evident from the graph that there was a steady acceleration in the rate of departure through the spring. Only 5% of the birds had departed by the end of February, and a further 20% left the following month. However, the rate of migration increased markedly through April, so that 50% of the population departed in a 15 day period in late April to early May. Only stragglers were left after May 10th; they too had departed within a week. Thus 90% of the population left in the two month period from early March to early May, with the majority leaving at the end of that period.

The departure dates of thirty-nine birds is known for both 1982 and 1983, and Figure 2.4 shows that there is a good correlation between the two; individuals left the study area on much the same date in both years. This result could have been produced spuriously, if my censusing had been biased so that certain areas were under-searched towards the end of both seasons. The estimates of departure dates for birds in such areas would then have been premature in both years, so possibly leading to a correlation in departure dates between years. However, that this is not the case is demonstrated by similar correlations when only the birds in one area are considered (e.g. taking only birds resident at Stevenston (n=11), correlation in departure dates between years $r_s = 0.763$, $P < 0.01$; similarly North Beach residents $r_s = 0.466$, $P < 0.05$). Thus it would appear that individual adult turnstone are consistent in their timing of

Fig.2.3. The timing of spring migration by adult turnstones, expressed as the percentage of residents known to be still present in the study area at successive five day intervals. Data combined for 1982 and 1983, n=116 birds.
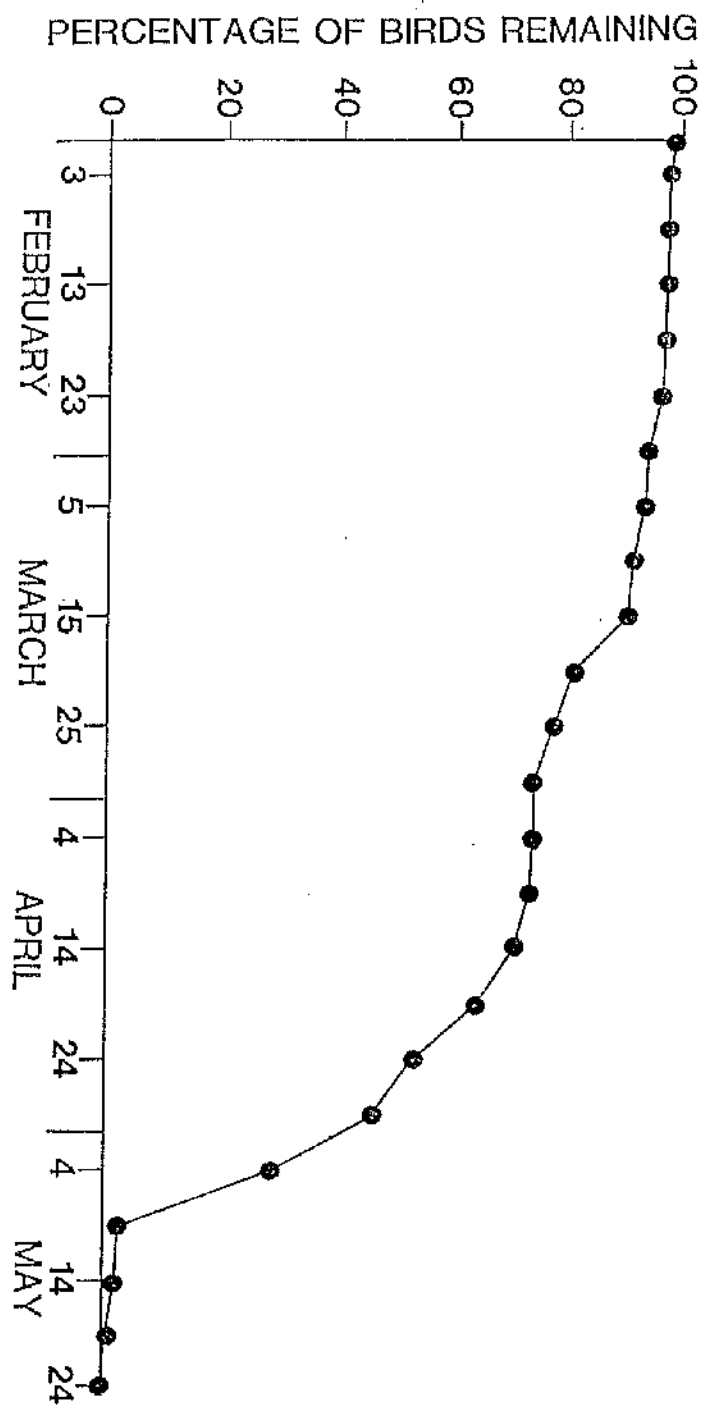
Fig.2.4. The date on which resident adult turnstones were last seen in the spring of 1982 plotted against the date of their last sighting in the spring of 1983. Larger dots and numbers indicate that several points are superimposed. The dashed line shows the result that would be obtained if birds were last seen on the same date in both years. Rank correlation between years: r_s = 0.744 (n=39), P<0.001.

MARCH 1982 APRIL MAY

1983
MAY
APRIL
MARCH
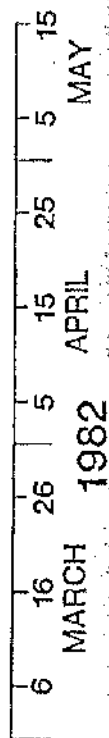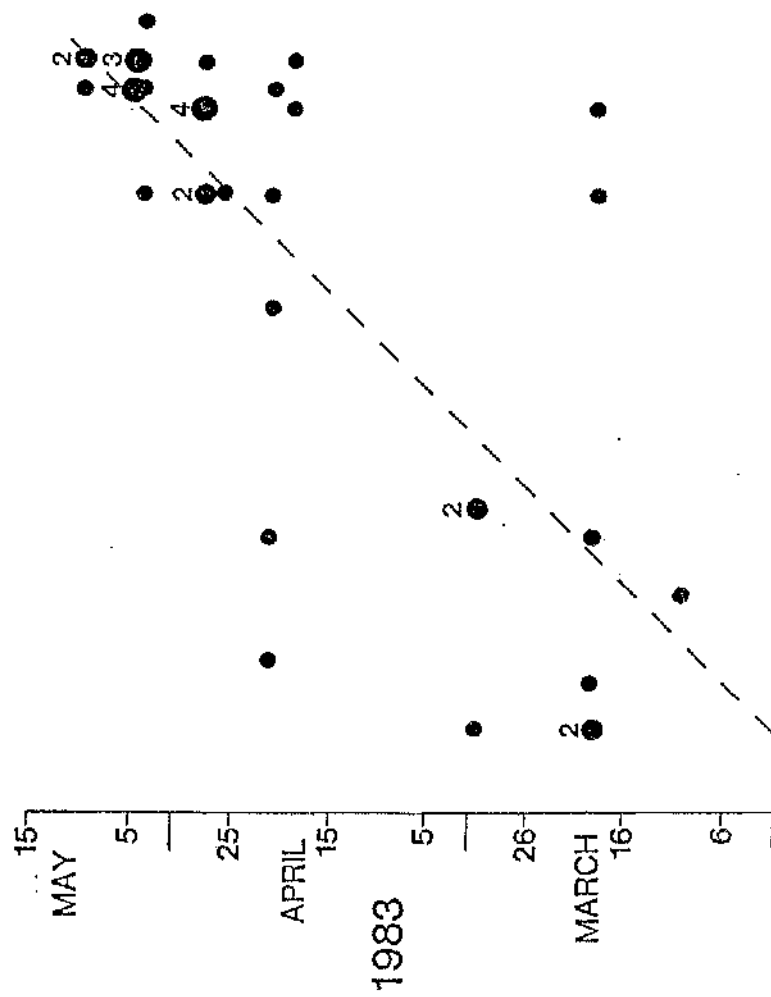
migration, with some birds regularly leaving their main wintering quarters well before the main exodus. Further evidence on this last point comes from the annual cycle of movements of the earliest bird known to depart (as opposed to die) in all three seasons. The 'spring' departure dates of this bird in the three years of the study were 27/1/82, 9/11/82 and 14/2/84. This bird's movements were clearly unusual, as can be seen from the fact that in 1982/83 it left the study area approximately 121 days before the next colour-ringed migrant!

Combining data for the first two years, seven out of the eight resident juveniles that were still alive in February were seen on or after May 4th in their first summer. Their dates of last sighting were thus significantly later than those of adults for the same combined years (Mann Whitney, $U = 6769$, $n_1=114$, $n_2=8$, $P < 0.01$).

Although fewer visits were made to the study site in 1984 than in the previous two years, with the result that estimates of departure dates were less accurate, it was evident that migration occurred earlier than in the previous two years. Figure 2.5 shows the departure dates in 1983 and 1984 for those individuals present in both years. Dates are significantly earlier in 1984 than in 1983 (Wilcoxon paired signed-ranks test, $T_S = 37$, $P < 0.001$), with only three out of 33 birds departing later in 1984 than 1983, and eight departing at least a month earlier. There was a general trend for all birds to leave earlier and in the same sequence, as shown by the significant rank correlation between a bird's date of last sighting in 1983 and 1984 ($r_S = 0.460$, $n = 32$, $P < 0.01$) and 1982 and 1984 ($r_S = 0.559$, $n = 17$, $P < 0.02$).

Changes in population size and the percentage of birds colour-ringed at Coalruffie are shown in Figure 2.6. The wintering population size was very stable (see also Figure 2.8), and did not

Fig.2.5. The dates of last sighting of resident adult turnstones in the springs of 1983 and 1984. For explanation of symbols see Fig.2.4. Correlation between years: $r_s = 0.460$ (n=32), P<0.01.
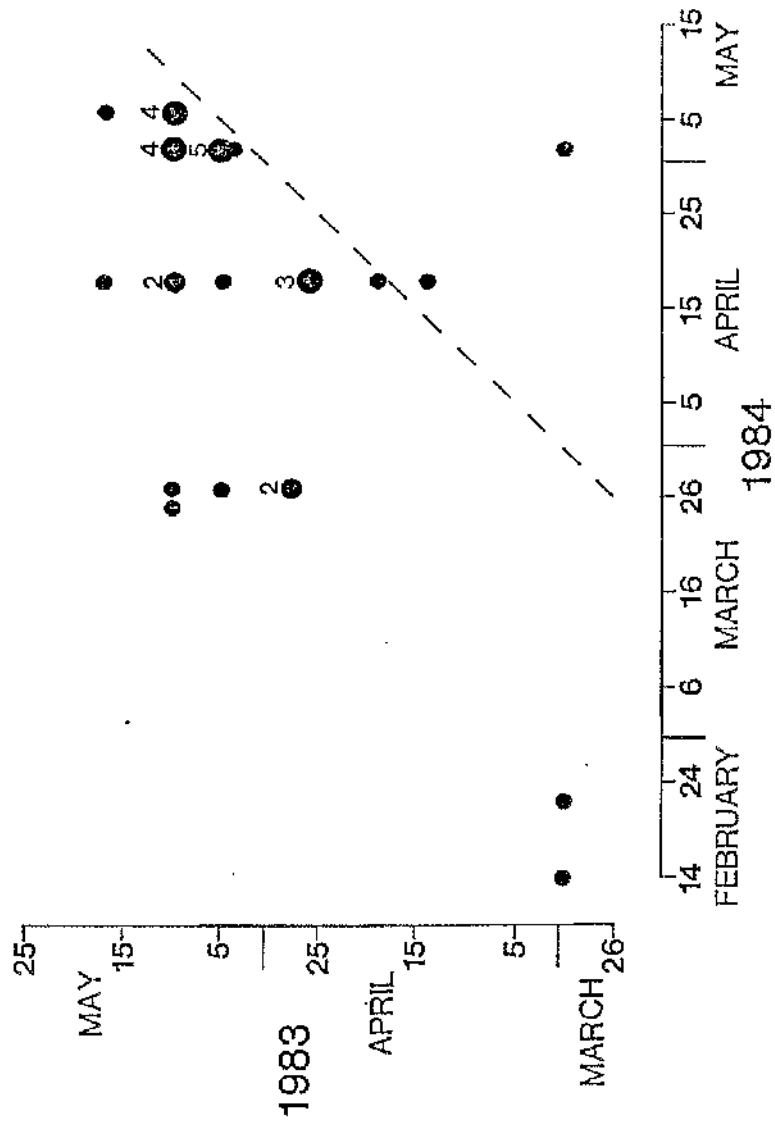
Fig.2.6. The mean number ($\pm$ S.E., with sample sizes) of turnstones

present at Coalruffie over the exposure period during the three years

of the study, and the percentage colour-ringed from 1983 to 1984.

Each year is divided into five periods:

1 = September to February
2 = March to 15th April
3 = 16th to 30th April
4 = 1st to 9th May
5 = 10th to 20th May

Comparisons between the number of turnstones present in winter

(period 1) and periods 2-5 in each year, by Mann-Whitney U test:

Year	Period 2	Period 3	Period 4	Period 5
1981/82	U=72,NS	Combined 3 & 4 —	U=53,NS	U=63,P<0.05
1982/83	U=77,NS	U=70, P<0.05	U=52,NS	U=72,P<0.02
1983/84	U=299,NS	U=18, P<0.05	U=256,P<0/01	U=207,P<0.05
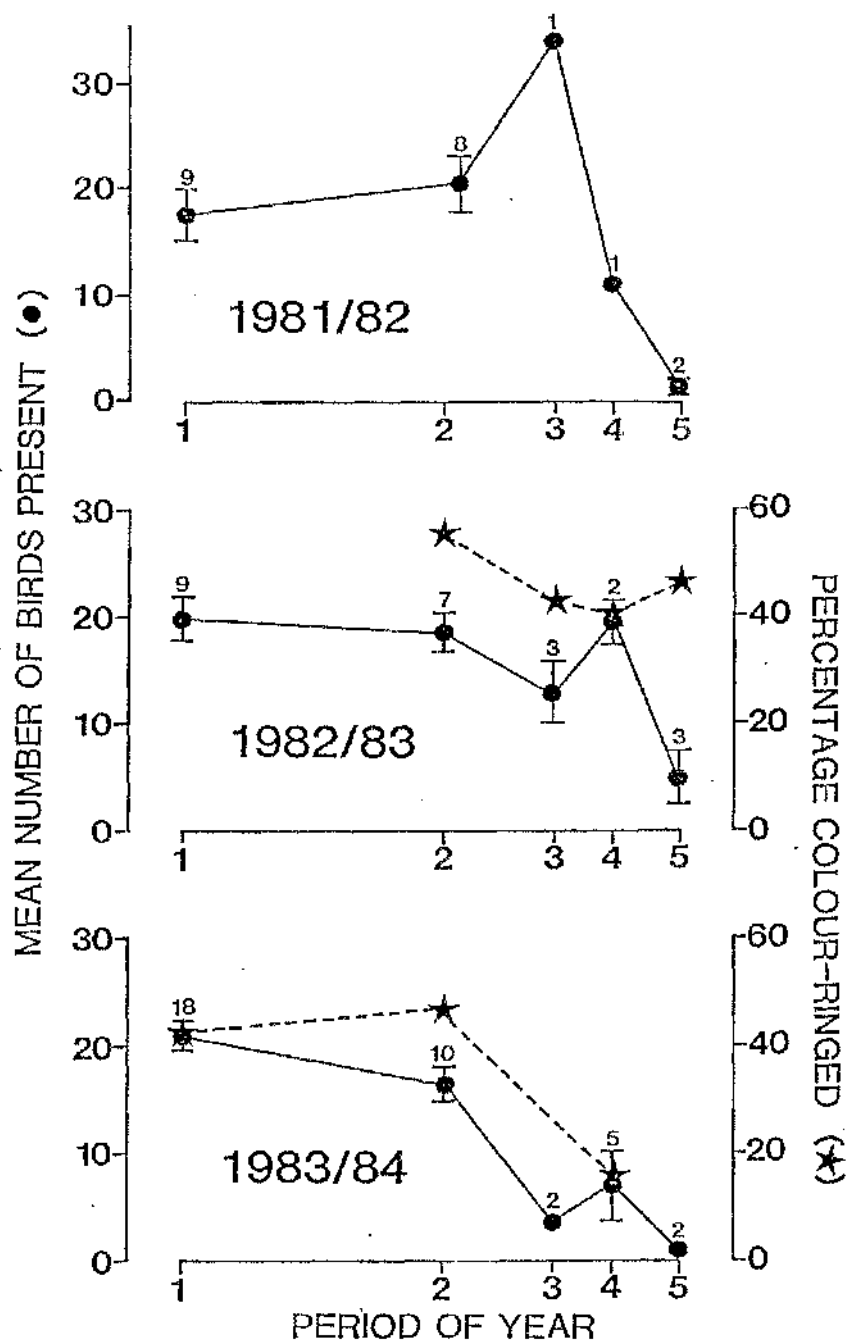
vary between years (there being no significant differences (using Mann-Whitney U tests) between years in counts made between September and April 15th). In the springs of 1982 and 1983 there was no significant decrease from the size of the wintering population until mid-May (although there were signs of fluctuation by late April). The lack of change in the proportion of birds colour-ringed in spring 1983 demonstrates that there was negligible immigration occurring during this period. This contrasts with the situation in the spring of 1984, when there was evidence of a slight (but not significant) decline in population size by early April. By late April the population was only approximately a quarter of that present in winter; furthermore, the reduction in the percentage colour-ringed indicates that some of these were immigrant birds passing through the area.

Therefore the counts at Coalruffie back up several of the conclusions reached from the analysis of the estimated dates of departure of individual birds: a negligible proportion of birds had departed by the end of March, thereafter the rate of departure increased markedly so that very few birds were left by mid May, and lastly that migration occurred earlier in the spring of 1984.

Figure 2.7 compares the changes in the proportion of birds colour-ringed at Coalruffie with changes over the same period in the three other areas that initially held high proportions of marked birds. No data are available for North Beach in spring 1984, as the area was not studied at that time. The results for the other areas in 1983/84 all show that no spring immigration had occurred up until mid April (even in this year of early migration). It can therefore be assumed that the percentages for the March-mid April period in 1983 represent the hypothetical values for the stable winter population

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Fig.2.7. The percentages of birds colour-ringed (with sample sizes) in four separate regions of the study area, from the spring following the 1982/83 winter until the end of the study in spring 1984. Year divided into five periods, as described in legend to Fig.2.6. No percentages are given where the sample size was less than 12 birds.

PERCENTAGE COLOUR-RINGED

NORTH BEACH

McCRINDLES/N. ROCKS

COALRUFFIE

STEVENSTON

1982/83

1983/84

PERIOD OF YEAR
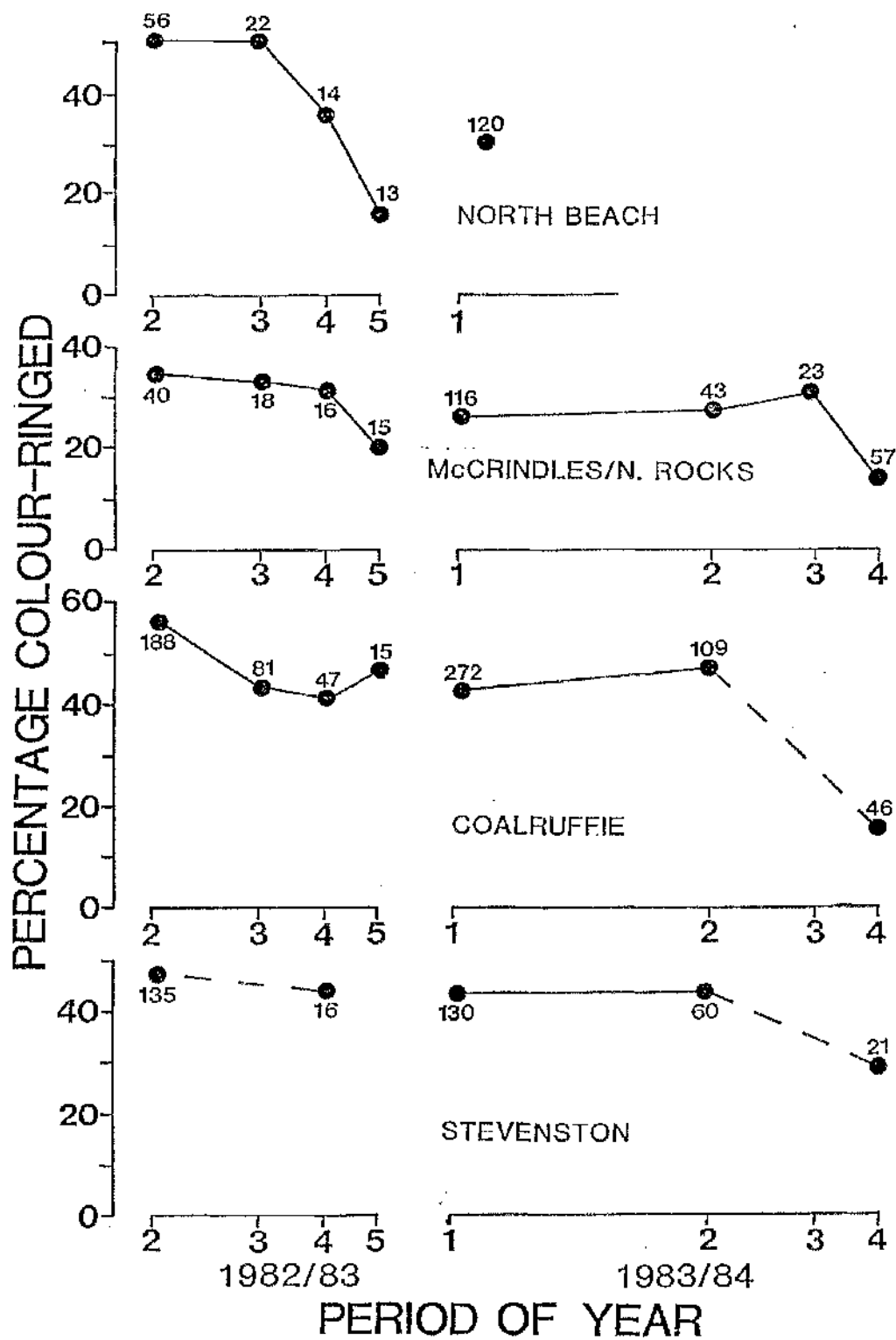
(the true values not being available, as birds were still being colour-ringed up until 15/2/83). While no immigration was evident at Coalruffie in 1983, this was not true of other areas. By mid May the proportion of marked birds had decreased on North Beach and the North Rocks/McCrindles areas, and all areas showed similar patterns in 1984. Therefore there was an overall trend for immigration to occur in May in both years (Wilcoxon ranked pairs test comparing periods 2 and 4 in four areas one year, three the next, $T_s = 0$, $n = 7$, $P < 0.02$), although its extent was not uniform over the study area.

Survival Rates

Table 2.2 illustrates that only eight out of 75 resident adult turnstones (and none out of eight resident juveniles) disappeared in the period from 1st October to February 1st. Combining this with the over-summer survival rate (Table 2.2) gives a minimum adult survival rate of 85.8%. The correct figure may be even higher, as it has been assumed that any bird that did not return to the study area had died, and section 2.2 has shown that a small minority of birds may alter their wintering areas. The sample size for juveniles was too small to calculate a realistic survival estimate for birds in their first year of life, but the indication is that the survival rate of resident juveniles cannot be greatly different to that of adults.

If survival rate is age independent, as is likely to be approximately correct in birds with moderately long lifespans, a one year old turnstone has an average life-expectancy of a further 6.25 years, and a quarter of the population will live for a further nine years. (The maximum recorded lifespan of a wild turnstone is 19 years 9 months (Cramp & Simmons 1982).)

Table 2.2 The winter and summer survival rates of resident turnstones

Period	Age Category	Initial No.	No. at end of period: Alive	No. at end of period: Disappeared	% Survival
Winter (Oct–Feb)	Adult	83	75	8	90.4%
	Juvenile	8	8	0	(100.0%)
Summer (Feb–Oct)	Adult	40	38	2	95.0%
	Juvenile	2	2	0	(100.0%)

Comparing between winter and summer mortality, it is evident that the long double-migration to and from the breeding grounds is not a major cause of mortality, as the entire 8-month summer period (including both migrations) accounts for only one third of the annual mortality.

Population Estimates

Estimates of the proportion of colour-ringed residents, the total number of residents and the total number of birds in each area are given in Table 2.3. Some indication of the reliability of the estimates is given by the number of birds seen at Coalruffie and South Rocks over the same period. These were the only areas that were small enough and of the right topography to allow complete censusses to be made with reasonable accuracy at most tidal levels. The average number of birds present in counts made between October and February was 21.0 ± 1.5 (n=18) at Coalruffie, and 12.6 ± 2.2 (n=9) at South Rocks, means which are 84.0% and 94.7% respectively of the estimated population sizes based on the number of marked residents utilizing the area. The slight discrepancy may arise partly from average counts having a tendency towards underestimation (through my failing to locate all the birds all the time), and partly from the assumption that all residents spent all their time within the study area being not entirely correct (so leading to over-estimation of the number of

resident birds normally present). A better figure for the total
population size may therefore be slightly less than that given in
column four of Table 2.3.

Table 2.3. Estimations of the number of residents, the proportions of
turnstones that were ringed, and the total number of turnstones
present in each part of the study area in the winter of 1983/84

Area	(1)	(2)	(3)	(4)
North Beach	21.1	30.0%	70.4	86.3
McCrindles/North Rocks	8.2	26.7%	30.7	33.6
South Rocks	2.5	19.6%	12.6	13.3
Saltcoats	3.0	10.2%	29.3	29.3
Coalruffie	9.4	42.3%	22.1	25.0
Stevenston	14.9	43.1%	34.5	44.3
Total	59		199.6	232.2

Notes: (1) The average number of ringed residents present in the
area
(2) The percentage of birds colour-ringed
(3) The estimated average number of residents (ringed +
unringed)
(4) The estimated average number of residents + visitants

2.3.3 Discussion

The rates of resighting of turnstones after capture were very
high, with the majority of the birds seen regularly in the study area
in the year of capture and in subsequent years. There is good
evidence that such specific site-fidelity is generally maintained
throughout a bird's life. One hundred and sixteen birds were caught
and (metal) ringed while roosting at McCrindles in September 1979; 13
of these birds were subsequently recaught and colour-ringed during
this study. Of the ten classified as residents, eight were still
present in the study area at the end of the project, when they were
at least 5.5 years old. A further three birds from the 1979 catch
have been found dead, all in the vicinity of Ardrossan. A similar
extent of site-faithfulness was recorded by Brearey (1982) in a
marked population on the Tees estuary, N.E. England. Turnstones are
faithful to roosting sites as well as feeding areas. In a long-term

ringing programme of the waders of the Wash, in eastern England, Branson et al. (1978) found that over 92% of retrapped turnstones were caught at the same roost at which they had been ringed.

However, both the present study and that of Brearey (1982) found variability in the frequency with which individual birds were seen; both have also recorded instances of birds apparently being absent from their previous home ranges for a complete year (also documented in the grey plover Pluvialis squaterola (Townshend 1982)). The variability in resighting rates in this study is probably largely caused by inevitable lack of complete overlap between the area searched for colour-ringed birds and the home ranges of all birds marked during the study. Sizeable populations of turnstones winter within 10km of the northern and southern limits of the study area, and movement between these populations was demonstrated by the four sightings of colour-ringed birds outside the area. In common with many waders, turnstones often fly several kilometres to a safe roost site. The major roosting site in the area was Horse Island, which lies just offshore from North Beach (Figure 1.1). This roost probably contained turnstones that normally foraged outside the study area, and so it is likely that such birds would sometimes be caught (and later seen) while moving to and from the roost.

While the evidence suggests that most (if not all) turnstones categorised as visitants were birds with foraging home ranges lying outside the study area, the possibility remains that some were more nomadic, utilizing the study area as only part of a much larger home range. This situation has been found to exist in the sanderling Calidris alba; some individuals winter on one short stretch of sandy beach, while others may range over 30km of coastline or more (Myers 1984, Evans 1981). This ranging behaviour enables them to take

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advantage of ephemeral super-abundant food resources. Myers (1984) describes one occasion where high densities of amphipods became available to the birds when a brackish lagoon in coastal California suddenly opened to the sea. Thirteen hundred sanderlings were feeding at the site within four days, including 37 marked birds normally resident at Bodega Bay, 23km away. Several of these then proceeded to move repeatedly between the two sites.

However, the real selective advantage of such vagility in the sanderling may only be apparent in bad weather, as sandy beaches are liable to suffer scouring and erosion from excessive wave action. Winter storms may therefore cause sudden reductions in invertebrate populations (Brown 1982), leading to local and unpredictable crashes in food supply (Evans 1981, Myers 1984). Similar local catastrophes may occasionally occur on estuarine mudflats (Yeo & Risk 1979, Radcliffe et al. 1981). Birds with knowledge of food supplies over a wide area may then have a selective advantage, as they will be able to switch to alternative feeding locations more rapidly and efficiently than those with only local experience. Thus there may be long-term benefits in adopting a strategy that over a shorter period is sub-optimal (due to the costs of sampling and movement).

This situation is unlikely to arise in turnstones, as rocky shores are far less likely to suffer sudden erosion by inclement weather. While wave action may remove some invertebrates such as mussels, major damage to musselbeds is infrequent in all but the most exposed localities (Paine & Levin 1981), and most prey species (e.g. barnacles and littorinids), being firmly attached to the substrate, are adapted to withstand such forces. The invertebrate communities upon which rocky shore waders feed are therefore less fragile and have greater temporal stability (and hence predictability) than do those of mudflats or sandy shores.

A second effect of weather on the 'soft substrate' wader species is that low temperatures may reduce prey availability, by causing both prey to burrow deeper (and so out of the range of the birds) and the substrate to freeze (Evans 1976, Goss-Custard 1980, Ratcliffe et al. 1981). Unusually cold winters may also cause heavy prey mortality. Crisp (1964) reported that the winter of 1962/63 caused the death of entire populations of the molluscs Scrobicularia plana and Cerastoderma edule, important constituents of the diet of oystercatchers, curlews and knots Calidris canuta in many areas. Thus cold temperatures not only increase the energy requirements of waders, but may also reduce their foraging efficiency, especially if coinciding with strong winds (Dugan et al. 1981). Therefore it comes as no surprise to find that estuarine and sandy shore species such as sanderling, knot, dunlin Calidris alpina, redshank and curlew have been found to have far higher mortality rates in severe winters than in average conditions (Pilcher et al. 1974, Evans 1981, Clark 1982, Davidson 1982). In soft substrate waders overwintering on the Tees estuary, over one-half the non-breeding mortality in a five year period (excluding deaths through shooting and other unnatural causes) occurred in just four months of severe weather (Davidson 1982).

In contrast, rocky shore waders such as turnstones and purple sandpipers are less affected by severe weather, as many of their prey types (e.g. Balanus balanoides, Littorina spp., Mytilus edulis) are sessile and also relatively unaffected by cold winters (Crisp 1964). Evans (1981) found that turnstone survival rates at Teesmouth were little reduced in the same cold winters that had so much effect on other species. This may partly explain their more northerly non-breeding distribution than any other western Palearctic

shorebirds (Cramp & Simmons 1982).

The estimates for adult turnstone survival rates obtained in this study are similar to (or higher than) those obtained elsewhere. The most comparable figure is that obtained by Evans & Pienkowski (in press) for return rates (autumn to autumn) of birds colour-ringed on the Tees. The adult annual survival rate averaged over six years was 85%, remarkably similar to the value of 85.8% obtained in this study. On the basis of two large catches of a discrete population in North Wales made in March and the following November, Sutherland (1981) estimated survival over this summer period to be 92.2%, a figure that tallies well with the estimate of 95% survival for adults obtained in the present study over approximately the same period. All estimates of survival based on return rates will have a tendency towards underestimation, as they assume that all birds still alive will return to their previous home ranges. Therefore survival rates in turnstones may be slightly higher than the estimates given here, as both this study and that of Brearey (1982) have shown that a small minority of birds change their wintering quarters between seasons. However, there seems to be at least as great a fidelity to the wintering area as to the breeding area, since Bergman (1946) estimated annual survival to be 77.8% on the basis of return rates to Finnish breeding sites. All these estimates from analyses of return rates to study populations are higher than that of 66% adult annual survival obtained by Boyd (1962) from ringing recoveries. This may be partly because he used data for all birds ringed up until 1954; some birds undoubtedly would still have been alive at the time of his analysis, which would lead to underestimation of longevity. Boyd's (1962) estimates for survival rates have also been found to be too low for many other shorebirds (Hale 1980).

The very low oversummer mortality demonstrates that, contrary

to expectations, a double migration of several thousand kilometres together with the hazards of an arctic breeding attempt do not consitute the major causes of turnstone mortality. The mortality rate per month over this period of migration and breeding is less than half that during the (sedentary) winter, even using the lower summer survival rates obtained by Sutherland (1981). Evans & Pienkowski (in press) also found that the majority of deaths occurred at Teesmouth in the winter, rather than over the summer.

While it is apparent (from within-species comparisons) that different techniques of measuring mortality produce different estimates, sufficient other studies have used the method of monitoring return rates of marked birds to allow tentative interspecific comparisons. The work of Evans and co-workers is especially useful in this context, as survival rates have been obtained for several species wintering in the same area. The average annual mortality of adult turnstones on the Tees is lower than that of sanderlings (17%), and curlews (23%), and similar to that of grey plovers (14%) (Evans & Pienkowski in press); the differences are mainly caused by the much higher mortality of the other species in cold winters. For instance, the percentage of grey plover annual mortality that occurred in the winter varied between 0 and 64%, leading to much greater year-to-year variation in survival than in turnstones. Other studies have estimated the annual mortality of adult ringed plovers Charadrius hiaticula, dunlins and redshanks to be between 25 and 30%, and the oystercatcher is the only western palearctic species of wader that has been found to have a substantially greater longevity than the turnstone, with return rates to the Exe estuary averaging 89% (Goss-Custard et al. 1982a). First year oystercatchers had a higher mortality than adults, and were most

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likely to disappear in the autumn, whereas immatures did so later in the winter. Most adults died either in the breeding areas or on migration, with a maximum of only 3.2% dying per year on the Exe (Goss-Custard & Durell 1984). This low winter mortality may be partly due to the Exe experiencing milder winters than most areas of Britain.

A greater proportion of juvenile turnstones disappeared from the Ardrossan area soon after ringing than did adults. This implies that either they suffer increased mortality, or that they may pass through a period of vagility before adopting the non-breeding range that is then usually maintained for the rest of their life. A similar tendency for juveniles to have a higher disappearance rate than adults has been found on the Tees, where over a given period the annual return rate was 90% for adults, but only 77% for juveniles (though the juvenile sample size was small) (Evans & Pienkowski in press). Tentative support for the hypothesis of increased juvenile mobility comes from the studies of the population on the Wash. Branson et al. (1978) found that the percentage of juveniles in samples of the population obtained in cannon-net catches at high water roosts drops in most years to near zero in midwinter, before increasing in the spring.

There are reasons for expecting differences between juveniles and adults in both movement patterns and survival rates. Groves (1978) found that juvenile turnstones at a staging post on their first autumn migration had lower foraging rates than adults, and were frequently involved in aggressive encounters with adults, in which they were consistently the losers. She attributed the differences mostly to juvenile inexperience, both in foraging and in the interpretation of signals from conspecifics that would have reduced the likelihood of their being attacked. Age-related differences in

foraging behaviour have been documented in other species (e.g. Burger 1980, Goss-Custard & Durell 1983, Greig et al. 1983); in all cases juveniles on average appear to be less efficient and hence at a possible selective disadvantage compared to adults.

This disadvantage will lead to their being more affected by an increase in selection pressure. If, for instance, conditions deteriorate so that birds find it increasingly difficult to meet their daily energy requirements (due, perhaps, to a decrease in food availablility or an increase in required intake), juveniles will tend to be affected before adults. They will therefore be the first to fall to the threshold below which birds will starve if they remain in the same location; they may therefore move in the hope of finding better conditions elsewhere. This may explain the movement of juveniles away from the Wash in mid-winter (the time of greatest energy demand and shortest daylight foraging period). There is some evidence of between-estuary movements at the onset of hard weather in other species (Clark 1982, Townshend 1982).

It is possible that the absence of juveniles from high tide roosts at the Wash is due not to their having moved away, but to their greater tendency to carry on foraging over the high water period. Brearey (1982) found that the proportion of juvenile turnstones present at roosts on the Tees was lower than that in the population as a whole, and studies on other waders have shown that birds will extend their time spent foraging into the high tide period in periods of increased stress (Heppleston 1971, Goss-Custard et al. 1977). Goss-Custard & Durell (1983) were able to link the greater tendency for juvenile oystercatchers on the Exe estuary to feed over high tide to their inability (through inexperience or competition) to feed on the preferred diet of adults. That this high tide feeding may

be crucial to the survival of the birds was demonstrated by Heppleston (1971), studying oystercatchers on the Ythan estuary (N.E.Scotland). He found that a period of three weeks of snow cover, which prevented birds from feeding in the fields at high water, caused the death of at least 25% of the population, with juveniles making a disproportionate contribution to the mortality.

However, in the turnstone these may only be general trends, and it is evident that many juveniles become established in the stable wintering population. Those juveniles that were classified as residents appeared to have similar sizes of home range (Chapter 3) and similar return rates as resident adults, and they were not noticeably subordinate to adults in aggressive encounters (Chapter 4). It is possible that in many individuals the learning process is rapid so that the inefficiencies recorded in early autumn by Groves (1978) are no longer apparent by the time the juveniles are a few months older. The process appears to be more prolonged in oystercatchers; the period of specialisation of diet and foraging behaviour may last four years (Goss-Custard & Durell 1983), which may account for the greater delay in sexual maturity in this species (birds first breeding after four years, as opposed to two in the turnstone).

As fieldwork did not commence each season until after the major influx of return migrants (which occurs in late July and August (Evans 1966, Marshall 1981)), no data were collected on the timing of arrival of individual birds. However spring migration was studied in detail; the results demonstrate that while the majority of birds depart within a short period in late spring, some birds consistently leave up to three months earlier. Ringing recoveries from birds marked on the Wash in winter have shown that some birds move west and northwards in Britain in the early spring (Branson et al. 1978).

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Similarly a bird colour-ringed on the Tees and present there until March had moved to the west coast by early April. It seems unlikely that these early 'migrants' actually depart from Britain until the main exodus in late spring, as there is no evidence from captures made in the spring in various parts of Britain that any birds put on the fat reserves necessary for the 1000km flight to Iceland (the first stage in the migration) until late April (Branson et al. 1979, Clapham 1979, Ferns 1981). It would therefore appear that some birds may include an extra stage in their annual cycle of movements, in that they move in early spring to areas further north or west, in which they put on the fat reserves required for the migration proper.

Brearey (1982) found that birds may be faithful to these migration stop-over points as well as their main wintering areas. Turnstones caught and colour-ringed on the Tees in early May while on migration were subsequently seen there in both the early autumn and late spring of the following season, indicating that their main wintering area was further south, and that the Tees was used on both northward and southward migrations.

There appear to be regional differences in the extent to which wintering areas are used by birds on passage. Turnstones take three weeks to build up the fat reserves required for the northward migration from Britain (Clapham 1979). The same period of weight gain was also found for birds fattening up on the Pribilof islands before migrating a similar distance (Thompson 1973). If birds that wintered further south were to use an area as the major stopping-off point at which to fatten up prior to the main migration one would expect them to be present by late April. A study carried out by Moser & Carrier (1983) on the population turnover on the Solway estuary (100km south of Ardrossan) in the spring of 1983 showed that the turnstone

population increased markedly in numbers in mid-April, with the peak count on May 9th being three times the wintering population size. Dye-marking showed that there had been no additional immigration after April 30th, and virtually all the birds had departed eight days later (the timing of final departure therefore being almost simultaneous with the Ardrossan population).

In contrast, the monitoring of the proportion of birds colour-ringed showed that very few immigrants were present in the Ardrossan area until early May (by which time the total number of birds present was declining). Similarly, from analyses of the proportions of birds that were already ringed, Clapham (1979) found that samples of birds caught at Morecambe Bay up until early May contained negligible proportions of immigrants, whereas a catch on 26th May, at the end of migration, was very largely composed of birds that had wintered elsewhere. The Solway thus appeared to be an area used by some migrant turnstones for the whole period of premigratory fattening, whereas the role of Ardrossan (and possibly Morecambe Bay) was as a temporary feeding site used by relatively small numbers of birds late in their migration northwards (as indicated by the lack of a spring peak in numbers and the very late and short-lived influx which occurred as the last winter residents were themselves departing).

In May 1983 certain parts of the study area contained immigrant birds while other areas did not. It is unlikely that this local variation was caused by passage birds selecting areas on the basis of their food supply, as the resident population (which would have far greater experience of local food distribution) showed no sign of selecting the same areas - the number of birds at Coalruffie (which, when censused, contained no immigrants) was as high in early May (when the total population size had decreased) as during the rest of the winter. As turnstones migrate in flocks (Bent 1929, p.279), the

situation may simply be that small flocks moving northwards up the coast stop off to feed opportunistically for perhaps only a matter of hours before continuing north; their dispersion at these sites is thus very patchy.

The cause of the earlier spring migration in 1984 is unclear; there is some evidence that this was not restricted to the Ardrossan area, as the pasage of waders through the Solway was also earlier in 1984 than in 1983 (M.Moser, pers.comm.). It is possible that the exceptional period of warm weather in Britain in the spring of 1984 hastened their departure.

2.4 The Purple Sandpiper Population

As only eight birds were colour-marked in this study, comparative data for the purple sandpiper are rather limited. However, those comparisons that can be made give interesting if tentative results.

2.4.1 The Frequency of Resighting Marked Birds

The turnstone categorisations (see section 2.1.1) were applied, except that the first observation day each autumn was taken as the first day of fieldwork in November (or the day of first sighting if earlier), as many purple sandpipers did not arrive until late autumn each year (see later). Five purple sandpipers were subsequently classified as residents, and three as visitants. The residents were seen on 25.0 - 55.6 % of observation days (mean 38.4 $\pm$ 5.23), which is significantly less than the resighting rate of resident turnstones (Mann Whitney U = 3462, $n_1 = 79$, $n_2 = 5$, P < 0.05). This lower rate of seeing marked purple sandpipers was probably due to a combination of three factors. Firstly, two of the resident birds were not first seen in the winter until early December, and so may well not have been present throughout November. A second point is that purple

sandpipers had a greater tendency to feed on the more exposed
offshore rocks, including some that could not be seen adequately from
a mainland vantage position. Hence there was probably a greater
likelihood of their escaping detection than turnstones. However it is
also possible that the resident purple sandpipers moved out of the
study area more frequently than did resident turnstones. Although
colour-ringed birds were most likely to be seen in the vicinity of
the place of capture within the study area (Table 2.4), there were
greater fluctuations in the number of purple sandpipers present (see
later), indicating that many birds were not in the study area
throughout the whole of the winter.

Table 2.4 The percentage of purple sandpipers in different sections
of the study area that were originally marked at North Rocks and
North Beach

Place of Marking	North Beach		North Rocks	
Place of Sighting	% Marked	(n)*	% Marked	(n)*
North Beach	10.0	(90)	0.0	(35)
McCrindles	1.3	(80)	8.9	(45)
North Rocks	0.4	(957)	8.4	(632)
South Rocks	0.0	(97)	0.0	(46)
Saltcoats	0.2	(650)	2.7	(557)
Coalruffie	0.1	(983)	0.8	(740)
Stevenston	0.0	(212)	0.0	(106)

*The sample sizes are not the same, as the two samples were caught at
different times.

2.4.2 Survival Rates

The sample size is too small to consider only resident birds;
consequently survival has been measured as the proportion of birds
known to be alive a year after the date of capture (and each year
subsequent to that). The rough estimate obtained in this way for
adult purple sandpiper annual survival is 80 % (n = 10 bird years).

2.4.3 The Timing of Migration, and Population Changes

Although a few purple sandpipers were seen in September, the main influx did not occur until later in the autumn. If the two North Beach birds are discounted in the final year (as coverage was incomplete in that area during that period), three birds were first seen in October, two in December, one in January and one in March. The two birds first seen in December were the two seen most regularly thereafter, and so were unlikely to have been present but not seen much earlier in the autumn. Most of the marked birds remained in the study area until late spring; for instance, five out of eight were seen on or after 5th May in 1983.

Population counts showed very much greater fluctuations for purple sandpipers than for turnstones. The frequency distributions of the number of purple sandpipers and turnstones seen at Coalruffie are given in Figure 2.8. While the turnstone counts vary according to an approximately normal distribution, ranging from 7 to 32 birds (discounting one occasion when no birds were present), the purple sandpiper population was far more variable, with a peak count of 98 yet five or fewer birds present on approximately 50 % of occasions. Similar variation was apparent in other parts of the study area. Therefore it was not possible to estimate the total study population from the averages of counts made in different parts of the study area, as these were so variable. However, a rough indication of the size of the population is given in Table 2.5, which shows the maximum number of purple sandpipers seen in one day in the study area for each month throughout the period of study. These totals will tend to be underestimates, due to the practical problems mentioned earlier of ensuring complete coverage of offshore rock outcrops in some areas. However, it is evident that there was a general tendency for the purple sandpiper population to increase towards the middle to late

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Fig.2.8. Frequency distributions of the numbers of (a) turnstones (n=54 counts) and (b) purple sandpipers (n=67 counts) present during the exposure period at Coalruffie. Counts are excluded when neither species was present; turnstone counts after 1st April, and purple sandpiper counts after 10th May, are excluded each year, due to the lowered population sizes resulting from spring migration.

(a)

(b)
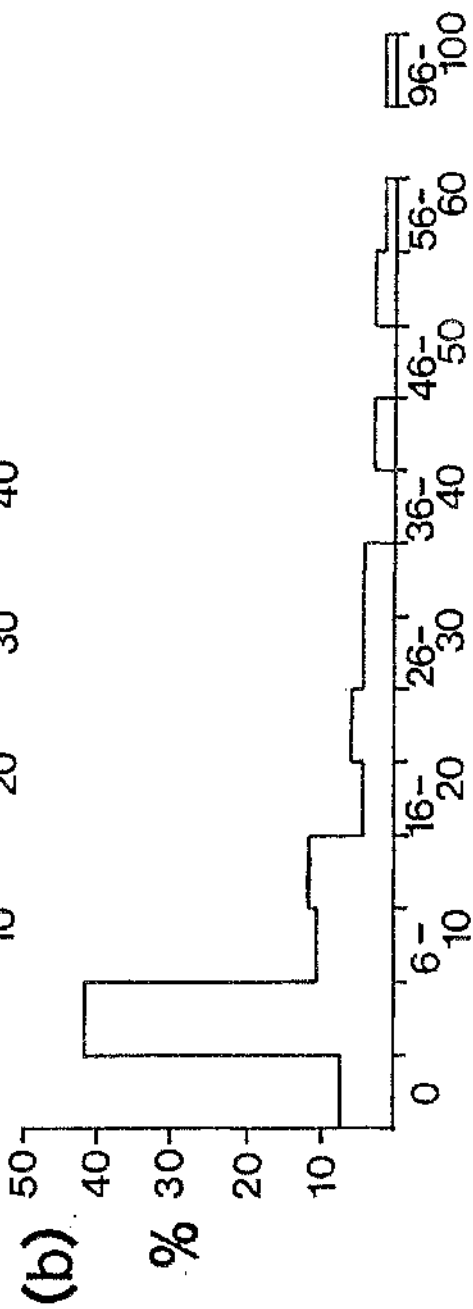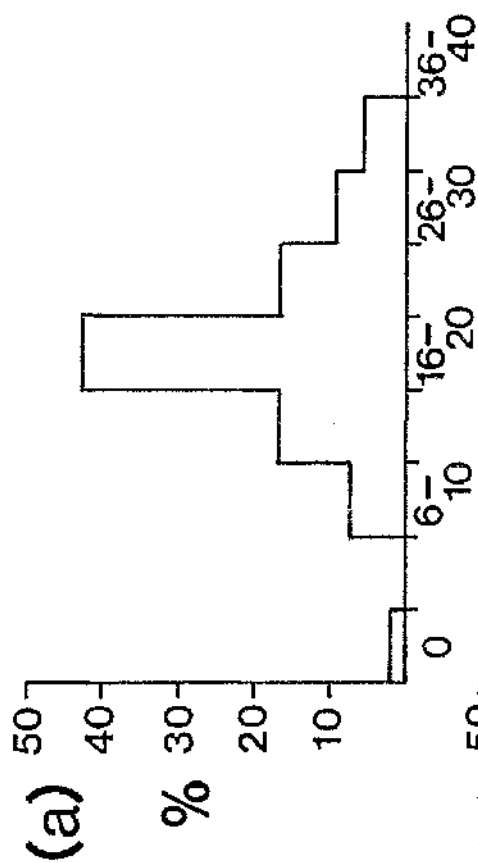
NUMBER OF BIRDS PRESENT

winter, with peak counts occurring after February in all three years. Nonetheless there was still considerable day-to-day variation in numbers even when this seasonal trend is taken into consideration. For instance, between January and April 1983 there were six counts of over 40 birds at Coalruffie, six of less than 5, and only two counts between these extremes.

Table 2.5 Maximum daily counts of purple sandpipers in the study area for each winter month of the study

Month	1981/82	1982/83	1983/84
September	–	2	–
October	10	52	9
November	41	38	27
December	18	14	38
January	32	100	41
February	33	69	43
March	67	118	35
April	78	58	65
May	92	56	36

2.4.4 Discussion

The timing of autumn arrival of purple sandpipers on the coastlines of Europe appears to depend on the location of the breeding grounds. Atkinson et al (1981) showed that birds wintering in south-eastern Scotland were largely of Norwegian origin, and the first birds arrived back in the wintering quarters in July. In contrast, Boere et al. (1984) found that, while some small birds (from Norway or Greenland) were present in Holland in early autumn, the majority of the population (thought to be of Canadian or Russian origin) did not arrive until November. A November arrival was also noted for birds wintering in eastern England (Feare 1966) and in the Outer Hebrides (Buxton et al. in press). The late timing of arrival therefore suggests that the majority of birds wintering at Ardrossan were not of Scandinavian origin. Further circumstantial evidence for this

comes from the biometrics of the eight colour-ringed adults; bill-lengths of these birds ranged from 28-36 mm, which indicates that they were more likely to belong to the breeding populations of Iceland and Canada than to that of Norway (Atkinson et al. 1981, Anon. 1984, Buxton et al. in press).

Although the estimate of annual survival/return rate produced by this study can only be regarded as very tentative, it is apparent that purple sandpipers may be quite long-lived for their size. There have been no other published estimates of survival; the oldest bird recorded from ringing recoveries was over 8 years old (Cramp & Simmons 1982), though this is undoubtedly an underestimate of maximum longevity, as so few have been ringed. Their high survival rate may be partly due to their being (like turnstones) relatively unaffected by cold weather. They are the most northerly wintering waders in the world (Cramp & Simmons 1982), and Britain is, in fact, towards the southern limit of their wintering range.

However, while both this study and that of Atkinson et al. (1981) have shown that many individuals return to the same general stretch of coastline each winter, they are not as restricted in their movements as turnstones. Atkinson et al. (1981) found that, although the majority of sightings of marked birds were at the site of marking, some birds moved over 20 km within a season. There is some evidence that purple sandpipers may become more mobile late in the winter; Feare (1966) found that his study population did not always frequent their early winter localities after mid-January, and birds caught on Vlieland (in the Dutch Waddensea) in spring were less likely to be subsequently retrapped there than those caught earlier in the winter (Boere et al. 1984). Late-winter short distance movements may explain why the time of peak population size over the

winter varied between sites in eastern Scotland, the greatest numbers being found in October at some localities but as late as March elsewhere (Atkinson et al. 1981). The great day-to-day variation in the numbers of purple sandpipers present at Coalruffie demonstrates that not only must the majority of individual birds utilise several feeding areas, but that they also move between them as a coordinated group. Despite this variation, colour-marked birds showed great fidelity to the area in which they were caught. The majority were caught early in the winter, and it is possible that the earliest birds to arrive show greater site-fidelity than those which appear from January onwards.

It would appear that the spring migration is as synchronised in purple sandpipers as in turnstones. While the maximum counts for May showed little decline from peak winter levels, numbers had dropped dramatically by the last day of fieldwork each year (e.g. from 92 to 13 birds by 19/5/82; from 36 to 6 by 16/5/84), and both Atkinson et al. (1981) and Boere et al. (1984) found that all birds had departed from eastern Scotland and Holland respectively by June.

In summary, this chapter has shown that the turnstone population was largely sedentary throughout the wintering period. The majority of the birds were seen regularly in the study area; those seen infrequently are thought to have had home ranges on the stretches of coast bordering the main study area. Although some birds left the area in early spring, the majority remained until the time of migration in late spring, and there was little evidence of population turnover until this time. The population structure was therefore more or less stable (with approximately 230 birds present in the study area) from October through to late April each year. Juveniles had a higher tendency to disappear than adults, but those

birds that became established as residents showed high site fidelity in subsequent years. This, coupled with high adult survival rates, meant that, on average, a bird surviving its first year would return to the same stretch of coast for a further six years.

The purple sandpiper population, in contrast, was slightly more fluid in composition, with evidence of birds moving into the area in late winter. Birds were also less predictable in their movements within the study area, although the small number of birds that were marked were more often seen at the site of capture than in other areas. These birds were also site-faithful in subsequent years; a rough estimate of 80 % of adult purple sandpipers present one year returned the next.

It has been shown in the previous chapter that the population of turnstones in the study area was very stable, in that negligible immigration or emigration occurred between October and late April each year, and population turnover from year to year was very low. The population size was also estimated to be approximately 230 birds within the study area. However, no indication was given of the degree of mixing of the population. Did each bird use the whole of the study area, mixing with all others, or were there limits to both individual associations and use of space? This point has clear implications for the subtlety of the social interactions in turnstones: the occurence of dominance through individual recognition, or of reciprocal altruism, is far less likely in a homogenous population of 230 than if that population is divided into ten groups which seldom mix. While hierarchies have been demonstrated in captive turnstones (Marshall 1981), laboratory studies of inter-individual relationships within small confined groups may indicate levels of interaction which simply do not exist in the wild due to the far greater fluidity of associations (Myers 1983).

There are two forms of assortative association between individuals in a population. The first is due to differential use of space; i.e. the association between two individuals is related to the extent of overlap of their home ranges. For example, Roell (1978) found that the frequency with which breeding jackdaws Corvus monedula were seen feeding together depended on the proximity of their nests. However, there may be a second, higher, level of association, as some pairings may be observed significantly more or less often than would be expected after correction for the amount of range overlap. In other words, there may be affiliation or avoidance between certain

individuals that use the same area. Examples of affiliation are persistent pair or family bonds, as found for instance in wintering Canada geese _Branta canadensis_ (Raveling 1969); conversely, subordinate mallard ducks _Anas platyrhynchus_ may avoid being in the same group as dominants, as dominants can outcompete them for food (Harper 1982).

Analysis of the first of these forms of non-random association would answer the question: with how many individuals does a turnstone regularly flock? However, the second is also worthy of investigation, since it is possible that populations as stable as those of wintering turnstones may move in flocks that are more than just random aggregations of the individuals present in one area.

The separate question then arises as to whether the flocks themselves are stable in composition. It is possible for individuals to be restricted in the number of birds with which they flock, yet for flocks to be continually changing in composition. The situation is best explained with reference to the position of individual home ranges. In gregarious species, home ranges may overlap either randomly or non-randomly with each other. In the latter case, the most common situation is for a group of individuals to have extremely similar home ranges; there is thus a 'group home range', which has little if any overlap with the collective home ranges of adjacent groups. All members of a group will therefore only flock with other group members, and the composition of a flock within a group home range is not site-dependent. In contrast, if ranges are positioned randomly with respect to each other, each bird will have a unique subset of individuals from the population with which it will flock, and the pool of individuals a bird can flock with at one end of its range is not the same as the equivalent pool at the other end. Therefore a flock will change in composition as it moves across

different individual home ranges.

This chapter therefore looks at the ranging behaviour of individual turnstones, to determine how great an area the average turnstone utilises and whether there is seasonal variation in its range use. The associations between individual turnstones are also examined, and their temporal stability, both in the short term (over the tidal cycle) and the long term (over the winter) is assessd. These two aspects are then combined, to determine the relationship between the home range overlap of a pair of birds and their association. This then allows analysis of the secondary form of association (the differential associations that occur once use of space has been taken into consideration) and the extent to which turnstones form discrete groups while on their wintering grounds.

3.1 Methods

3.1.1 A Rationale for the Method of Home Range Determination

Most methods of home range determination have been developed for use upon small mammals. As a consequence, the majority of techniques (including all those based on trapping grids) were inappropriate in this situation, as they mostly made assumptions that were not satisfied. In particular, the method to be employed had to take account of the facts that (1) the functional home ranges of the turnstones were likely to be discontinuous, as areas of suitable habitat were separated by stretches of sea, promenade, dockland and so on, and (2) individual birds were almost always found feeding within an area only a few hundred metres in diameter, yet they might fly up to 5 km to a roost each high tide; there was therefore a possibility that they would occasionally be seen en route, well outside their normal feeding home range. Thus, a method such as the Maximum Polygon (Sanderson 1966), which uses the most extreme

sightings to determine the home range boundary, is clearly inappropriate, since only a single aberrant sighting might produce anything up to a ten-fold increase in home range size.

A more suitable choice would therefore be a probabilistic technique, which would estimate the area within which a bird spent, for instance, 90% of its time. However, such methods as the probability circle and probability ellipse (reviewed in Sanderson (1966) and Van Winkle (1975)), have the disadvantages that they are still greatly affected by extreme locations in range and are over-sensitive (such that any new sightings, even within the previously-calculated home range, would cause changes in its boundaries). They also do not allow for a discontinuous home range, and impose a pre-determined geometrical shape on the distribution of sightings. While this may be adequate for some comparative purposes, the shape may have little biological justification, and cannot reliably be used to determine the home range overlap of two individuals.

However, there is one technique that overcomes many of these obstacles. It is based on harmonic, rather than arithmetic, means, and has been termed the Harmonic Mean Measure of home range (Dixon & Chapman 1980). Use of harmonic means makes it relatively insensitive both to the location of extreme points and to further sightings within the main home range. The technique also allows the range to be composed of several discontinuous patches, which can be of any shape. Furthermore, the location calculated to have the highest probability of containing the animal (the 'centre of activity' (Hayne 1949)) must be positioned <u>within</u> a region of observed activity. (In contrast, arithmetic mean methods may generate a 'centre' of activity that is <u>between</u> two patches of activity).

The method uses a grid, superimposed over a map of all

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observations of an individual. For each intersection (j) of the grid, the reciprocal mean distance deviation (D_j) (Neft 1966) to the observations is calculated as:

$$D_j = \cfrac{1}{\cfrac{1}{N}\sum_{x=1}^{N}\cfrac{1}{R_{jx}}} \qquad (1)$$

where N = number of observations

R_{jx} = distance from intersection j to point x.

Calculating D_j for each intersection of the grid produces an array of values; the magnitude of D_j increases outwards from each cluster of observations, and the minimum value of D_j gives the centre of activity. Isopleths can then be constructed, spreading concentrically outwards from the centre of activity and from other 'hotspots'; these lines are in effect contours on a map of the spatial probability distribution of the location of the individual. If the home range is defined as the space within which the animal spends 90% of its time, then the range area can be found by constructing successive isopleths out from each hotspot until just 90% of the observations fall within the enclosed area. The location of isopleths is more or less independent of grid size, as their position can be approximated by interpolation between adjacent intersections. Further explanation of the technique is given in Chapman & Dixon (1980).

3.1.2 The Specific Procedure for Home Range Determination

The basis for the loci of individual birds were the sightings recorded on maps as described in Chapter 1. To ensure some independence of the data points, a minimum period of one hour had to elapse between successive sightings of a bird, and no more than three sightings of the same bird were included per day. In practise, the tidal cycle generally ensured that birds were continually on the move

and so were rarely recorded in the same position in successive hours, and my own movements between regions of the study area in the course of a day resulted in very few birds being recorded more than twice per day, usually with several hours between each sighting. In addition, sightings from the high tide period (Chapter 1) and those of roosting birds were treated separately, as few birds roosted or spent high water in the same areas in which they had foraged during the period of exposure.

Turnstones tended to be more mobile (often being seen outside their normal winter range) in the late spring. Therefore, to avoid these anomalous late spring movements biasing the estimation of range size, all sightings after 15th April each spring were omitted from the calculations of the wintering range.

The map locations of sightings of each bird not ruled out by the above constraints (i.e. all independent sightings of non-roosting birds obtained during the exposure period and before April 16th each season) were converted to Cartesian coordinates, by superimposing a transparent grid composed of 100x100m squares over the maps of flock locations. The entire study site could thus be mapped as a grid of 20 by 70 such squares, the longer axis (of 7km) running along the coastline. Sightings were mapped to the nearest 10m; while this may imply undue accuracy, the technique used to determine the range size is, as previously explained, relatively insensitive to the precise location of any one point, and so it is assumed that any slight errors in the recording of locations of points will tend to cancel each other out and have a negligible effect on range determination. One constraint with the method is that no sighting must be too close to a grid intersection (as the value of D_j tends towards zero for increasingly small values of R_{jx} (Chapman & Dixon 1980)); therefore all sightings were recorded as being at least a tenth of a grid

square (i.e. 10m) away from any intersection.

A computer program was used to calculate values for D_j for each set of sightings coordinates. Home range areas were measured electronically, using a cursor to trace around scale drawings of range boundaries on a Summagraphics graphic digitiser linked to a Commodore Pet microcomputer.

Surveys of habitat usage showed that only 0.6% of all sightings of turnstones were on sand during the exposure period, despite its prevalence as the most extensive habitat (Chapter 1). Therefore any areas of sand enclosed within the boundaries of an exposure period home range were omitted from calculations of its area, as were areas of sea below the mean spring low water mark and ground above the mean spring high water mark. Other habitats that were used infrequently (such as rock pools) covered relatively insignificant fractions of the total area (Chapter 1).

With most techniques of measuring home range size, the estimated range initially increases in size with the number of observations obtained, although it may reach a stable plateau once a threshold number of observations is reached. To examine the effect of the number of sightings on the harmonic mean estimation of home range size, a test was therefore carried out using a sample of ten birds seen over 30 times. For each of these birds, the home range (90% isopleth) was successively calculated on the basis of the first 5, 9, 13, 17, 21 and 25 sightings, and the results compared to the estimation produced by 30 sightings. The results showed that, while on average the estimation given after 9 sightings was very close to that given by 30, there was a great deal of individual variation about this mean (Fig.3.1). However, by 21 sightings the variance had reduced, and the addition of a further nine loci changed the

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Fig.3.1. The estimated home range area as a function of the number of sightings used in its calculation, expressed as a percentage (mean of 10 birds ± S.E.) of the area calculated using thirty sightings.
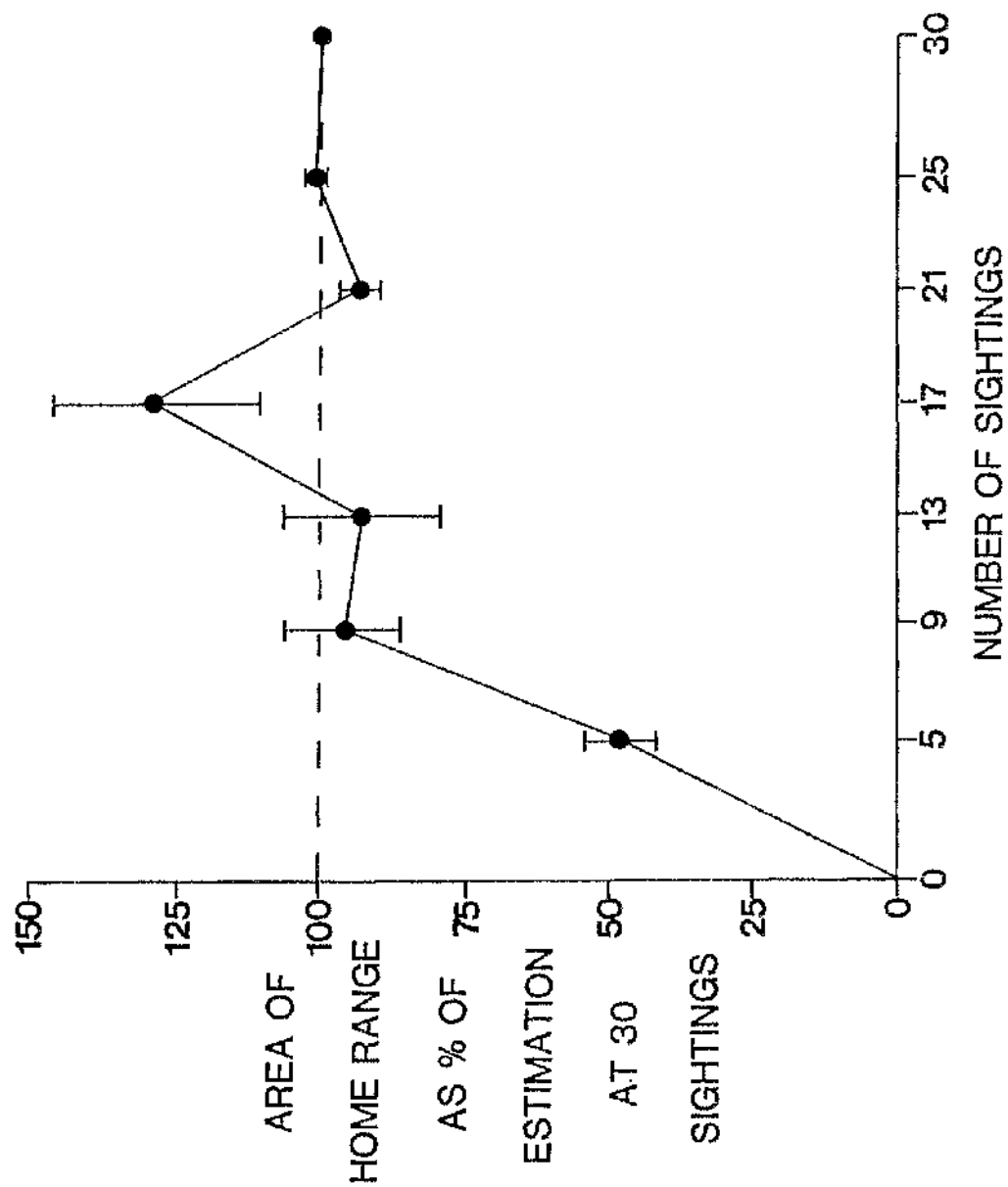
estimation very little. In fact, for the most frequently seen bird, a further 51 sightings resulted in a change in range size of only -0.4% of the home range calculated after 21 sightings. In addition, the centre of activity for the sample of ten birds shifted a maximum of 500m between the 9th and 30th sighting, and in all but one case this shift was less than 200m.

This test therefore showed that the estimate of home range size changed little with increasing number of sightings above a minimum of around 20, which proved that (a) above this minimum the method produced estimates of range size that were not biased by sample size, and (b) individual turnstones maintained the same ranges over long time periods (the period of data collection being over two years in some cases). Therefore exposure period home ranges were calculated for all birds with at least 20 appropriate sightings.

Most birds spent the period of high water on (the inaccessible) Horse Island. However, those birds that foraged on North Beach during the exposure period were also often found there at high tide, feeding on amphipods and dipterans in the sand and accumulations of dead wrack. It was therefore possible to calculate the high water home ranges of such birds. As fewer sightings were made at high water than during the exposure period (due to its shorter duration), the criterion for inclusion was relaxed to a minimum of 16 per bird, with the additional constraint that each bird had to have been seen on at least 60% of the visits I made to North Beach at high tide while it was alive.

High water ranges were determined using the same procedure as for the exposure period, except that areas of sand were included in the range, as this habitat was used to a greater extent over high water (Chapter 1). The upper and lower shore limits to ranges were defined as 25 m above and 50 m below the mean spring high water mark

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respectively.

To allow comparison between the location of home ranges of two birds (A and B) and the extent of association between them, an index of the degree of overlap of their home ranges was developed. This was defined as:

$$R_{AB} = \frac{c}{(a+b+c)} \qquad (2)$$

where a = area of A's home range that does not overlap with B

b = area of B's home range that does not overlap with A

c = area of overlap of ranges of A and B.

The index, an adaptation of Jaccard's Coefficient of Association (Janson & Vegelius 1981), is therefore the proportion of the overall area covered by the two birds that overlaps; it thus varies between zero (no overlap) and one (ranges identical and completely overlapping). Although this indicates the extent to which birds used the same area, it is not equivalent to an index of the random expectation of their being seen together, as it takes no account of the size of the ranges in question; a pair of birds moving at random within closely overlapping, but large, ranges would less often be in close proximity to each other than if those ranges were much more restricted. Therefore the coefficient of range overlap was corrected for range size by dividing by the overall range area of the pair (measured in hectares):

$$\text{Corrected } R_{AB} = \frac{R_{AB}}{(a+b+c)} \times 10 \qquad (3)$$

The ten-fold multiplication factor was used to make values of the corrected index the same order of magnitude as those of the association index (see later). Although in theory there is no upper limit to the value of the index shown in equation (3), in practice

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the smallest home ranges were of the order of 2 ha, so that a maximum value in this situation (corresponding to two very small and completely overlapping home ranges) would be five.

3.1.3 The Measurement of Association Between Birds

The level of association adopted was whether or not a pair of birds were together in the same flock (as defined in Chapter 1). In the majority of cases this was clear-cut, as the identity of every marked flock-member was recorded. However, there were many occasions when this was not so, due to factors such as the flock taking flight before I had completed the check of colour-rings. Such instances, when I could not be sure that the two birds were not in the same flock, were discounted, unless the birds in question were seen in two different flocks within an hour. A minimum period of two hours had to elapse between successive recordings of a pair's association, to ensure some independence in the data. Jaccard's Coefficient was used as the index of association, as this is one of the best measures of coexistence (Janson & Vegelius 1981), and makes this study compatible with those of Ekman (1979) and Myers (1983). Jaccard's coefficient of association of birds A and B (A_{AB}) is defined as:

$$A_{AB} = \frac{c}{(a+b+c)} \qquad (4)$$

where a = number of sightings of A alone

b = number of sightings of B alone

c = number of sightings of A and B together.

As with the analagous coefficient of range overlap R_{AB} (equation 2), the value of A_{AB} ranges from zero (pair never seen in the same flock) to one (always seen in the same flock). The coefficient was calculated for different period of the tide and different times of year as appropriate (e.g. to compare between associations during the exposure period and at high tide, or between winter and spring). The

association between two birds was measured only up until the spring departure of the earlier migrant of the pair each year, or until the disappearance of one of them; this avoided measuring a 'lack of association' when in fact only one member of the pair was present. Each analysis was carried out on a sample of birds (see below), and a value of A_{AB} determined for all possible pairs of birds for each period in question; the result was a one-sided similarity matrix (Morgan et al. 1976). The sum of (a+b+c) was at least 10 (and often over 30) for all coefficients in each matrix. The matrix was then submitted to one or more of the following statistical procedures for data simplification and representation:

(1) Single Linkage Cluster Analysis (SLCA). Cluster analysis is a technique which determines how readily the data fall into groups ('clusters') of birds that were found together. Full details of the procedure can be found elsewhere (e.g. Morgan et al. 1976; Roell 1978). The relevant points to be noted here are that SLCA is hierarchical (i.e. birds placed in the same cluster at one level of association will be in the same one at a lower level), a bird cannot be in two clusters at once, and that the output of a SLCA analysis can be represented as a dendrogram. SLCA has been used to test whether the birds formed separate distinct sub-populations. Since SLCA is less stringent in its cluster formation than many other clustering techniques (in that it requires a lower average association between individuals placed in the same cluster (de Ghett 1978)), a failure to produce tight clusters would indicate that the turnstone population was not made up of such groups of fixed composition.

(2) The Sibson-Jardine B(2) Clustering Method. This is a more flexible clustering algorithm, as it allows a bird to be in more than

one cluster at the same time, and is thus non-hierarchical (Morgan et al. 1976). Therefore it was used (in conjunction with multi-dimensional scaling - see below) as an alternative to SLCA when the latter produced results which indicated that the sample of birds did not fall into tight clusters. The results of a B(2) analysis cannot be represented as a dendrogram because of the presence of overlapping clusters.

Both clustering methods were run using programs from the CLUSTAN computer package (Wishart 1978).

(3) <u>Multi-Dimensional Scaling</u>. Multi-dimensional scaling (MDS) is a method of data representation which places each data point (i.e. bird) at a particular locus in an n-dimensional space, so that the interpoint distances correspond to the dissimilarity of the points. Thus two birds that were highly associated would be positioned close together, whereas a pair that were seldom seen together would be widely spaced. Theoretically, there is no limit to the number of dimensions used to define the locations of the points. A solution in two dimensions is obviously easiest to portray, but may be distorted (in the way that maps of the 3-dimensional Earth are distorted when drawn in two dimensions). However, the amount of distortion imposed by a 2D representation can be assessed using Kruskal's Stress Formula One (see Spence 1978). While MDS does not itself produce objective groupings, it is the best method of visualizing the groups produced by a Sibson-Jardine B(2) analysis, as it shows both the relative association of birds within a cluster, and the degree of separation between clusters.

Various types of MDS procedure exist, including both metric and non-metric algorithms. Jaccard's coefficient of association is a composite index, based on the separate presence/absence scores for each bird of the pair. Therefore a doubling of the proportion of

times bird A was seen without bird B would not necessarily lead to an exact halving of their association (as this also depends on the proportion of times B was seen without A). Thus the coefficient is not truly metric, and so non-metric methods are more appropriate, as they aim to produce a configuration whose interpoint distances are in an order that is as close as possible to the observed ordering (rather than absolute magnitude) of the dissimilarities (Spence 1978). The scaling program used was the MINISSA algorithm from the MDS(X) compute package (Lingoes & Roskam 1973).

3.2 Results

3.2.1 Turnstone Home Ranges Over The Exposure Period

An example of the distribution of sightings of one bird, and the 90% probability space of the home range subsequently calculated, is shown in Figure 3.2. The outer boundary of the range is defined as the isopleth which encloses 90% (i.e. 33 out of 36) of the sightings. Points to note are (1) that the sightings that are not included in this range are those furthest from the main body of sightings, (2) that the range is patchy, and (3) that the 'buffer zone' (between sightings and boundary) is widest for the patch containing the most sightings, indicating that the technique attaches more importance to the core patch than to the peripheral patches (which may be created or disappear with just one additional sighting). All these would seem to be biologically meaningful properties of the method of range determination.

A total of 34 birds (32 adults and 2 juveniles) met the criterion of being seen while foraging a minimum of twenty times during the exposure period between September and April 15th. There was no correlation between the estimated home range size of these birds and the number of times they were seen (r_s = 0.013, n = 34,

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Fig.3.2. The 36 exposure period foraging sightings of adult turnstone number 121, and the 90% probability space home range (shaded) calculated from these sightings by the harmonic mean method. The bird's home range was centred on Coalruffie and Salcoats (see Fig.1.1).
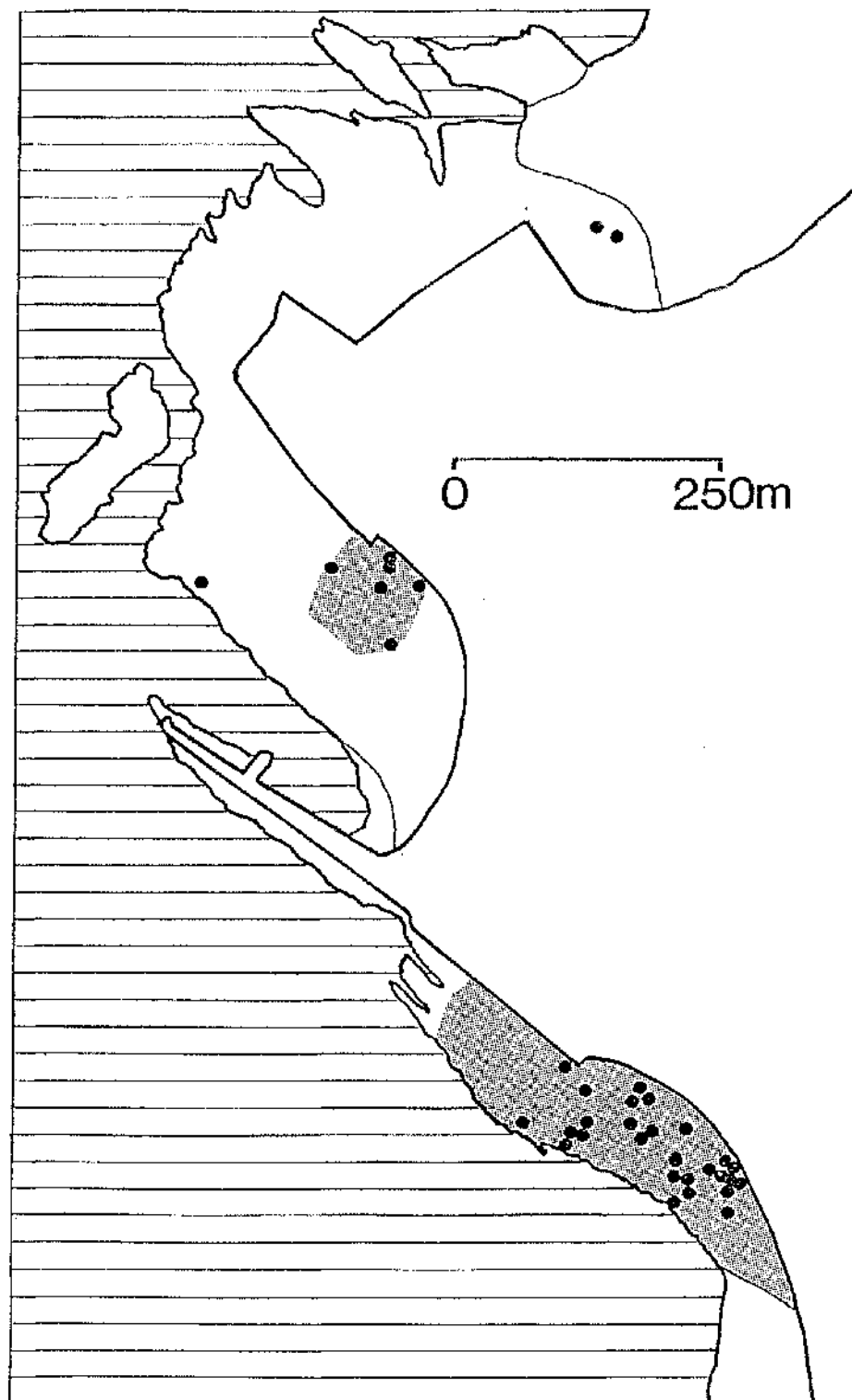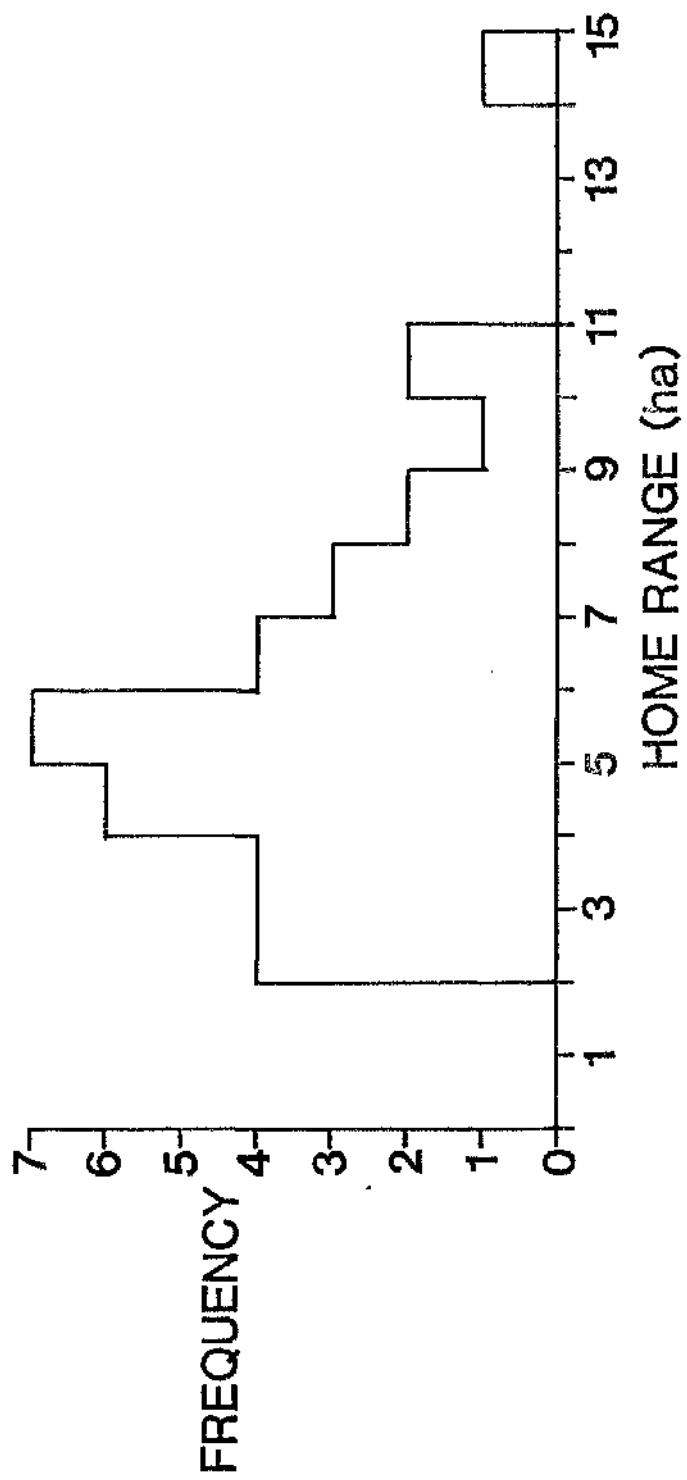
0   250m

Fig.3.3. Frequency distribution of the size of exposure period home ranges (measured in hectares) for 34 resident turnstones.

NS), nor their departure date (r_s = -0.048, n = 34, NS). The frequency distribution of home range sizes is shown in Figure 3.3; the range is from 2.7 to 14.6 ha but is positively skewed, with a median of 5.4 ha and with over 80% of birds having a range of less than 8 ha.

The bird with the largest range (010) was exceptional in that it was the only one to change its range markedly during the study. For the first three months after capture, its range and centre of activity were based on North Beach; subsequently, however, it was almost always seen at Saltcoats, regulary over the next ten months but only sporadically in the final winter. Its centre of activity thus shifted 2.1 km during the study (and possibly further, if the bird was using a third, undiscovered, range in the final year). As its range was calculated using all the sightings (so effectively combining two ranges), its large size is at least partly an artefact. If this individual is ruled out, the largest home range of a resident turnstone in the sample was 10.4 ha. The two juveniles had ranges of 5.5 and 6.4 ha, similar to the overall median value. They showed no indication of altering their range size or location between their first and second winters.

Examples of home ranges of birds in different parts of the study area are shown in Figure 3.4 (a) - (i). These demonstrate the variability between individual ranges in both location and compactness. For instance, bird 057 (Fig.3.4 (b)) spent most of its time just on North Rocks, whereas 004 (Fig 3.4 (a)) utilized this same area but also a large section of North Beach. The possibility that 057 was forced to use several areas because the quality of habitat on North Beach was too low to fully support a turnstone is made unlikely by the finding that many birds (such as 701 (a

Fig.3.4. (a) to (i) Examples of turnstone home ranges over the exposure period. (j) Examples of turnstone foraging home ranges over the high tide period. Home ranges are indicated in black, while areas of suitable, but unutilised, habitat are speckled.
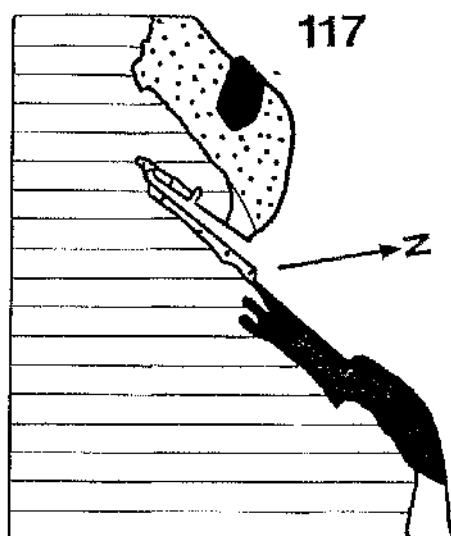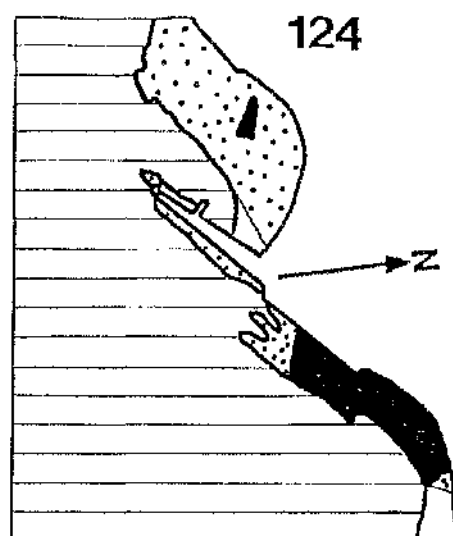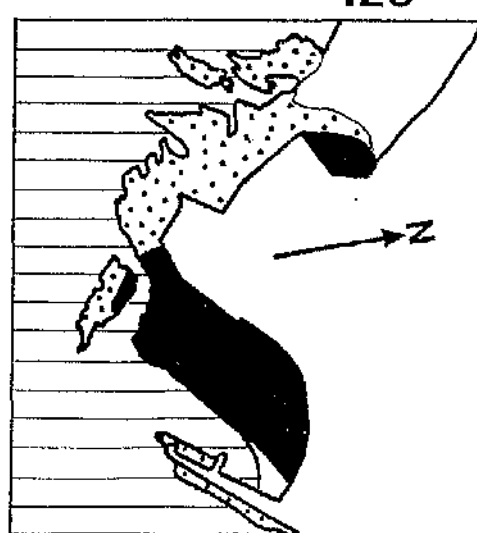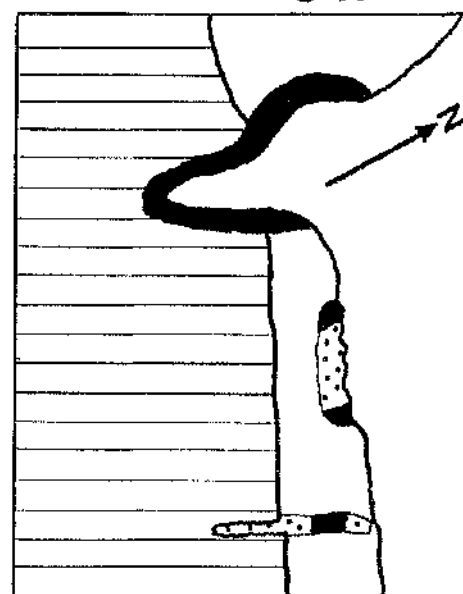
(a)

004

0   500m

(b) 057

(c) 107

N

0   500m

(d) 117

(e) 124

0   500m

(f) 126
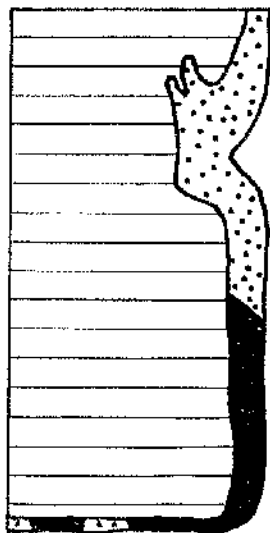
(g) 047

(h)

701

(i)

007

N
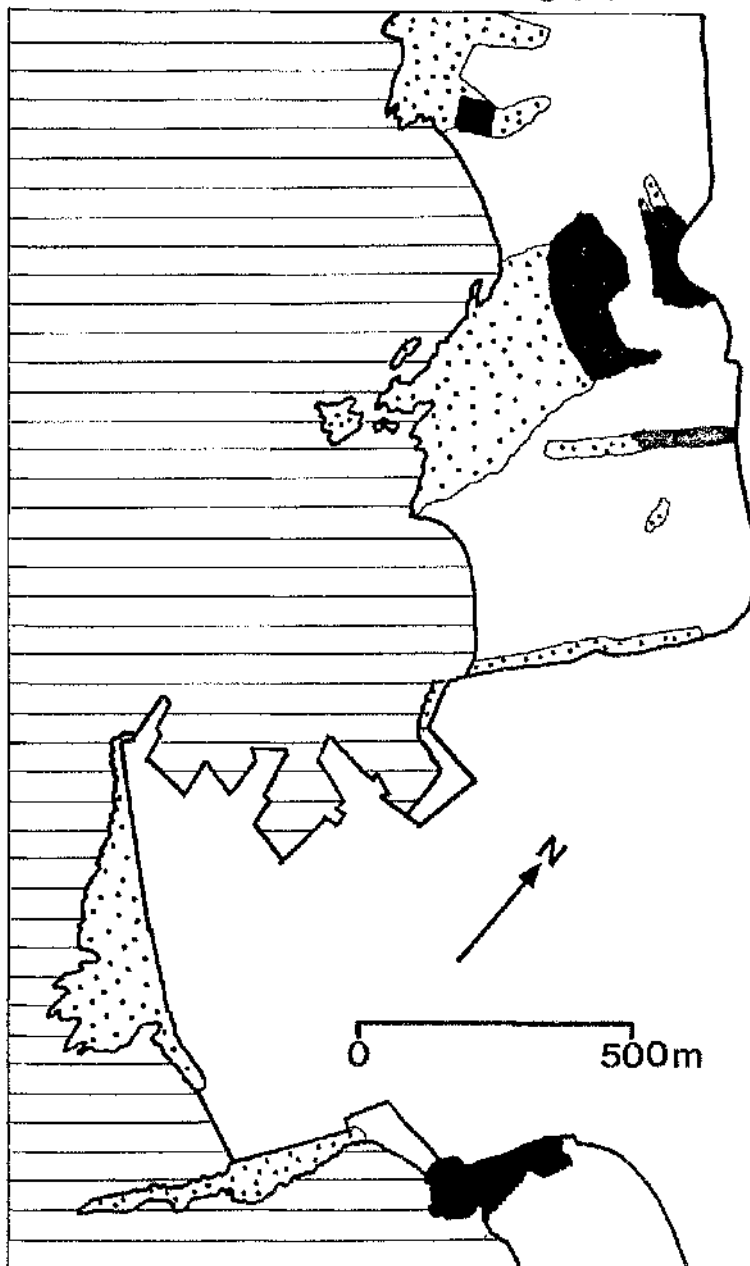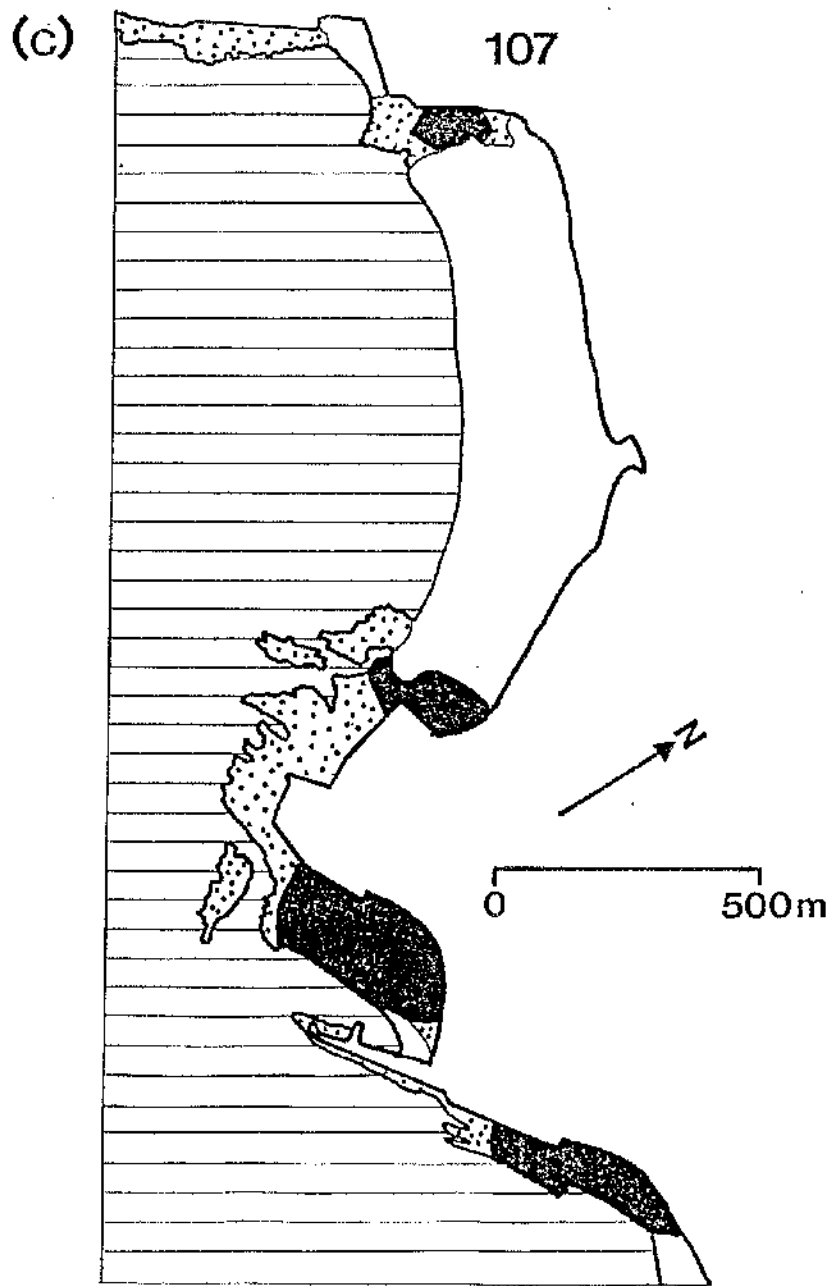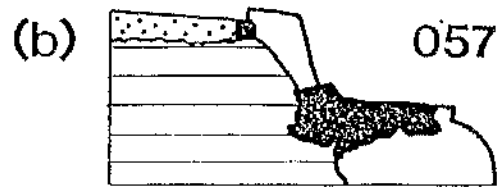
0   500m

(j)
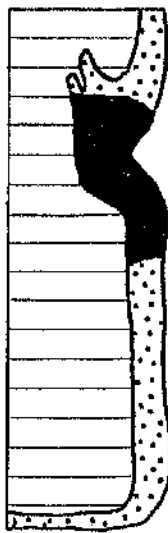
701   007   013   019

juvenile) and 007, Fig.3.4 (h) & (i)) were only ever found on North Beach. Similarily bird 124 was almost always found at Coalruffie (e), whereas 107 moved between Coalruffie, Saltcoats, South and North Rocks (c). The proportion of birds that were seen at both ends of the study area was very small; of the 494 exposure period sightings of resident birds of North Beach, only 1.4 % were at Stevenston, while only 0.2 % of 550 sightings of Stevenston residents were made at North Beach. Therefore movements of as little as 6 km were rare, both within and between winters. Some birds had remarkably similar ranges – for instance 121, 117 and 124 (Figs.3.2 and 3.4 (d) & (e) respectively). All three used Coalruffie at low water, and the remaining part of Saltcoats that was still exposed when Coalruffie was covered by water. At the higher tidal levels they would therefore come in contact with 126 (Fig.3.4 (f)), a bird which however remained in the area of Saltcoats as the tide dropped.

There is some evidence that a link exists between the size of a bird's home range and its dominance status; this will be examined in Chapter 4 with the analyses of dominance.

There were seasonal changes in the regularity with which birds were seen outside their normal home ranges. By definition, 10 % of exposure period sightings between September and April 15th were outside a bird's home range; this rose to 23.0 % (40 out of 174) in the late spring period, from April 15th until the birds had migrated to the breeding grounds (Goodness of fit test, $x^2 = 32.4$, 1 df., P < 0.001). Several of the 'aberrant' spring sightings were from the McCrindles region of the study area. By late spring, fewer birds were to be observed in other areas, and so McCrindles tended to be searched more frequently in that period than in winter (being visited on average every 2.3 days in late spring, but only every 8.4 days of fieldwork in winter). Thus the apparently greater vagrancy in spring

could have been due to my failing to search for birds at McCrindles during the rest of the year. However, no vagrant birds were seen on the visits that were made to McCrindles during the winter, and there was still a significantly greater probability of seeing a bird outside its home range in late spring even when sightings at McCrindles were excluded (Goodness of Fit, x^2 = 6.82., 1 df., P < 0.01).

Figure 3.5 shows the proportion of sightings at different periods of the winter and spring that were at least 500 m from the nearest part of a bird's home range; it is clear that many of these aberrant movements took birds well outside their normal home ranges (which were often less than 500 m in diameter). The proportion is given for late spring both with and without the inclusion of sightings made at McCrindles (no aberrant sightings were made at McCrindles during the rest of the year). There are clear seasonal trends in the extent of mobility of birds, with their being most restricted in their movements in mid-winter, and more vagile in autumn and especially late spring. In the latter period, the proportion of sightings more than 500 m from the home range is significantly greater (even excluding McCrindles data) than during mid-winter (November-mid April) (x^2 = 4.34, 1 df., P < 0.05), whereas the difference between autumn and mid-winter periods is not significant (x^2 = 1.05, 1 df., NS). There was no correlation between the number of sightings more than 500 m from a bird's home range and the size of that range (correlation including McCrindles sightings: r_s = 0.062, n = 34, NS; correlation excluding McCrindles sightings: r_s = -0.005, n = 34, NS). These movements could have been due to birds moving into the preferred areas as the density of birds in the study area decreased; however, there was no evidence for moving birds

Fig.3.5. The percentage of observations of resident turnstones that were more than 500m from their home range, during different periods of the year. The total number of observations is given adjacent to each point; the point for mid-April to May linked by the dashed line includes sightings made at McCrindles, while that linked by the solid line excludes them. See text for details.
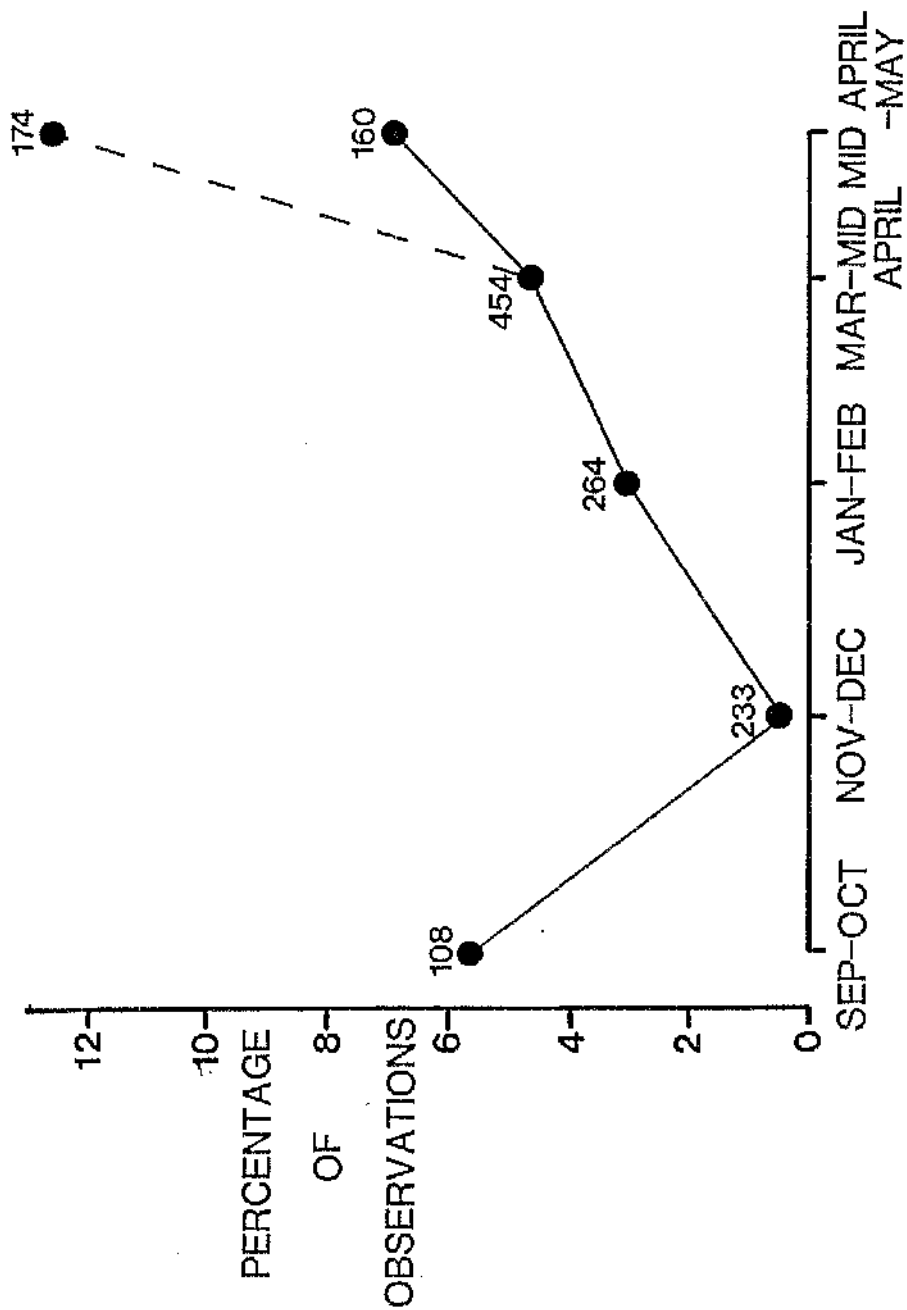
to concentrate in particular areas. For instance, five of the eleven spring sightings of birds normally resident at Stevenston that were greater than 500m from their home range were made at Coalruffie or Saltcoats, while nine out of ten such spring sightings of Coalruffie and Saltcoats residents were at Stevenston.

3.2.2 Turnstone Home Ranges over the High Tide Period

Only four birds satisfied the criteria set for determining a bird's home range — other marked North Beach birds were not seen frequently enough due to either having been marked late in the study or presumably spending some high tides on Horse Island. The ranges are shown in Figure 3.4 (j); their areas ranged from 2.4 to 5.1 ha, with a median of 3.5 ha. Even with this small sample it is again apparent that some birds have very similar ranges; this is shown more strongly in the analysis of the associations between a larger sample of North Beach birds at high tide.

3.2.3 Associations Between Individual Turnstones

Single Linkage Cluster Analyses of the associations between birds, uncorrected for the extent of range overlap, generally produced rather diffuse clusters. The results of one such analysis are illustrated in Figure 3.6 (a); the dendrogram shows the associations between birds commonly seen on North Beach during the exposure period, in the period from December 1981 (when all the birds were marked) to May 1983 (or until a bird died). The sample has been limited to birds found in only part of the study area so as to reduce the proportion of pairs of birds that were never seen together.

The lines indicate the linkages between birds; the higher up the diagram two birds are linked, the greater was the association between them. Thus the most closely linked birds were 022 and 701, followed by 016 and 020. The latter pair were also quite often seen

Fig.3.6. Dendrograms illustrating the SLCA of associations between 14 turnstones resident on North Beach. (a) Associations during the exposure period. (b) Associations in foraging flocks over the high water period. See text for details.

(a)

COEFFICIENT OF ASSOCIATION

(b)

COEFF. OF ASSOCIATION
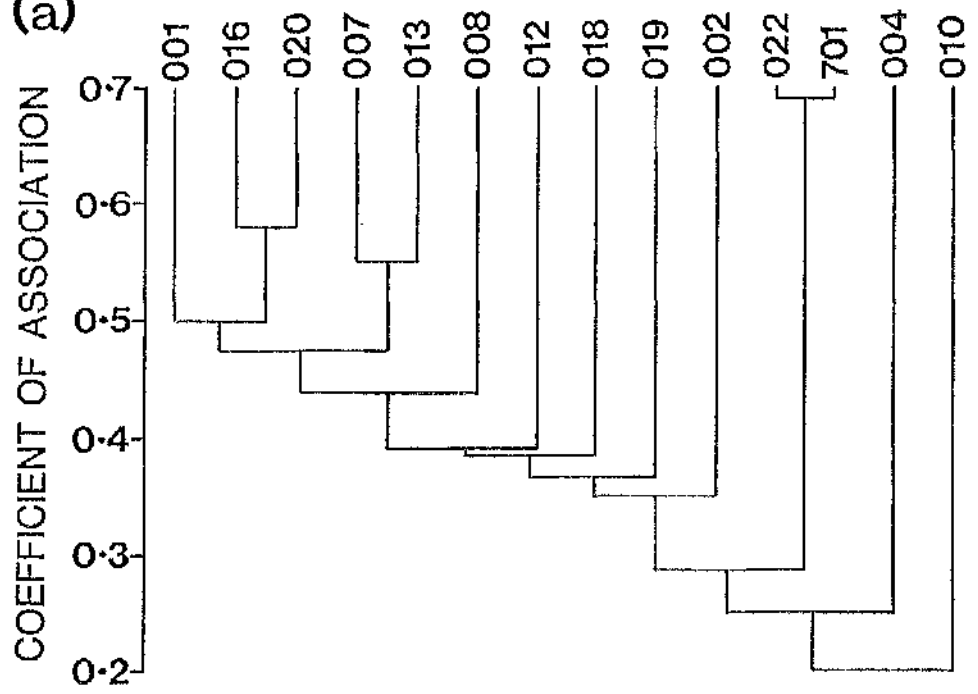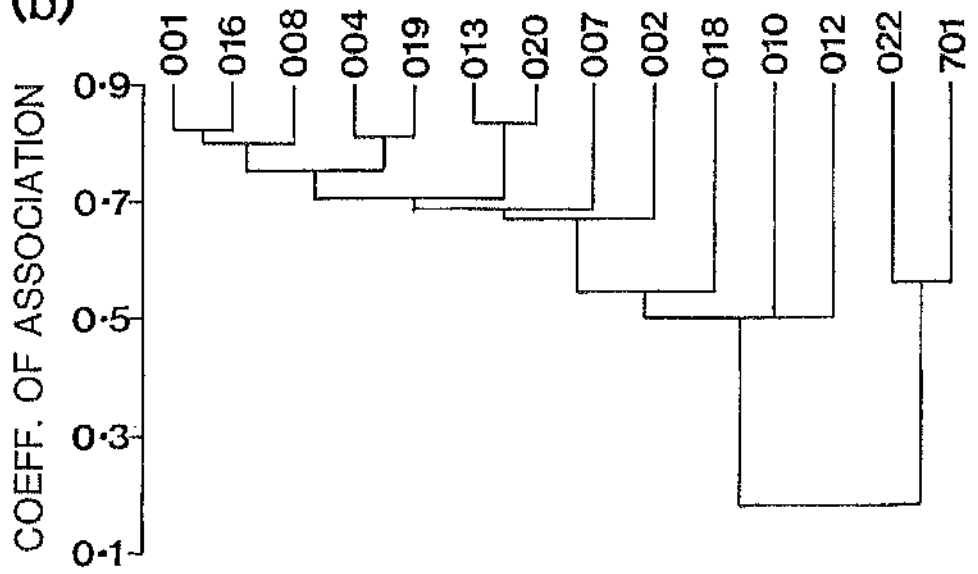
with 001, 007 and 013, while less attachment to this group was shown by 008, 012, 018 and so on.

Thus the general pattern is of a small core of closely associated birds (e.g. 001, 016, 020, 007 and 013) to which other birds are peripherally linked. A similar result was obtained for another sample of 14 birds based on Saltcoats and Coalruffie. A slight contrast was found in the pattern of associations the same North Beach birds exhibited when foraging at high water (Fig.3.6 (b)). The overall level of association was higher than during the exposure period, with the majority of birds placed in the same cluster at an association level of 0.65. However, birds 018, 010 and 012 were less often seen with this main group, while 022 and 701 (the same pair as were closely associated in Figure 3.6 (b)) showed some indication of forming a separate group. Despite this, the general pattern is not one of very tight clusters.

As these preliminary SLCA tests showed that turnstones did not live in discrete groups of fixed membership ('closed groups'), but in groups of a rather more fluid nature, further analyses were conducted using Sibson-Jardine B(2) clusters coupled with multi-dimensional scaling, as these allowed a more flexible representation of the data.

Association Patterns in Relation to Season at Coalruffie

Figure 3.7 is the multi-dimensional scaling portrayal of the inter-relationships of 14 birds that regularly used the Saltcoats and Coalruffie areas. The data have been divided into two periods of the year: 'winter' (September to February) and 'spring' (March to May). Two-dimensional solutions did not unduly distort the data (Kruskal's Stress Formula 1 being equal to 0.09 for winter and 0.11 for spring, values which indicate 'fair' and 'moderate' levels of stress respectively (Lingoes & Roskam 1973)). The proximity of a pair of

Fig.3.7. Multidimensional scaling diagrams of the associations between 14 turnstones resident at Coalruffie and Saltcoats. Also shown are the Sibson-Jardine B(2) clusters existing at the level of the median coefficient of association (solid line) and the median + 0.1 level (dashed line).

(a) Associations between September and February. (b) Associations between March and May. See text for details.

(a)

126

030
124
039 119 120
121 125
118
117
025
107

115

123

(b)

025

123

126 107
117
039
115 118 119 121 120 030
125
124
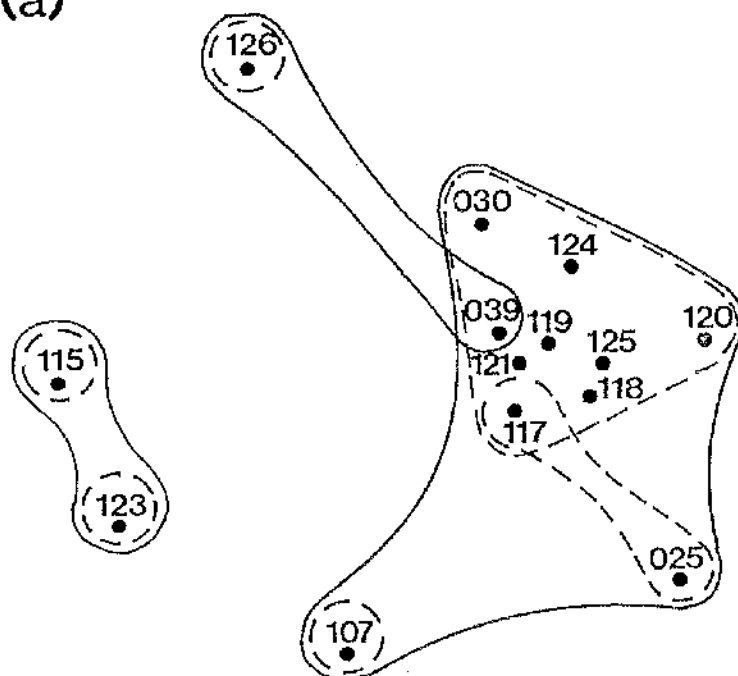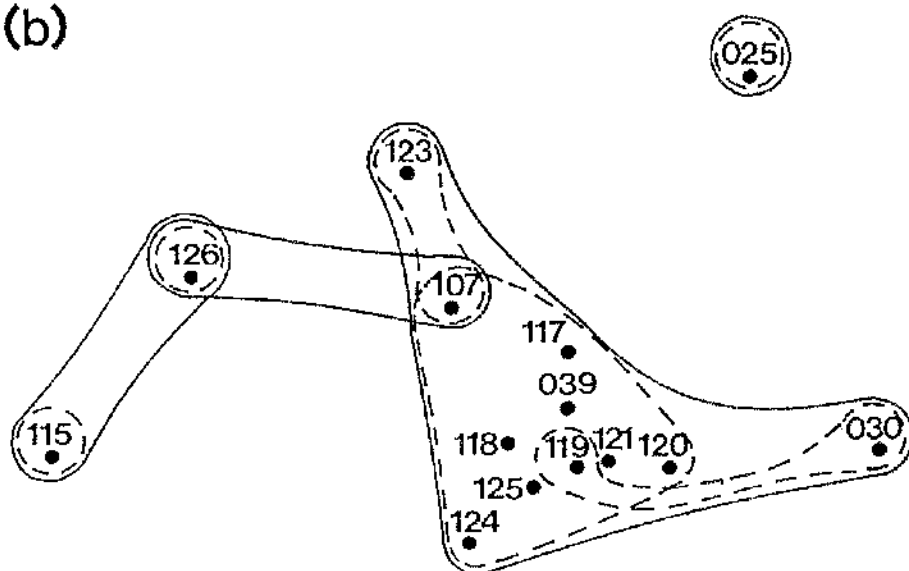
points indicates the frequency with which those birds were seen together. For example, in winter, bird 117 was seen far more frequently with 121 than with 107, and bird 126 was rarely seen with any of the other birds in the sample. A point to remember is that the <u>absolute</u> position of a point is irrelevant; it is its position relative to others that is important. Also shown on the diagram are clusters identified by the B(2) method. The levels of association at which the clusters were drawn were predetermined, so as to give unbiased and objective assessments of the groupings formed by the sample. The two levels chosen were that of the median Jaccard's coefficient of association between birds in the sample, (i.e. 0.111 in winter, 0.200 in spring), and the median coefficient + 0.100 (i.e. 0.211 in winter, 0.300 in spring). Birds in separate clusters at the higher level of association may be placed in the same cluster at the more relaxed level (an example in Figure 3.7 (a) being birds 115 and 123).

The diagrams also illustrate the concept of overlapping clusters. For instance, in (a) the presence of bird 025 in the large cluster at the lower association level is evidently largely due to its link with 117. This is a good example of the general point that many 'peripheral' birds were included in a cluster due to their having often been seen with particular core members of the cluster, rather than due to an association with the group as a whole. This indicates that birds within a core group did not move as one unit.

There are various differences between winter and spring in the patterns of association in the sample. Birds 107 and 123 were more often seen with birds in the main cluster (and with each other) in spring than in winter. The composition of the main cluster changed comparatively little; eight of the nine birds in the inner cluster in winter were still within it in spring, and the ninth (030) was linked

72

to it by a cluster overlap. These diagrams only indicate relative levels of association, and the apparently greater isolation of 025 in spring is in fact caused not by a decrease in its association with other birds, but by a failure to increase its associations in step with the population as a whole. Figure 3.8 shows that there was a significant overall increase in the coefficients of association in spring. There was no increase in the proportion of birds that were very highly associated; rather, the change was caused by a drop in the proportion of birds that were never seen together. In winter, 21 of the possible 91 pairings were never observed, whereas in spring this dropped to only two out of the 91. Figure 3.8 also shows the separate frequency distributions of the association coefficients for within-cluster and between-cluster pairings. In neither winter nor spring are the two categories distinct. Had the situation been one of closed groups, the distribution would have been clearly bimodal, with birds showing either high or no association with each other.

Association Patterns in Relation to Tidal State on North Beach

The same data of exposure period and high water associations on North Beach that were presented as a SLCA in Figure 3.6 are shown in Figure 3.9, after MDS and B(2) cluster analyses. Much the same pattern exists during the exposure period as in Figure 3.7. However, at high water the clusters are very much more distinct (Fig.3.9(b)), with very little indication of any link between the large and small clusters of 12 and 2 birds respectively. The frequency distribution of association coefficients (Fig.3.10) shows that while the average association coefficient was much higher at high water, between-cluster associations were still very low. This results in a distinctly bimodal distribution, which indicates that the individual composition of groups was more fixed at high water. The distribution

Fig.3.8. Frequency distributions of the coefficients of association between all possible pairings (n=91) of the same 14 turnstones resident at Coalruffie and Saltcoats which were portrayed in Fig.3.7. The frequency distribution of associations for those pairs placed within the same Sibson-Jardine B(2) cluster at the median level of association is indicated by shading.

(a)

FREQUENCY

30
25
20
15
10
5

0   0·1   0·2   0·3   0·4   0·5   0·6

(b)

FREQUENCY

15
10
5

0   0·1   0·2   0·3   0·4   0·5   0·6

COEFFICIENT OF ASSOCIATION
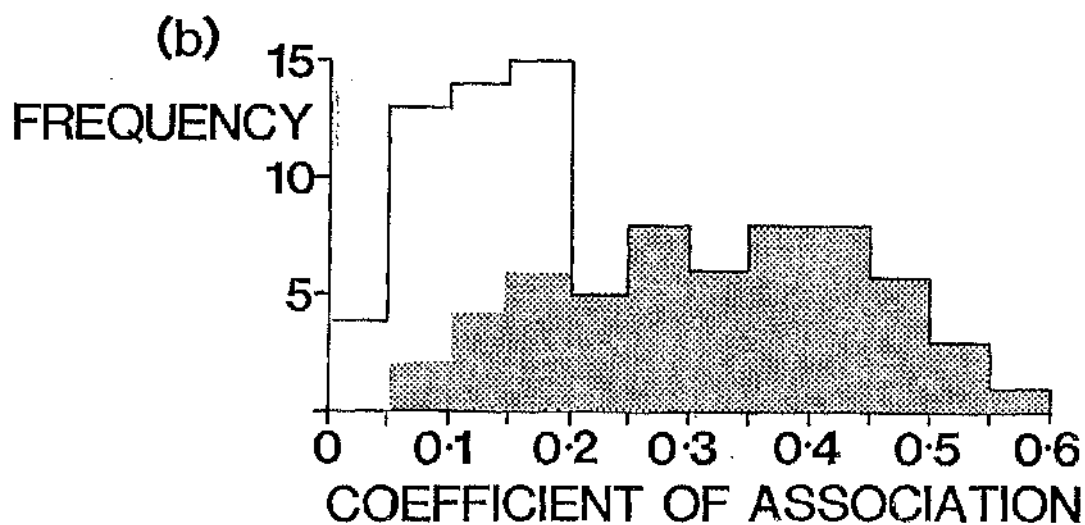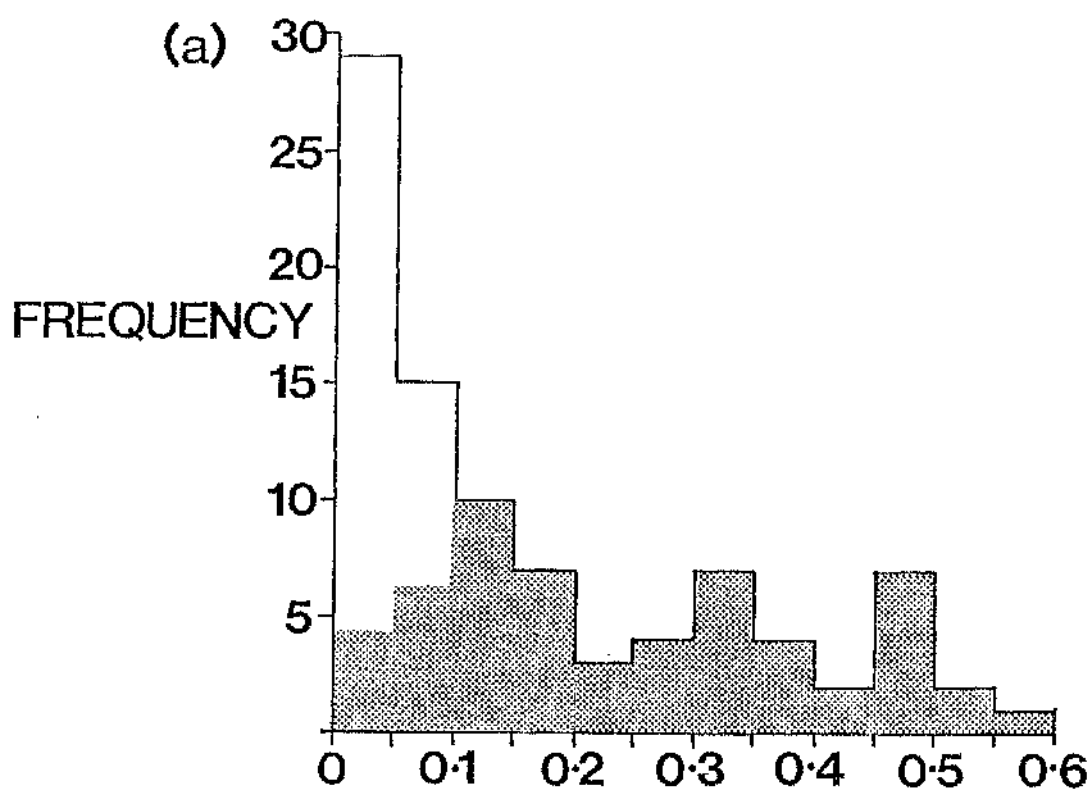
Fig.3.9. Multi-dimensional scaling diagrams of the associations between 14 turnstones resident at North Beach; birds linked within the same Sibson-Jardine B(2) clusters are indicated by shading as in Fig.3.7.

(a) Associations during the exposure period. (b) Association among foraging birds over the high water period; the relative distance apart of the two main clusters is shown within the box, while the clusters are enlarged beneath to illustrate the details within them. Kruskal's Stress Formula 1 for (a) is 0.142, and for (b) 0.000 (levels described by Lingoes and Roskam (1973) as "moderate" and "excellent" respectively) indicating that 2-D representations do not distort the data.

(a)

(b)
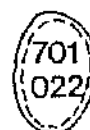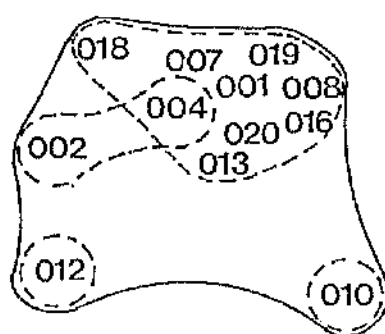
Fig.3.10. Frequency distributions of the coefficients of association between all possible pairings (n=91) of the same 14 turnstones portrayed in Fig.3.9. For further details see text, and legend to Fig.3.8.

(a) — FREQUENCY vs COEFF. OF ASSOCIATION histogram

(b) — FREQUENCY vs COEFF. OF ASSOCIATION histogram
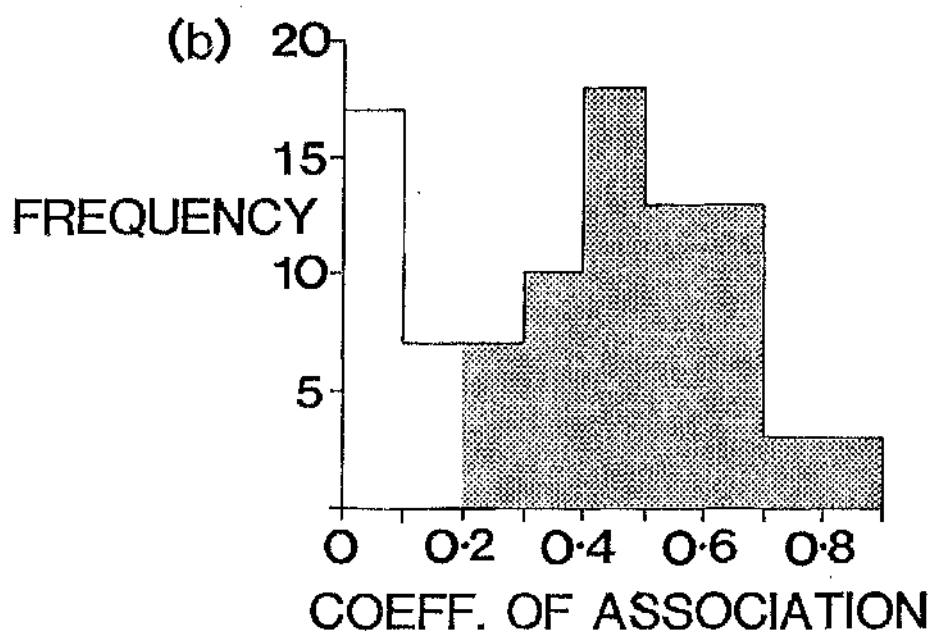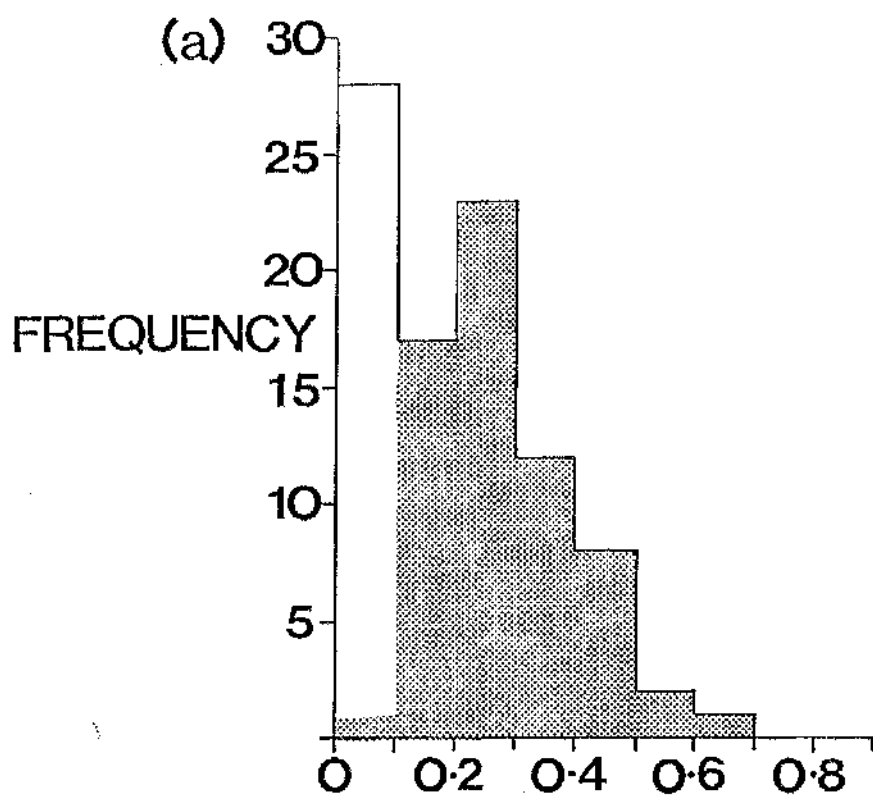
of high water sightings of the two groups (Fig.3.11) shows that the separation is partly spatial; the two birds in the smaller cluster (022 and 701) were only seen at the southern end of the beach, and showed restricted overlap in range with the twelve other birds. Sightings were concentrated at the points where dead wrack was most frequently deposited.

3.2.4 The Affilations between Turnstones, Correcting for Home Range Overlap

Referring back to Figures 3.2, 3.4 and 3.7, it is clear that the extent of association between birds was largely dependent on whether they were utilising the same areas of the coast. For instance, birds 117, 121 and 124 had very similar home ranges and were consequently often see together. In contrast, all three were infrequently seen with 126 due to only a small overlap in home ranges, and while the range of 107 overlapped considerably with most other birds in the sample, it was so large an area that the bird's degree of association with any other was actually quite low. Therefore, before a more detailed analysis of the affiliations of birds could be carried out, the connection between range overlap and level of association had to be examined. As the size of a home range might be affected by habitat type or quality, the sample of birds used in this analysis was restricted to those resident in one particular region of the study area. The largest such sample for which both home range size and degree of association were known were those at Coalruffie and Saltcoats. The sample is the same as that shown in Figure 3.7, except for the omission of bird 115, due to it not having been seen frequently enough for its range to be determined.

Figure 3.12 shows the relationship between the corrected coefficient of range overlap (R_{AB} – see equation 3) and the

Fig.3.11. Distribution of sightings on North Beach over the high water period of the 14 turnstones portrayed in Fig.3.9. Sightings of the 12 birds placed within the larger cluster are shown as open circles, while those of the 2 birds placed within the smaller cluster are shown as solid circles.
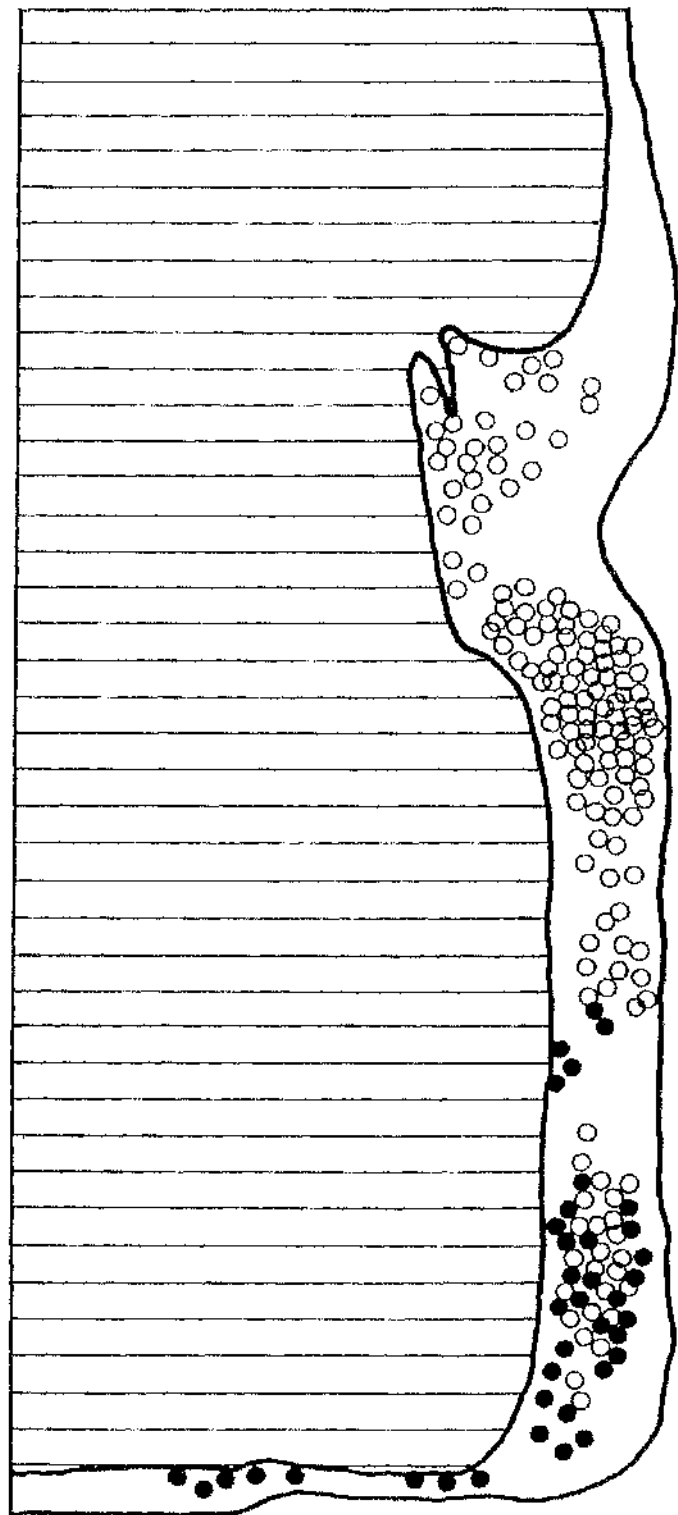
250m

Fig.3.12. The relationship between the co-efficient of association of a pair of birds and the coefficient of their home range overlap, for the 78 possible pairings of 13 birds resident at Coalruffie and Saltcoats. Both coefficients were calculated using observations made over the same time period. The best fit to the data was an exponential regression line:

$$y = -0.399e^{-1.37x} + 0.419; \quad r = 0.678, \quad P < 0.02$$
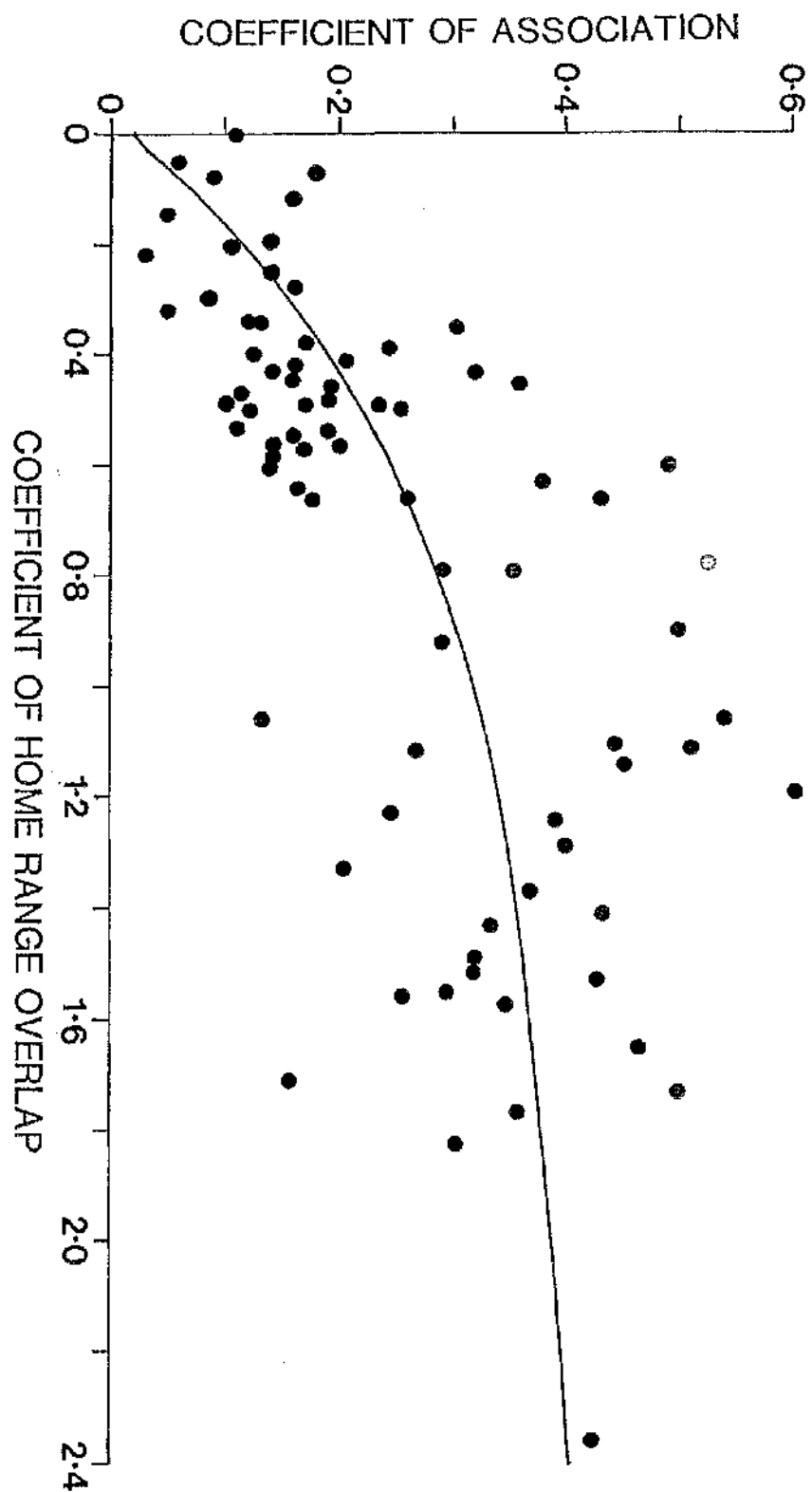
coefficient of association (A_{AB} – equation 4) for the 78 possible pairings of the 13 birds examined; all data refer to exposure period sightings over the period from September to April 15th. The relationship is exponential rather than linear, and although the positive correlation is highly significant, there is still scatter about the line. This indicates that some pairs of birds were seen together either more or less frequently than would (on average) be expected on the basis of their home range overlap. The extent of this departure from an expected degree of association can therefore be used as a corrected index of affiliation (or avoidance) between birds, with positive and negative residuals indicating respectively higher and lower associations than expected.

The coefficient of range overlap (R_{AB}) was most prone to error in situations of only a small overlap in range, as only a slight change in range boundaries could lead to disproportionately great changes in the area of the overlap. In addition, the slope of the overlap/association curve was steepest when the amount of overlap was small (Fig.3.12), so that a small error in R_{AB} would lead to a much greater difference in the expected A_{AB} than for pairs with greater overlap. Therefore this final analysis was restricted to the nine marked birds with greatest overlap, which were the same nine birds as placed in the main cluster in Figure 3.7(a). In this subgroup, the minimum value for R_{AB} was 0.45, and only 14% of the values were less than 0.75 (compared to 60% in the complete sample).

The discrepancies between the expected and actual association coefficients were entered as the measures of similarity in a final multi-dimensional scaling analysis, the results of which are shown in Figure 3.13. It is clear that bird 030, shown to be at the edge of the main cluster in Figure 3.7, is still peripheral even after

Fig.3.13. A multi-dimensional scaling diagram of the associations between nine turnstones, after correction for home range overlap. Kruskal's Stress Formula 1 = 0.098 ("fair" according to Lingoes and Roskam (1973)), indicating that a 2-D representation is not distorting the data.

117

125

121

118

119 039

124

120

030
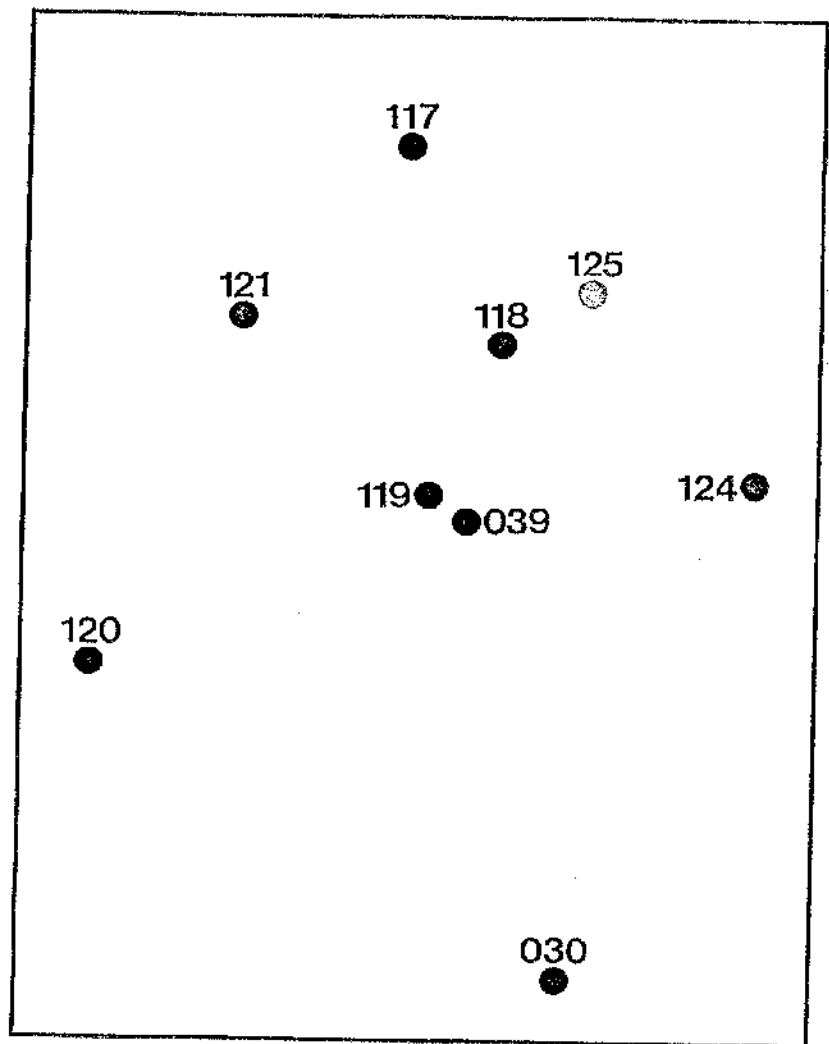
corrections for range overlap. Conversely, birds 039, 118, 119 and 125 are more centrally located, having the greatest affiliations of any birds in the sample. The relationships between the affiliations of birds and their dominance rank will be examined in the section on dominance (section 4.2.2) in Chapter 4.

3.3 Discussion

The harmonic mean method of home range determination used in this study clearly gives a more accurate description of a bird's range than most (if not all) other probabilistic techniques; methods such as the probability ellipse produce range shapes that often bear little resemblance to the distributiuon of observations (e.g Baker & Mewaldt 1979). While the harmonic mean method can produce discontinuous ranges which focus on patches of observations, it was still necessary in this study to discount some areas of a calculated range on the grounds that they constituted an unsuitable (and therefore unused) habitat. The technique had failed to exclude such areas due to their contiguity with suitable habitats (e.g. sea and rocks). However, use of a method that produced a discontinous range was still justified, as it allowed the exclusion of areas of suitable but unutilised habitat in the 'middle' of a bird's range.

The variation in home range size was not primarily due to diff erences in habitat, as there were several examples of small ranges being completely enclosed within much larger ones. The differences were therefore at least partly due to individual differences between birds. If the largest range is excluded (on the grounds that its size was due to the bird changing range during the study, as discussed earlier), the next largest range was approximately four times the size of the smallest. There remains the possibility that some ranges were larger, if they extended beyond the

limits of the study area; however, no resident birds were ever seen outside the study area (Chapter 2), and there was negligible movement between the groups of birds found at either end of the study area.

There was a tendency for birds to move outside their home ranges in autumn and (especially) spring. Similar findings have been reported in the sanderling in autumn (Myers 1984). It is possible that upon their arrival back in the non-breeding grounds in autumn, birds 'sample' different areas adjacent to their normal home range, to assess them for prey abundance. This is analogous to the situation of a predator (which lacks perfect knowledge) being faced with a choice of foraging patches which it must sample before being able to choose the most profitable (Krebs et al. 1978). However, in both sanderlings and turnstones it would appear that this vagrancy does not usually result in any changes in range; rather, the vast majority of birds readopt the same range they used the previous winter (possibly because large-scale changes in prey distribution between years are rare). Nonetheless the experience gained by such sampling could be beneficial in times of stress, and the short-term costs of exploratory behaviour are lowest at that time, as the combination of high prey biomasses, low energy requirements and long daylength ensure that birds can afford to risk these short periods of possibly sub-optimal foraging.

Turnstones are most restricted in their ranging in mid-winter. This is possibly because they can best overcome the constraints imposed by the short daylight foraging hours by remaining in the areas where they have the greatest knowledge of food distribution. The spring peak in mobility may have been caused by birds being forced to extend their ranges due to prey depletion by the end of the winter. There are very few data on the extent to which invertebrate prey supplies are depleted on rocky shores during winter. Marshall

(1981) found that turnstone prey biomasses were reduced by approximately one-third between September and March at his study site in eastern Scotland; however this loss had been replaced by increased reproduction and growth by May. Thus the time of the lowest food abundances may not coincide with the peak in turnstone mobility. Other possible causes of spring vagility could be the changes in flocking behaviour that occur at that time, or the shift of birds into the more preferred habitats as the density of birds declines; discussion of these points will be left to the appropriate section of Chapter 7.

Whatever the cause, the increased mobility in spring leads to some changes in the association patterns between birds, notably an increase in the local mixing of the population. This leads to an overall increase in the association levels between birds. A similar increase in association from autumn to late winter was found by Myers (1983) in a wintering population of sanderlings in California. In this latter case the trend was due to beach erosion reducing the number of potential feeding sites, so producing increases in flock sizes.

The size of the pool of birds with which any one individual associates has implications for the complexity of its interactions, as discussed in Chapter 2. Myers (1983) found negligible departures from a model of random association amongst the population of 500-700 sanderlings on a 4 km stretch of beach, and suggested that each sanderling might well associate with all others in the population during the course of a winter, due to the continual forming and dividing of flocks. The same processes of dynamic flocking occur in turnstones, due to the changes in flock size in synchrony with tidal rhythms (Chapter 6); in addition, all the birds of one area may roost

together, due to a limited number of potential roost sites (Furness 1973) and anti-predator advantages of roosting communally (Lack 1968, Ydenberg & Prins 1984).

However, this study has found that the patterns of association in foraging turnstones are far from random. Although territorial behaviour has never been recorded in turnstones (Myers et al. 1979a, Marshall 1981, Brearey 1982, Cramp & Simmons 1982, Fleischer 1983, this study), individuals consistently restrict their movements to relatively small home ranges. As there is a good correlation between the extent of home range overlap between two birds and the frequency with which they feed in the same flock, the number of potential flock mates a bird has while foraging is quite limited. For instance, marked birds resident at Coalruffie were seen with only eight other marked birds regularly over the course of two winters; if unmarked birds are added the total is only approximately 25 (Chapter 2, Table 2.3). The Coalruffie sub-population also mixed to a small extent with that found at Saltcoats; including this increases the pool of birds with which an individual interacted to around 50. The same pattern is true for other parts of the study area: birds resident at Stevenston rarely foraged in any other areas, and as a consequence they were regularly associated with as few as 35 other individuals. (Table 2.3). The maintenance of the same range in successive years and the low rate of population turnover ensure that this restricted rate of population mixing will be maintained from year to year. Thus individual turnstones in the study area may have foraged regularly with as few as one-tenth of the birds with which they roosted.

This limited mixing of the population might also extend to the roost itself. Although it was not possible to study the behaviour of individual birds at a roost in this study, Furness & Galbraith (1980) showed that non-random associations may persist even in a large wader

roost of 5000 birds.

Thus while species such as the sanderling may move in flocks that are random and fluid subsets of a much larger population, it would appear that turnstones are more restricted in their associations, primarily because of their great fidelity to a small home range. This is not to imply that their social system approaches that of closed groups, where all group members have exactly the same range. Instead, turnstone exposure period home ranges vary both in size and location, so that although one individual may only flock regularly with a particular section of the population, another member of that section will have a slightly different subset as its own group of regular flockmates, and so on. As a result, the cluster analyses of associations do not reveal tight clusters but straggling groupings; no doubt such 'chaining' would have been even more obvious had an analysis been carried out that included birds from more than one small section of the study area.

One of the reasons why turnstones do not form closed groups is presumably that the small flocks in which they feed are periodically being forced to aggregate by the incoming tide. There are examples of animals which both roost or sleep communally yet forage in smaller groups of constant composition; hamadryas baboons Papio hammadryas sleep at night in large aggregations, yet break up into the same male-dominated groups during the day (Kummer 1968). However, the benefits in keeping the same groups are obviously greater for male baboons, guarding their harem, than for wintering turnstones. Indeed, the costs for turnstones of attempting to reform exactly the same group as before when the tide recedes are likely to outweigh any advantages, and instead birds may move away from a high tide roost or feeding flock in any flock that is moving in the direction of their

exposure period home range. This process might explain some of the movements of birds outside their home range, as it is possible that they might get 'carried' by a flock moving to a different location, and the risk of leaving a flock might be greater than the drawbacks of spending one exposure period with unfamiliar birds in a different section of the beach.

In many of the species that form closed non-breeding groups (e.g. oregon and slate-colored juncos Junco oreganus and J. hyemalis (Sabine 1956, Fretwell 1969, Ketterson 1979) and blue jays (Racine & Thompson 1983)) neigbouring groups rarely meet. Therefore there may be few opportunities for birds to change flocks without first breaking away as solitary individuals; the risks involved may help maintain group stability. It is interesting that turnstones which foraged over the high water period did so in flocks which were (if anything) of greater stability (in terms of individual composition) than those of the exposure period. Thus although high water flocks were much larger, they were by no means random coalescences of flocks present during the exposure period. These assortative associations were again partly spatially induced; on North Beach there were often just two high water feeding flocks, one always at the southern end of the beach and the other usually around the promontary 500 m further north. The distribution of sightings and cluster analysis showed that marked birds associated with just one of the flocks, and interchange between the two was very rare. This was especially apparent when trying to move flocks in cannon-netting attempts (see Chapter 1). Even large amounts of human disturbance at one end of the beach rarely succeeded in causing birds from one flock to join the other; instead the disturbed flock would attempt to feed within its normal 'flock range'. Constraints on mixing may be especially adaptive in high tide flocks, as the higher densities at which birds must feed

lead to increased rates of aggression (Chapter 4); the mutual advantages of a dominance hierarchy based on individual recognition (which is only possible with stable groups) would thus be greater at high water than during the exposure period. Birds may therefore restrict their high tide foraging to as few sites as possible, as there will be large numbers of birds present at each site.

CHAPTER FOUR - AGGRESSION AND DOMINANCE

It is evident from the previous chapters that wintering turnstones and purple sandpipers have stable resident populations with (in turnstones at least) differential associations between individual birds that persist over the course of several winters. The basis upon which these associations are built is the flocking behaviour of the birds, which will be described in more detail in Chapter 6. In Chapter 5 one of the principal benefits of such flocking, that of a reduced predation risk and an associated decreased investment in anti-predatory behaviour, is investigated. This chapter, however, concentrates on one of the costs of grouping: aggression between individuals.

Aggression is costly for both contestants involved in a fight, in terms of time lost, energy expended, and the risk of injury. In addition the loser must pay a cost in terms of lost resources, status, or both. Increases in the density or size of a feeding group will tend to lead to increased pressure on the resources the group is attempting to exploit. In effect, there is likely to be greater local competition for those resources, with consequent increases in the likelihood of aggressive interactions between individuals. Therefore, unless cooperation is required between birds to catch prey or unless the presence of other birds otherwise assists in the finding of prey items, it is likely that increases in group size will lead to decreases in average food availability per bird, with possible resultant increases in aggressive behaviour.

If there are consistent differences between individuals in status (with some winning more encounters than others), the pay-offs of group living will clearly vary according to dominance status (Fretwell 1969, Pulliam & Caraco 1984). Failure of individuals to compete successfully will lead to their losing prey items to more

dominant birds, and may result in their avoidance of, or exclusion from, occupied prey patches. This may lead to different distributions of subordinates on a large as well as a small scale, as subordinates disperse in an attempt to avoid the competitive effects of dominants (Fretwell 1969, 1972, Dittus 1977, Gauthreaux 1978, Ketterson 1979). There may also be life-history implications, as subordinate individuals may be excluded from breeding (Watson & Moss 1970) and have reduced chances of survival (Fretwell 1969, Murton et al. 1971, Dittus 1977, Gauthreaux 1978).

Therefore the nature and extent of aggression and dominance are important facets in studying the ecology of social behaviour. They are potentially very important factors influencing group structure, and the spacing and movement of individuals both within and between groups. The aims of this chapter are firstly to describe the nature of the aggression which was observed in wintering flocks of turnstones and purple sandpipers, the contexts in which it was observed, and the factors that affected its rate of occurrence. The second approach of the chapter is an investigation of the variation in dominance status between individuals, and an attempt to elucidate the effects such status variation might have on the social structure of the population.

4.1 Methods

In order to investigate the rates and natures of aggressive interactions, minute-long observations (timed with an electronic audio timer) were made on single foraging turnstones or purple sandpipers, selected opportunistically. The following details of any aggressive encounter in which the bird was involved during the observation period were noted:

(a) whether the bird was the initiator of the interaction;

(b) <u>the species of the other bird</u>, and if possible its identity if individually colour-ringed;

(c) <u>the intensity of the encounter</u>, measured on a four point scale of increasing intensity:

(1) THREAT: the outcome was decided by the use of threat postures only (usually the hunched body with tail depressed posture described by Groves (1978) and Marshall (1981)), with no overt aggression shown by either bird.

(2) RUN: either one or both birds ran at the other, sometimes making contact but with no physical follow-up to this impact.

(3) FLY: as above, except that movement was achieved by a short flight towards the other bird.

(4) ATTACK: This involved one bird physically attacking the other, by pecking or wing-beating.

(d) <u>the distance apart of the two birds</u> at the time of the perceived initiation of the encounter. The distance, initially measured as bird-lengths, was then assigned to the closest of the following categories: 0.5, 1, 2 or 3+ metres;

(e) <u>whether a food item (or feeding location) was involved</u> in the dispute. Food-related encounters were defined as those where the initiating bird attempted to take over an item of food, or, after supplanting a bird from a feeding location, immediately began to feed at precisely the same site;

(f) <u>the outcome of the encounter</u>.

At the end of the minute of observation, the separate densities of all wader species were recorded, measured as the number of individuals within an estimated 10 m of the focal bird. However, the nature of the habitat often prevented neighbouring birds from being able to see one another, due to the presence of intervening

structures such as rocks and boulders. Therefore, apart from this 'overall' density, a second type, the visible density, was noted, measured as the number of birds of each species within 10 m that the focal bird was judged to be able to see. Visible densities were therefore the same as overall densities when there were no obstructions to vision, but sometimes considerably lower when, for example, birds were feeding amongst boulders. Visible density was measured, as it was possibly a more realistic measure of density as far as the focal bird was concerned (as was also found to be the case for the effect of density on individual vigilance (Chapter 5)). As well as these densities, a note was also made of the habitat in which the focal bird had mainly been feeding. Any observations during which either wader densities changed markedly or the focal bird changed habitat were discarded.

To compare observed rates of food-related aggression in different habitats with those that would be predicted on the basis of opportunities to steal food, data were collected on prey manipulation times and rates in different habitats. The term 'manipulation time' is defined as the time taken to expose and handle a prey item. It is used in preference to purely the handling time, as birds foraging in some habitats (e.g. dead or live wrack) would spend considerable amounts of time digging into and turning over the substrate to expose buried food items. It was therefore often profitable for dominants to supplant subordinates that had thus manipulated the substrate, but before they had handled any prey. Therefore the important parameter that determined the availability of chances to kleptoparasitise was not just the time taken to handle the prey, but also the time spent prior to this in exposing it. Manipulation times in different habitats were measured by spot observations on birds picked at random, timing the duration of their next manipulation using a

digital stopwatch. The manipulation time was measured as the period from the bird first coming into contact with the substrate to it moving away from that feeding site, deducting time spent vigilant during that period (since vigilance rate varied according to flock density and habitat visibility (Chapter 5)). Manipulation rates were recorded as the number of such manipulations that occurred during a minute of observation of a focal bird. Overall and visible densities of wader species were recorded as earlier at the end of these observations, to allow determination of whether manipulation rates altered with bird density.

The minute-long observations on aggression rates enabled some data to be collected on interactions involving individually colour-marked birds; these were supplemented by incidental recording of the outcome of encounters between marked birds observed at other times. These results were examined for evidence of individual differences in dominance and the presence of a dominance hierarchy.

4.2 Results

4.2.1 The Nature of Aggression in Mixed-Species Flocks, and its Relationship to Flock Density

(a) Intraspecific Aggression

In both species the majority of aggressive encounters involved food items or feeding sites, although the proportion of interactions involving food was significantly lower in purple sandpipers ($^{79}/_{136}$, or 58.1%) than in turnstones ($^{219}/_{274}$, or 79.9%) ($x^2 = 22.70$, 1 df, P<0.001). Those encounters that did not involve food were usually defences of 'individual distance' (Conder 1949). In both species, the initiator of an encounter was almost invariably the victor, irrespective of whether the contest was over food or not (Table 4.1).

Table 4.1 The percentage of interactions between conspecifics won by the initiator

| | Turnstone | | Purple sandpiper | |
	% won	n	% won	n
Interactions over food	95.9	219	97.5	79
Interactions not over food	96.4	55	98.2	57
All interactions[*]	95.8	286	98.0	148

[*]This category contains small numbers of cases where the presence of food could not be ascertained, and thus has sample sizes slightly larger than the sum of the other two.

There were very few occasions when the birds involved in an interaction were initially more than a metre or so apart (Table 4.2). No interactions occurred between purple sandpipers initially more than two metres apart, and the proportion that took place between birds only 0.5 m apart was greater than in turnstones ($x^2 = 19.79$, 1 df., P<0.001), which is probably a reflection of their smaller size and consequent smaller individual distance. In both species there was a tendency for a greater proportion of interactions to involve food as the initial distance separating the birds increased; however this was not significant in either case, possibly due to small sample sizes in the greater distance categories (comparing the proportion involving food in the 0.5 m category with that in the lumped 1-3 m grouping: turnstone $x^2 = 1.94$, 1 df., NS; purple sandpiper $x^2 = 0.98$, 1 df., NS). Table 4.2 also shows the intensity of interactions, classified according to the four categories Threat, Run, Fly and Attack in order of increasing cost. In both species the most common forms of aggressive intensity were threats, followed closely in frequency by encounters involving one bird running at another. Both flying assaults and actual physical attacks were rare, although attacks made up a higher proportion of the total in purple sandpipers than turnstones (comparing the number of attacks observed to the number of less aggressive interactions, $x^2 = 6.01$, 1 df., P<0.02). In both species, encounters over food were more likely to be of higher

intensity (i.e. running, flying or attacking) than were those not over food (turnstone: $X^2 = 6.53$, 1 df., $p<0.02$; purple sandpiper: $X^2 = 5.65$, 1 df., $P<0.02$). Virtually all encounters were over within a couple of seconds.

In summary, aggressive encounters , which were short-lived and almost always won by the initiator, frequently involved food items or feeding locations, especially in turnstones. They invariably occurred between birds initially close together, and were often resolved just by use of threatening postures. However, those interactions over food were more likely to involve more costly aggressive behaviours (both in terms of energy and risk of injury), although actual physical fights were rare.

(b) Interspecific Aggression

Relatively small numbers of interactions were observed between species (Table 4.3). Overall, the proportion of interactions involving food was lower for interspecific than intraspecific encounters (turnstone: $X^2 = 28.15$, 1 df., $P<0.001$; purple sandpiper: $X^2 = 12.19$, 1 df., $P<0.001$), with the majority being concerned with individual distance. However, in those cases when a turnstone was aggressive to a purple sandpiper, the proportion involving food was not significantly different to when the victim was another turnstone ($X^2 = 1.55$, 1 df., NS). Both species lost almost all interspecific encounters (which were won by the initiator on every occasion), except when interacting together (when turnstones usually dominated purple sandpipers).

Table 4.2 The frequency of aggressive encounters between conspecific turnstones or purple sandpipers, classified according to their intensity, whether food was involved, and the initial separating distance of the two birds

Intensity		Initial Separating Distance (m)				Total No.
		0.5	1	2	3	
(a) TURNSTONE						
THREAT	Food	71	6	2		79
	Non-food	26	4			30
	Total*	102	10	2		114
RUN	Food	23	33	22	5	83
	Non-food	3	5	2		10
	Total	30	41	24	5	100
FLY	Food	1				1
	Non-food		1			1
	Total	1	1			2
ATTACK	Food	1	1			2
	Non-food	1				1
	Total	2	1			3
TOTALS	Food	96	40	24	5	165
	Non-food	30	10	2	0	42
	Total	135	53	26	5	219
(b) PURPLE SANDPIPER						
THREAT	Food	31				31
	Non-food	34	1			35
	Total*	70	1			71
RUN	Food	27	13	3		43
	Non-food	13	5	1		19
	Total	43	19	4		66
FLY	Food					0
	Non-food					0
	Total	1				1
ATTACK	Food	5				5
	Non-food	3				3
	Total	10				10
TOTALS	Food	63	13	3	0	79
	Non-food	50	6	1	0	57
	Total	124	20	4	0	148

*See footnote to Table 4.1. This table omits 67 encounter between turnstones where the intensity and separating distance were not noted

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Three-quarters ($^{21}/_{28}$) of turnstone and $^{28}/_{34}$ purple sandpiper interspecific encounters occurred when the interactants were initially 0.5 m apart, similar ratios to those for encounters between conspecifics (turnstone: $x^2 = 1.37$, 1 df., NS; purple sandpiper: $x^2 = 0.003$, 1 df., NS). In turnstones there was no difference between inter- and intraspecific encounters in the proportion resolved by threat displays ($x^2 = 0.50$, 1 df., NS). This was not true for purple sandpipers, where the proportion involving running, flying or attacking was lower in interspecific interactions ($x^2 = 5.67$, 1 df., P<0.02).

Table 4.3 The frequency of aggressive encounters (a) between turnstones and other species,and (b) between purple sandpipers and other species, classified according to initiating species, intensity and the proportion that involved food. The initiating bird always won the encounter

(a) TURNSTONE

Initiator	Victim	n	Intensity Threat	Run,fly,attack	Proportion involving food
Gull[*]	Turnstone	8	4	4	3/6
Oystercatcher	Turnstone	12	10	2	1/12
Redshank	Turnstone	5	2	3	1/2
Purple sand.	Turnstone	1	0	1	0/1
	Total	26	16	10	5/21
Turnstone	Purple sand.	2	1	1	1/1

(b) PURPLE SANDPIPER

Initiator	Victim	n	Threat	Run,fly,attack	Proportion involving food
Gull[*]	Purp.sand.	5	5	0	0/5
Oystercatcher	Purp.sand.	11	10	1	0/11
Redshank	Purp.sand.	3	2	1	0/2
Turnstone	Purp.sand.	13	7	6	7/12
Ringed plover	Purp.sand.	1	0	1	0/1
	Total	33	24	9	7/31
Purple sand.	Turnstone	1	0	1	0/1

[*] 'Gulls' were predominantly herring gulls _Larus_ _argentatus_

To summarise this section, encounters in which turnstones or purple sandpipers were involved with other species took much the same form as conspecific interactions, except that they were less likely to involve food (unless between the two species), and (in the case of

purple sandpipers) were less intense. Both species almost invariably lost in interspecific encounters, although turnstones dominated purple sandpipers.

(c) The Effect of Density

To test whether aggression rate (interactions per bird per minute) was more related to overall or to visible flock densities, two linear correlations were calculated; that between intraspecific aggression rate and overall conspecific density, and that between intraspecific aggression rate and visible conspecific density. The correlations were measured over the density range 0-15 birds within 10 m of the focal bird (either visible or overall, as appropriate). Data from higher densities were omitted, as they were obtained from a limited number of situations and habitats, and so might produce habitat-biases in the density-aggression relationship (which was also not linear above densities of approximately 15 birds within 10 m of the focal individual -- see later).

Although aggression rate was significantly correlated with both types of density measurement, Pearson correlation coefficients were greater for visible than overall densities, indicating that aggression was more affected by the apparent density of conspecifics than by the actual density (Table 4.4). Therefore visible density has been used as the measure of density in subsequent analyses.

Table 4.4 Pearson Correlation Coefficients of the Relationships between Intraspecific Aggression Rates and either Overall or Visible Conspecific Densities

| Species | Measure of density and sample size | | | |
	Overall	n	Visible	n
Turnstone	0.177	818	0.268	829
Purple sandpiper	0.279	434	0.311	446

As mentioned earlier, in neither species did aggression rate continue to increase linearly once the density reached a certain level; the best fits to the complete data set were obtained using exponential regression, a finding which indicates that the rate reached a plateau as density increased (Figs. 4.1 and 4.2). Similar results were obtained when the rate of aggression between the focal turnstone or purple sandpiper and all other waders (i.e. including interspecific encounters) was plotted against the sum of visible densities for all wader species (Figs. 4.3 and 4.4). As the highest densities were only observed in a few habitats, and as the type of habitat affects the aggression rate (see later), the position of the plateau (which is largely determined by these high density observations) cannot be used to compare between the curves reliably. However, comparisons can be made over the linear portions of the graphs (i.e. the density range of 0-15 visible birds within 10 m of the focal individual) using covariance analysis. The results showed that for aggression not involving food, there was no difference (in either species) between the two aggression rate/density relationships (i.e. conspecific aggression against conspecific density, and all aggression against total wader density) (Fig.4.5).

However, where food was involved, the regression line of conspecific aggression rate against conspecific density was steeper than the comparable multi-species regression line (relating the rate of combined intra- and interspecific aggression to wader density) in both species (Fig.4.5). This means the rate of aggression over food was greater at a given density of birds in flocks composed only of conspecifics than if the flocks contained other species. In effect, turnstones and purple sandpipers were more likely to be involved in aggression over food with birds of their own species than with other waders.

Fig.4.1. The relationship between turnstone visible density and the rate of intraspecific aggression. Data represented as means $\pm$ S.E., with sample sizes shown. Exponential equation:

$$y = -0.569e^{-0.149x} + 0.562; \quad r = 0.284, \quad n = 909, \quad P < 0.01$$
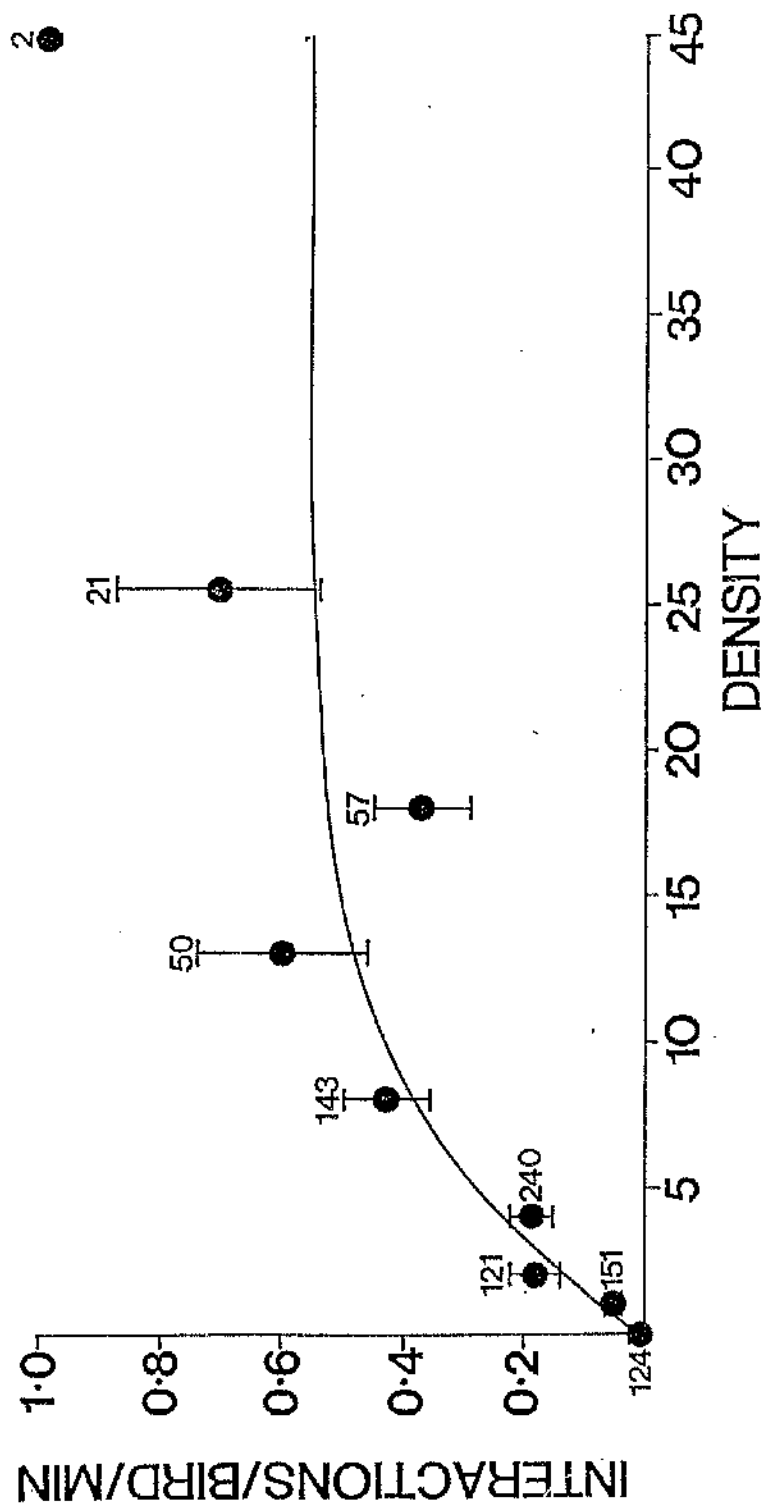
Fig.4.2. The relationship between purple sandpiper visible density and the rate of intraspecific aggression. Data represented as in Fig.4.1. Exponential equation:

$$y = -0.902e^{-0.062x} + 0.913; \ r = 0.405, \ n = 529, \ P<0.001$$

Fig.4.3. The relationship between wader visible density and the rate of interactions involving turnstones. Data represented as in Fig.4.1. Exponential equation:

$$y = -1.06e^{-0.030x} + 1.089; \quad r = 0.298, \quad n = 909, \quad P<0.01$$
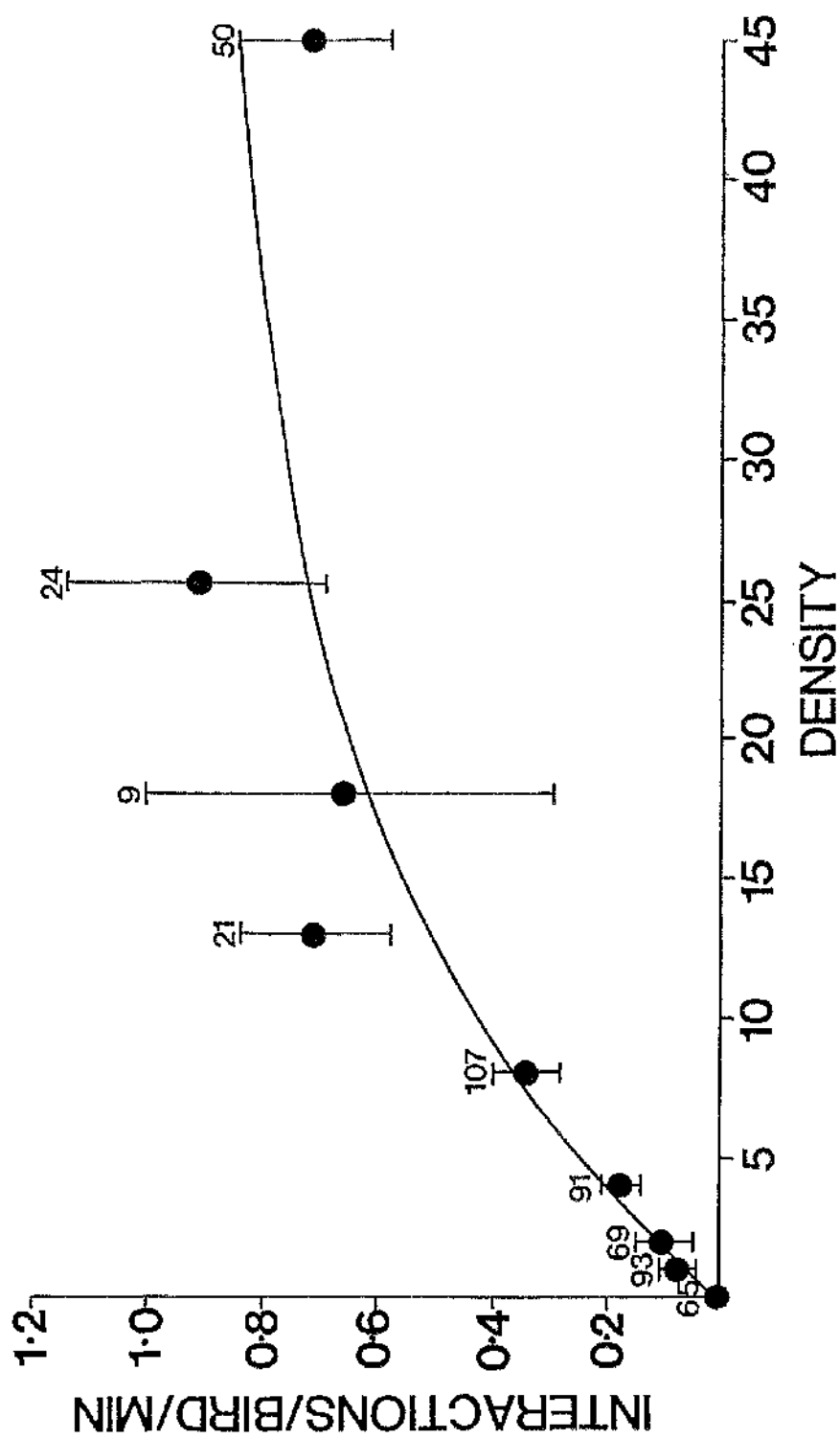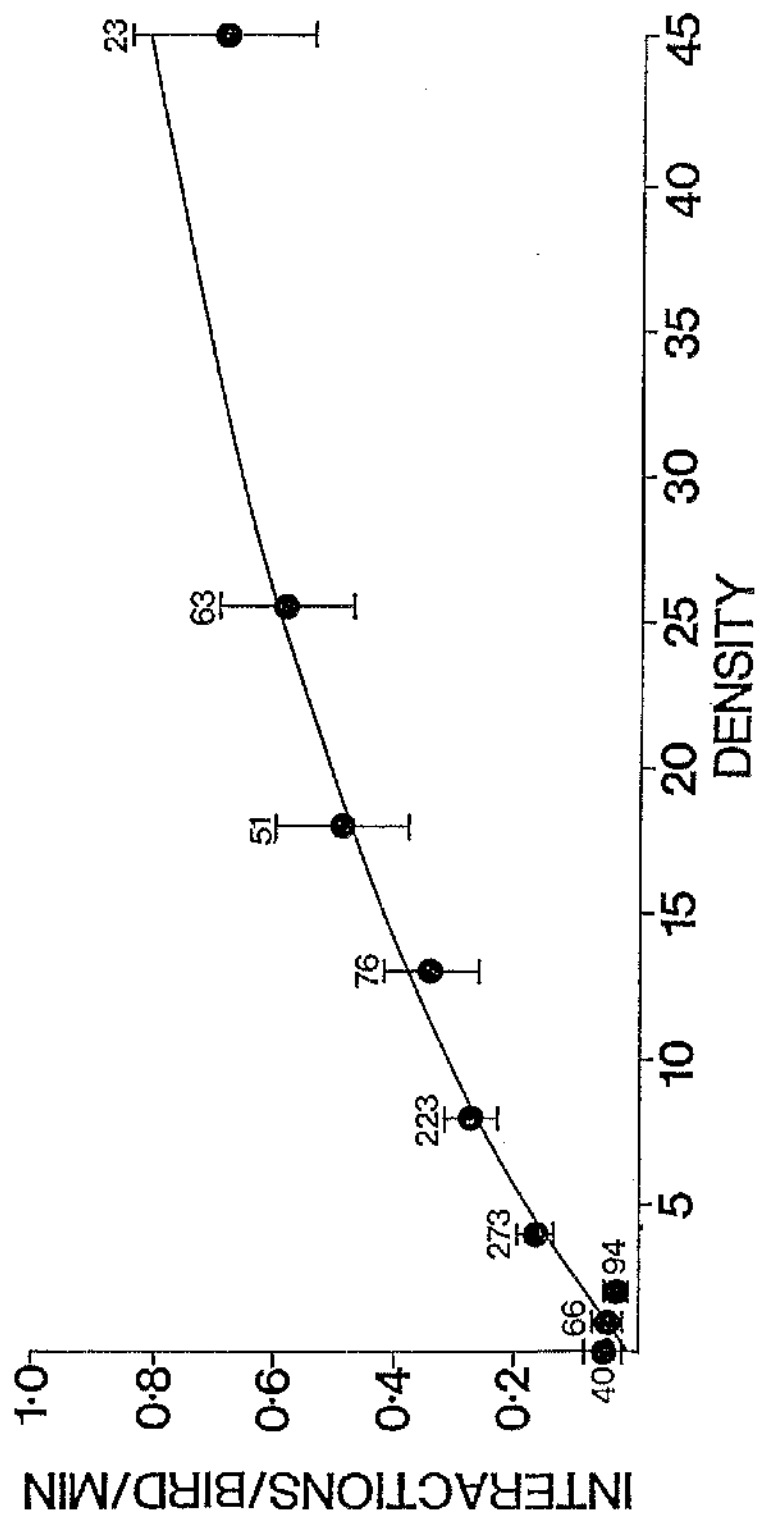
Fig.4.4. The relationship between wader visible density and the rate of interactions involving purple sandpipers. Data represented as in Fig.4.1. Exponential equation:

$$y = -1.23e^{-0.035x} + 1.193; \quad r = 0.395, \quad n = 529, \quad P < 0.001$$
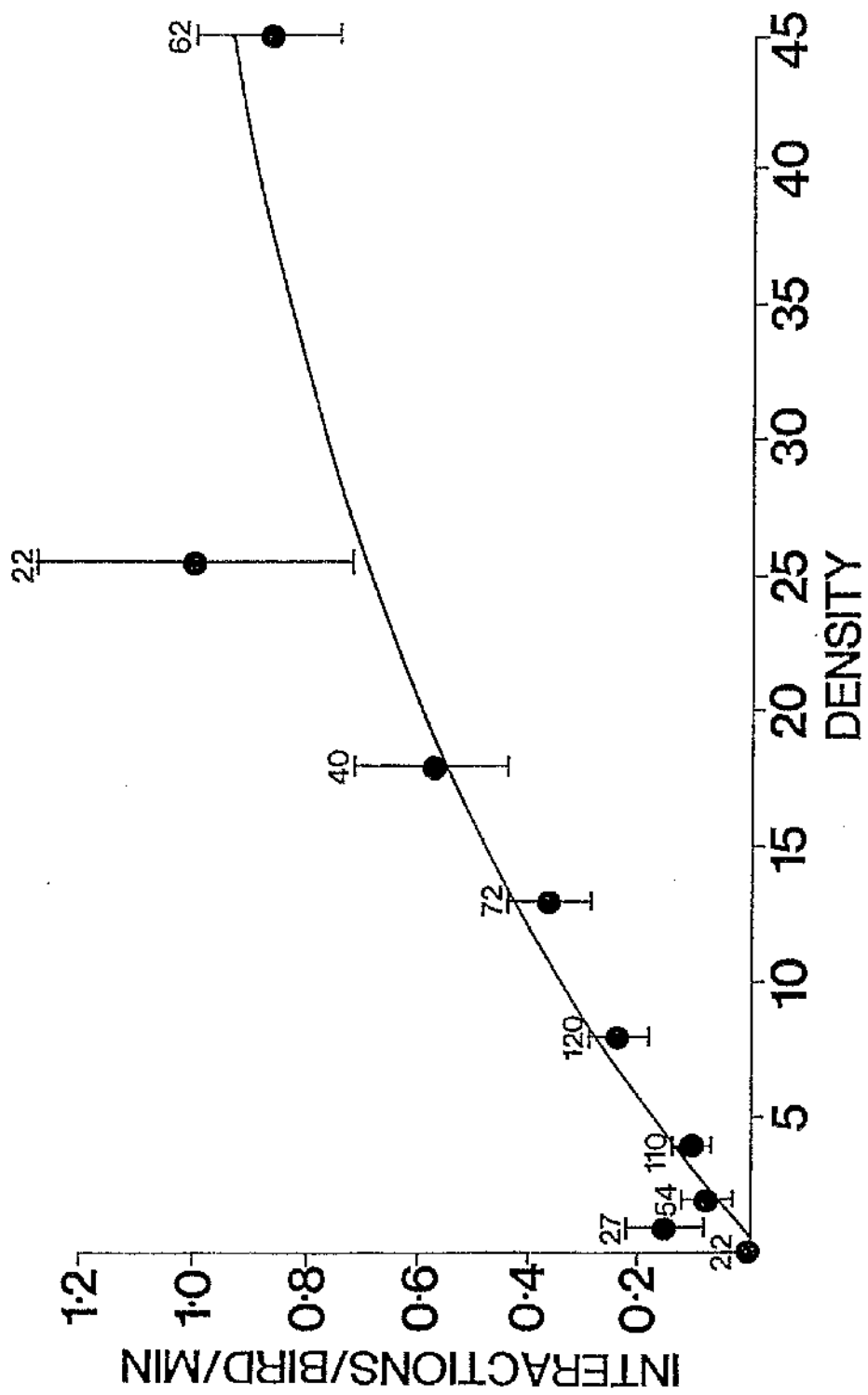
Fig.4.5. Comparisons between the regressions of conspecific aggression rate against conspecific density (solid lines) and those of wader aggression rate against wader density (dashed lines) for food related and non-food related aggression. See text for details.

(a) Turnstone: covariance analysis comparing regression line slopes for food related aggression $F_{1595,2}$ = 3.40, P<0.05; for non- food related aggression $F_{1595,2}$ = 0.38, NS; comparing elevations $F_{1598,1}$ = 0.11, NS.

(b) Purple sandpiper: Covariance analysis comparing slopes of food related aggression $F_{845,2}$ = 4.47, P<0.05. For non-food related aggression, comparing slopes $F_{845,2,}$ = 1.49, NS; comparing elevations $F_{848,1}$ = 1.67, NS.
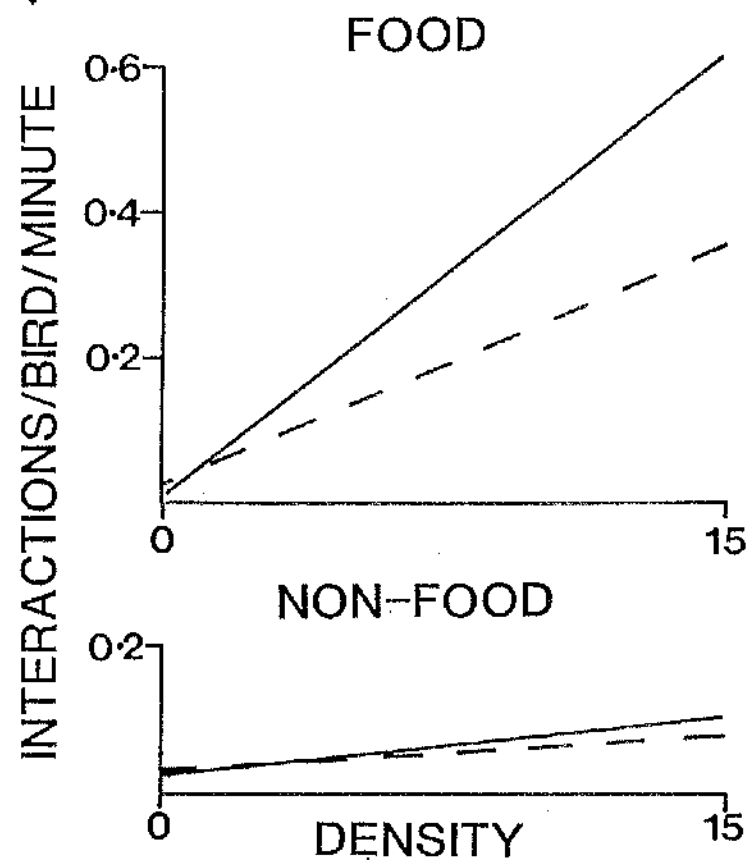
As spring pre-migratory fattening was found to affect the allocation of time to vigilance (Chapter 5), analyses were carried out to determine whether changes in aggression rate occurred at the same time. The pre-migratory fattening period was taken to be the same three weeks prior to migration as in the vigilance analysis (i.e. from 28th April to the time of the last birds' departure in mid May), and intraspecific rates of aggression w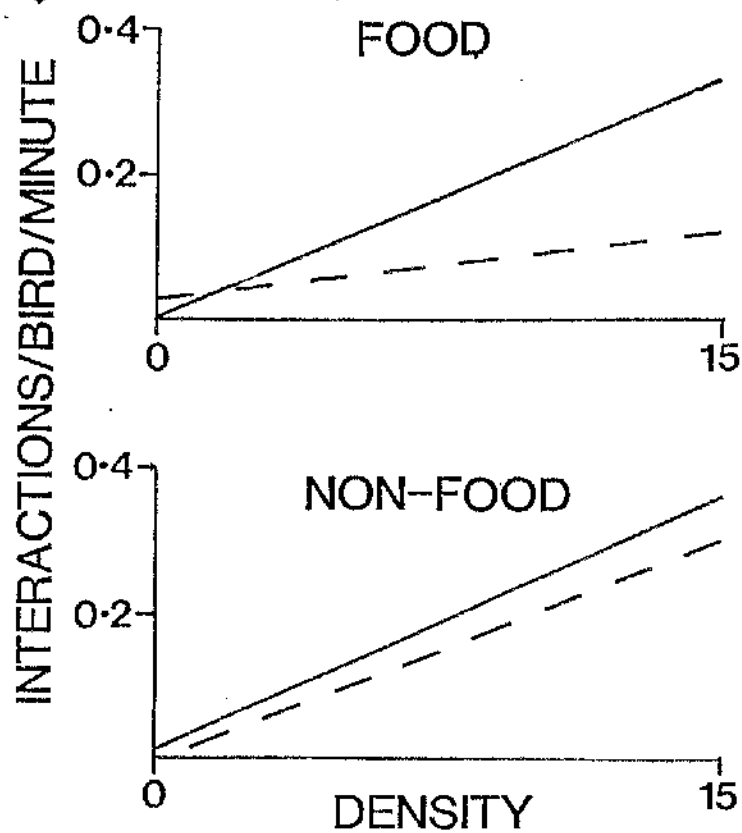ere compared in this period to those during the rest of the wintering period, controlling for conspecific density. The results showed that in neither species did aggression rates appreciably alter during the pre-migration period (covariance analyses, comparing slopes: turnstone $F_{823,2} = 0.24$, NS; purple sandpiper $F_{440,2} = 0.002$, NS; comparing elevations: turnstone $F_{826,1} = 1.30$, NS; purple sandpiper $F_{443,1} = 0.09$, NS).

4.2.2 Dominance Hierarchies, and Relationships between Dominance, Use of Space and Associations in Turnstones

The small group of marked birds that regularly foraged in the Saltcoats and Coalruffie area during the exposure period (Chapter 3) were seen frequently enough for their individual performances in aggressive encounters to be compared. There were marked differences in the proportion of interactions won, both in encounters with other marked birds and with those of unknown identity. Following the procedure of Ens & Goss-Custard (1984), the percentage of encounters won has been used as an indication of dominance; the range was from only 4.2% for the most subordinate bird in the sample to 93.3% for the most dominant (Table 4.5). There was no evidence that the extremes in the percentage of encounters won were artefacts due to smaller sample sizes, as there was no correlation between the number of encounters observed and the dominance status assigned ($r_{sp} = 0.266$, 10 df., NS).

Table 4.5 shows that, for contests between two marked birds, only five outcomes out of thirty went against the hierarchy based on overall percentage of wins. This implies that the hierarchy was both stable and approximately linear and transitive. All five 'reversal' outcomes involved similarly-ranked pairs, which may indicate that they were incorrectly placed, although in three of the five cases the losing bird was the winner on at least one other occasion of that pair interacting. There was no correlation between a bird's size (measured as its wing-length) and its dominance rank ($r_{sp} = 0.004$, 10 df., NS).

Table 4.5 Dominance Hierarchy for Resident Saltcoats/Coalruffie Birds

WINNER	030	010	124	121	117	120	119	025	125	118	126	039	Total won	Total no.	% won
030	XXX									1		2	14	15	93.3
010		XXX											8	9	88.9
124			XXX	1		1	1			3			8	11	72.7
121		2		XXX			1		1	1		3	10	14	71.4
117		1			XXX		2						7	12	58.3
120						XXX						2	4	7	57.1
119							XXX		3			1	12	22	54.5
025								XXX					1	4	25.0
125						1	1		XXX	2			4	17	23.5
118										XXX			2	12	16.7
126											XXX		1	12	8.3
039												XXX	1	24	4.2

Note: the totals columns include interactions with unmarked birds

The home range was determined for all twelve birds in Table 4.5, although the size of the range for bird 010 was probably seriously overestimated, as it changed range halfway through the period of observations (as discussed in section 3.2.1). Omitting this bird, there is a significant negative correlation between dominance rank and home range size (Fig.4.6). The sample size is necessarily small, as few marked birds were observed in encounters frequently enough for their dominance status to be assessed. However, a further gross comparison can be made using all birds for which home ranges were

Fig.4.6. The relationship between dominance rank (measured as the
percentage of enounters won) and home range size (in hectares); r_s =
-0.645, n = 11, P< 0.05.
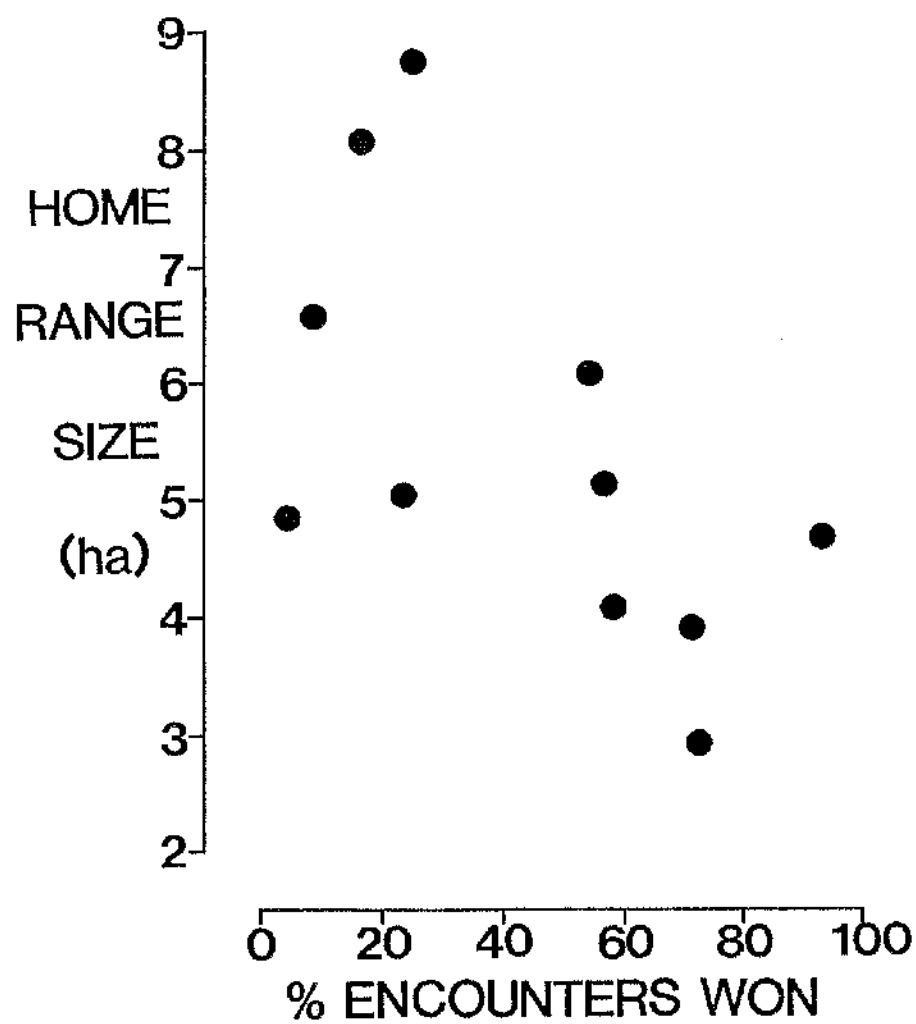
determined. If the sample is ranked in order of increasing home range size, and the overall proportion of encounters won by the top third (~ the third predicted to be the most dominant section of the population) is compared to the proportion won by the bottom two-thirds, the third with the smallest home ranges won a far greater proportion of their encounters ($^{42}/_{58}$, or 72 % (n=11 birds), as against $^{40}/_{124}$ (32 %, 23 birds); $X^2 = 24.14$, 1 df., P<0.001).

Table 4.6 Matrix of Corrected Coefficients of Association between Coalruffie Turnstones, Ranked in Order of Decreasing Dominance

	Decreasing dominance ──								
	124	121	117	120	119	125	118	039	Median
030	−0.11	−0.12	−0.23	−0.10	−0.02	−0.19	−0.09	−0.03	−0.105
124	**−0.12**	−0.09	−0.03	−0.06	0.07	0.12	0.15	0.04	0.005
121		**−0.10**	0.02	−0.05	0.22	0.06	0.24	0.08	0.040
117			**−0.04**	−0.08	0.11	0.07	0.12	0.12	0.045
120				**+0.09**	0.01	−0.05	0.01	−0.02	−0.050
119					**+0.07**	0.18	0.20	0.27	0.145
125						**+0.12**	0.24	0.05	0.065
118							**+0.24**	0.17	0.160
039								**+0.17**	0.065

Values given are the deviations from expected associations; negative values indicate less than expected association. Values in bold are the medians of the indicated diagonals

There was also a relationship between the dominance rank of a bird and its level of association with other birds. Chapter 3 examined associations between the group of marked birds resident at Coalruffie, correcting for home range overlap. Figure 3.13, illustrating these relationships, is reproduced as Figure 4.7, showing the dominance rankings within the sample. It is apparent that dominant birds (especially bird 030, the most dominant) had weaker

Fig.4.7. Multi-dimensional scaling diagram of the associations between nine birds, corrected for home range overlap. The nine birds are numbered according to their dominance rank, 1 being the most dominant.
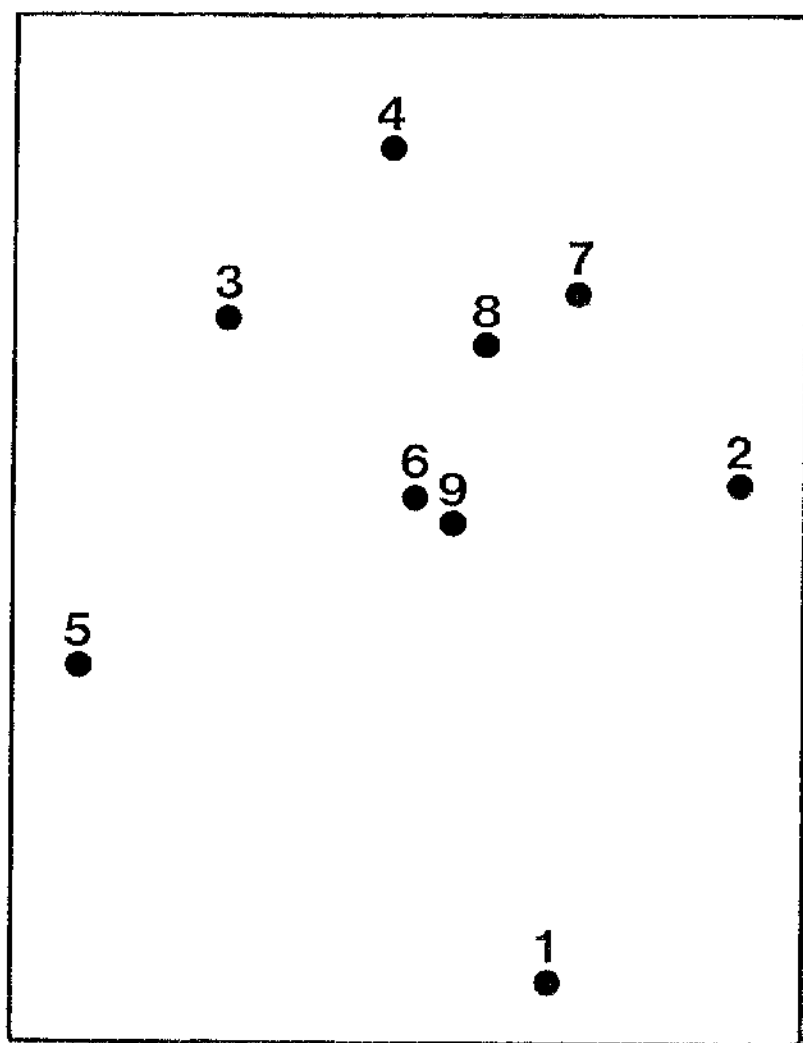
associations with other birds than did subordinates. The coefficients of association between birds in the sample, correcting for range overlap, are given in Table 4.6. There is a significant negative correlation between a bird's dominance rank and its average (given as the median) level of association with the other birds ($r_{sp} = 0.804$, 7 df., $P<0.01$). There is also a clear trend towards greater associations moving diagonally down across the table, such that two subordinates were seen in the same flock more frequently than were subordinate-dominant pairs, which in turn were seen together more frequently than pairs of dominants.

Table 4.7 Mean Sizes of Exposure Period Flocks in which Coalruffie Turnstone were found[*]. Birds Ranked in Decreasing Order of Dominance

Bird	Mean Flock Size	S.E.	n
030	10.64	1.55	22
124	11.41	1.48	37
121	12.76	1.59	33
117	12.79	1.88	28
120	13.50	1.79	26
119	13.81	1.66	42
125	13.10	1.26	39
118	14.11	1.96	35
039	14.12	2.03	33

[*] observations made after April 15th each spring excluded

Thus there was a tendency for increasing dominance status to be correlated with a decreasing tendency to be seen in the same flocks as other marked birds, especially if they were also of high dominance status. This can readily be seen in Figure 4.7; the five most dominant birds are almost equally spaced around the periphery of the cluster of subordinates, indicating that they had a tendency for greater affiliation with the subordinate cluster than with each other. Since birds were recorded as being associated if they were present in the same flock, the implication is that dominants tended to be seen in smaller flocks that therefore contained fewer of the

other marked birds. Table 4.7 shows that this was indeed the case; there was a significant negative correlation between the mean flock size a bird was seen in and the proportion of encounters it won (and thus its dominance rank (r_{sp} = -0.950, 7 df., P<0.01).

4.2.3 The Effect of Habitat on the Aggression of Shorebirds

Sample sizes of greater than 20 observations were obtained for turnstones feeding in eight, and purple sandpipers feeding in four, of the eleven habitat types in the study area (categorised in Chapter 1). The aggression rate/density relationships were compared between these habitats, using covariance analyses over the density range of 0-15 visible conspecifics within 10 m of the focal bird, as previously. Intraspecific aggression was divided into food-orientated and non-food interactions, the two types being analysed separately, to further determine whether the habitat type affected both forms of aggression.

In neither species did rates of non-food aggression vary between habitats, controlling for density (testing homogeneity of slopes of aggression rate/density relationship: turnstone $F_{760,8}$ = 0.62, NS; purple sandpiper $F_{400,4}$ = 1.39, NS; testing homogeneity of elevations: turnstone $F_{777,7}$ = 0.58, NS; purple sandpiper $F_{405,3}$ = 1.03, NS).

However, while habitat type also had no effect on food-related aggression in purple sandpipers (comparing slopes, $F_{400,4}$ = 2.37, NS; comparing elevations $F_{405,3}$ = 1.32, NS), the rates at which turnstones fought over food differed significantly between habitats (comparing slopes, $F_{760,8}$ = 5.59, P<0.01; the relationships for each habitat are shown later in Table 4.11). These differences might be predicted if there were consistent differences between habitats in the times taken by turnstones to manipulate prey and/or the rates at

which they found prey items. These would produce differences between habitats in both the opportunities available for kleptoparasitism, and the profitability of such behaviour.

Table 4.8 shows that there were indeed significant differences in the times taken by turnstones to manipulate prey items in different habitats, whereas there were no differences between habitats for purple sandpipers. Similarly, there were differences between habitats in the number of manipulations made per minute by turnstones, but not in the number made by purple sandpipers (Table 4.9). (Mean manipulation rates were used, irrespective of conspecific density, as density had no effect on manipulation rate in eleven out of the twelve categories (Table 4.9)).

Table 4.8 Mean Manipulation Times (in seconds) for Turnstones and Purple Sandpipers in Their Main Habitats

Habitat	TURNSTONE Manip. time $\pm$ SE (n)		PURPLE SANDPIPER Manip. time $\pm$ SE (n)	
Rock	2.69 $\pm$ 0.61	(91)	1.27 $\pm$ 0.14	(59)
Boulder	3.62 $\pm$ 0.42	(138)		
Musselbed	2.16 $\pm$ 0.32	(121)	1.79 $\pm$ 0.25	(60)
Pools	1.75 $\pm$ 0.37	(87)	1.22 $\pm$ 0.14	(33)
Loose rock	2.21 $\pm$ 0.40	(100)		
Dead wrack	3.65 $\pm$ 0.58	(108)		
Live wrack	5.04 $\pm$ 1.11	(66)		
Algae	1.44 $\pm$ 0.22	(75)		

One-way Analyses of Variance comparing between habitats:

Turnstone $F_{778,7}$ = 4.57, P<0.001; Purple sandpiper $F_{149,2}$ = 2.53, NS

Data given for all habitats used in analyses of effect of habitat on aggression rates, except that no manipulation times were obtained for purple sandpipers on loose rock

The hypothesis that food-orientated aggression might be dependent on the availability of opportunity was therefore examined by modelling aggression rate as a consequence of parameters such as manipulation time and search time, and then comparing observed aggression rates in each habitat with those predicted by the model.

Table 4.9 Mean Manipulation Rates (manipulations/min), and Correlations between Manipulation Rate and Conspecific Density, for Turnstones and Purple Sandpipers in their Main Habitats

Habitat	TURNSTONE				PURPLE SANDPIPER			
	Manip. rate $\pm$ SE	(n)	Corr.		Manip. rate $\pm$ SE	(n)	Corr.	
Rock	14.1 $\pm$ 0.9	(46)	-0.192		19.8 $\pm$ 1.6	(12)	0.098	
Boulder	9.2 $\pm$ 0.6	(75)	0.106					
Musselbed	14.5 $\pm$ 0.8	(51)	0.048		17.0 $\pm$ 1.1	(32)	-0.077	
Pools	21.5 $\pm$ 1.6	(15)	-0.495*		21.0 $\pm$ 1.4	(22)	0.086	
Loose rock	13.2 $\pm$ 0.9	(41)	-0.232		20.2 $\pm$ 3.1	(10)	0.472	
Dead wrack	14.7 $\pm$ 1.2	(58)	-0.212					
Live wrack	9.8 $\pm$ 1.4	(17)	-0.118					
Algae	22.8 $\pm$ 1.6	(15)	0.221		* = P<0.05			

One-way Analyses of Variance comparing between habitats:

Turnstone $F_{310,7}$ = 13.89, P<0.001; Purple sandpiper $F_{72,3}$ = 1.63, NS

A Model of Aggression Rate in Different Habitats

The purpose of this model is to assess whether the variation in turnstone aggression rates in different habitats were caused by variation in the opportunities of kleptoparasitism; it aims to do this by producing predictions of the relative rates of aggression to be expected on the basis of prey manipulation times.

Due to the great variety of prey types taken by both species, it was generally not possible to identify prey items by observation of feeding birds, nor hence to assess their profitability. Therefore the simplifying assumption is made that a kleptoparasite should be interested in any prey item judged worthy of consumption by a conspecific, since the costs of attempting to kleptoparasitise were apparently very low (the interactions always occurring between closely-adjacent birds, being very short-lived, and virtually never producing retaliation). Thus the model assumes that a bird will attempt to steal food (or a foraging position in those situations where food can only be gained by manipulating the substrate) from any neighbouring subordinate if given the opportunity. The probability of a focal bird displacing a conspecific is therefore the probability

that it is not engaged in handling prey itself, multiplied by the probability that it is within striking range of a subordinate bird that is manipulating prey or substrate at that moment. For comparing between habitats, it is assumed that the probability of the focal bird being dominant to its neighbours is constant. Therefore, for a given density and relative dominance rank of the focal bird, the probability of an attack is given by:

$$A = k \left(1 - \begin{array}{l} \text{Probability of focal} \\ \text{bird handling prey} \end{array} \right) \left(1 - \begin{array}{l} \text{Prob. that no neighbour} \\ \text{is vulnerable to an attack} \end{array} \right)$$

where k is a constant, and 'vulnerable to attack' is defined as manipulating prey for a period as least as long as the minimum required by a neighbour to attempt a kleptoparasitic attack. The expected number of encounters per bird per unit time period is therefore:

$$A = k \, (1 - ND) \, [1 - (1 - T)^n] \tag{1}$$

where
   N = number of manipulations per unit time
   D = mean duration of a manipulation (- the manipulation time)
   T = proportion of time a bird is vulnerable to attack
   n = number of subordinate neighbours within striking distance

The value of T is given by:

$$T = N_L \, (D_L - L) \tag{2}$$

where
   L = minimum time period required by kleptoparasite to detect an opportunuity and start an attack
   D_L = mean duration of manipulations that take longer than period L
   N_L = number of manipulations per unit time that take longer than L

Thus if a bird can manipulate and consume a prey item in under L seconds, it cannot be attacked by neighbouring kleptoparasites, and if all manipulations take less than L seconds, T will be zero, and it is predicted that no aggression will occur. If, however, the majority of manipulations are lengthy, T will tend towards one (i.e. there will always be vulnerable neighbours). The other major term in the equation concerns the proportion of time birds spend moving between

prey items; the larger it is, the more often they will be able to take advantage of any kleptoparasitic opportunities. If, however, food is superabundant such that search time is minimal, little would be gained through kleptoparasitism, and observed aggression rates will be low.

One complication with the model is that (as described in section 4.1) in some habitats the greater part of the manipulation time is taken up with substrate manipulation rather than prey handling; an example being the turning-over of wrack to locate hidden amphipods and dipteran larvae. In this situation dominant birds may take advantage of subordinates by supplanting them from a feeding site once the groundwork of wrack excavation has been done; they thus obtain most of the food without having to spend time exposing it. This results in dominant birds having shorter manipulation times than the average for the population as a whole. Therefore two values of D (the average manipulation duration) may be required: one for the kleptoparasite (to determine the proportion of time it spends moving between prey items), and one for its neighbours (to determine the amount of time they are vulnerable to attack). This distinction is only important in those habitats where substrate manipulation times are considerable, namely dead and live wrack.

Aggression Rates Predicted by the Model

The rates of aggression predicted by the model were only calculated for turnstones in different habitats, as purple sandpipers showed no habitat differences in manipulation times or rates. Table 4.10 gives the various parameters required by equation 1, except for values of D and N, which have already been given in Tables 4.8 and 4.9 respectively. For the purposes of comparison between habitats, predicted relative rates of aggression have been calculated assuming

that in each habitat the flock density equals eight visible turnstones within 10 m of the focal bird, of which four are subordinate to it and within striking distance (i.e. n=4), and that L, the time required to detect a kleptoparasitic opportunity and carry out an attack, is three seconds. Turnstones spend 8.3% of their time vigilant at the given density (Fig.5.7); manipulation times (which are given with the time spent vigilant subtracted in Table 4.8) have therefore been increased by this proportion. Mean manipulation times and rates for dominant birds were obtained for the dead wrack habitat by filming feeding flocks, and then measuring these parameters for those individuals seen to supplant others (but not be supplanted themselves); a maximum of 10 manipulation times and a single manipulation rate were recorded per individual. The mean values for D and N obtained for these dominants (2.82 secs (n=65) and 12.2/min (n=9) respectively) were then used to determine the proportion of time dominant birds spent moving between food items on dead wrack, while the proportion of time neighbours were vulnerable to attack was calculated using the values of D and N for the population as a whole (from Tables 4.8 and 4.9). Unfortunately this correction could not be made for the live wrack habitat, as no video film was obtained of birds feeding in this situation, and so the manipulation times and rates of dominants could not be measured.

Table 4.10 shows that while there is relatively little variation between habitats in the proportion of time the dominant kleptoparasites spent moving between food items, there was much greater variation in the proportion of time at least one neighbouring bird was vulnerable to attack; the values in the given situation range from 39% (algae) to 97% (live wrack). This results in moderate variation in the relative rates of aggression predicted by the model.

Table 4.10 The Calculation of Expected Relative Rates of Aggression amongst Turnstones in Different Habitats -- see text for explanation

Habitat	D_L	N_L	(A)	(B)	Expected relative aggression rate (AxB)
Rock	10.51	2.64	0.316	0.830	0.262
Boulder	8.03	3.22	0.298	0.749	0.233
Musselbed	7.87	2.52	0.435	0.634	0.276
Pools	8.83	2.71	0.321	0.739	0.237
Loose rock	8.01	2.64	0.474	0.665	0.315
Dead wrack	10.46	3.95	0.379	0.952	0.360
Live wrack	12.40	3.40	---- *	0.968	----
Algae	6.04	2.12	0.408	0.389	0.159

Notes: D_L, N_L -- see equation 1.
(A) Proportion of time potential kleptoparasite spends moving between prey items (i.e. $(1 - ND)$ in equ.1)
(B) Proportion of time at least one neighbour is vulnerable to attack (i.e. $[1 - (1 - T)^n]$ in equ.1).
* no measurements were made of manipulation rates or times of kleptoparasites

When these predictions are compared to the observed aggression rates (Table 4.11), there is a significant correlation between the predicted and observed values ($r_{sp} = 0.929$, 5df., P<0.01). Further indirect support for this correlation comes from two habitats which would have been placed at either ends of the spectrum of aggression rates had enough data been collected to include them. As explained earlier, it was not possible to generate an expected rate of aggression for birds feeding on live wrack; however, it is calculated that birds spent a greater proportion of their time vulnerable to kleptoparasitic attack in this habitat than any other (Table 4.10), and indeed the rate of aggression in live wrack was observed to be the highest for any habitat. In contrast, measurements of manipulation rates and times of birds feeding on the tideline indicated that birds were taking very small prey items, at a fast rate, from the water surface. As a result, neighbours of dominant birds were calculated to be vulnerable to attack only 5.1% of the time (cf.97% of the time in live wrack), and the expected relative rate of aggression was 0.038, the lowest of any habitat. While only

18 observations were made of birds foraging in this habitat, too few to calculate an aggression rate/density regression, not a single instance of aggression over food was recorded, lending support to the prediction of an extremely low aggression rate. Thus the general conclusion is that relative rates of food-related aggression could be predicted purely on the basis of the availability of kleptoparasitic opportunity.

Table 4.11 Observed Relationships between Food-related Aggression Rates and Conspecific Density in Turnstones Feeding in Different Habitats, Given in Order of Magnitude, with Rankings of Predicted Rates (from Table 4.10).

Habitat	Correlation	(n)	Regression equation	Rate at density = 8 Obs.	Rank of Pred.
Live wrack	0.649***	(36)	$y = 0.171x - 0.303$	1.07	----
Dead wrack	0.231**	(109)	$y = 0.045x + 0.165$	0.53	1
Musselbed	0.275***	(213)	$y = 0.039x - 0.001$	0.31	3
Loose rock	0.222**	(158)	$y = 0.036x + 0.014$	0.30	2
Rock	0.234**	(120)	$y = 0.031x + 0.012$	0.26	4
Pools	-0.002	(21)		0.19	5
Algae	0.046	(25)		0.08	7
Boulder	-0.060	(96)		0.01	6

**P<0.01   ***P<0.001
The observed aggression rate at density = 8 is given as the mean for all observations where the correlation with density is not significant

4.3 Discussion

The majority of interactions involving turnstones or purple sandpipers involved either specific food items or feeding sites, and both species were more likely to fight over food with conspecifics than with other species. In fact, there were very few interspecific aggressive interactions over food, the majority of encounters between species being situations where the smaller bird was forced to move out of the path of the larger. Since turnstones and (especially) purple sandpipers are smaller than redshanks or oystercatchers, the most abundant of the other species in the study area, they invariably

lost such encounters. Similar size-related interspecific dominance in mixed-species wader assemblages has been found by Burger et al. (1979) and Stawarczyk (1984).

Thus while interspecific interactions were chiefly over individual distance, aggression between conspecifics was mainly concerned with food, and increased in rate with increasing conspecific density, up to at least intermediate densities (as also found in many other studies of waders, for instance Recher & Recher (1969), Goss-Custard (1977a), Burger et al.(1979), Fleischer (1983) and Stawarczyk (1984). Two of these studies (Recher & Recher 1969 and Stawarczyk 1984) have suggested that aggression rates in some situations may actually decrease again, through some form of aggression suppression, as density reaches high levels, though the evidence for this is not unequivocal. In the present study too few observations were made at the highest densities for the trend to be clear, though it was apparent that the aggression rate/density relationship was not linear over the entire density range.

The increase in kleptoparasitism with increasing conspecific density indicates a probable cost of flocking with conspecifics. The greater loss of food items and feeding places at higher densities might have a serious effect on the food intake rates of birds, especially subordinates. Food intake was not measured in this study, due to the breadth of both diet and feeding techniques making it difficult to quantify food intake rates and diet by observation. However, much previous work on waders has shown that intake rates are reduced at high densities (reviewed in Goss-Custard 1980, also Zwarts & Drent 1981, Sutherland & Koene 1982, Fleischer 1983, Ens & Goss-Custard 1984). While in some cases this may be due to food depletion, it is often apparent that the reduction in intake is reversible, and

that it is the presence of the birds themselves (rather than any reduction in prey biomass) that is causing the drop in feeding rate. This phenomenon of interference may have several causes, such as increased aggression rate and kleptoparasitism, reduced efficiency of searching, and depression of prey availability (Goss-Custard 1980). One of the more complete studies of interference, that by Ens & Goss-Custard (1984) on oystercatchers feeding on musselbeds, showed that all but the most dominant birds in the population suffered interference, with decreasing intake rates as density increased. It had been shown previously that losing food items to kleptoparasites reduced a bird's intake rate, and that individuals differed in the rate at which they attacked other birds (Goss-Custard et al. 1982b). Ens & Goss-Custard (1984) concluded that the interference experienced by most of the population was a result of both losing food items to more dominant birds, and spending time avoiding them; this avoidance may also have forced subordinates into using alternative, secondary feeding areas when densities were highest.

Studies on captive birds of other species have also shown differential foraging benefits of flocking for individuals of different rank. For instance, dominant great tits Parus major and dark-eyed juncos Junco hyemalis may exploit the food-finding abilities of other members of a flock, monopolising any caches of food that are discovered (Baker 1978, Krebs 1980a, Baker et al.1981). In this situation dominants experience an increasing food availability as flock density increases, whereas the opposite is true for the rest of the flock.

Such differential benefits of flocking will only arise if there are consistent differences between individuals in their abilities to kleptoparasitise. This study has shown that the outcome of interactions between turnstones or purple sandpipers is often decided

on the basis of simple threat displays, and are almost invariably won by the initiating bird; the implication is that outcomes of encounters are highly predictable to the interactants on the basis of assessment cues obtained prior to the contest (Barnard & Burk 1979). In addition, it was apparent from a sample of interactions between marked birds that some form of hierarchy existed in turnstones. Thus the predictability of outcomes of encounters was unlikely to be due merely to some form of arbitrary decision rule (Maynard Smith & Parker 1976) such as 'initiator wins'. Detailed work by Marshall (1981) on captive turnstones demonstrated that a group of 14 birds formed an approximately linear hierarchy within two days, which was consistent in both feeding and non-feeding contexts. It lasted for over six months, and had as low a frequency of initiators losing interactions as in the present study. Furthermore, the more dominant bird of a pair would usurp the subordinate from feeding sites and food items in the same manner as observed in the wild, and subordinates would often escape confrontation by actively avoiding dominants (Marshall 1981). While in some cases hierarchies produced in small, confined captive populations may bear little resemblance to social structures in the wild (Myers 1983), the similarities in behaviour between captive and wild turnstones, and the fact that wild turnstones may flock regularly with as few as 50 other individuals over the course of a winter (Chapter 3), make it highly probable that wild turnstones have very stable dominance hierarchies based on assessment cues.

There is some evidence that aggression is greater (both in terms of rate and intensity) in the wild in autumn than during the rest of the winter (Marshall 1981), which may be the result of a dominance assessment period during which the hierarchy is reformed. The long-

term stability of the population may result in many adults retaining much the rank as they held the previous winter. However, juveniles in their first autumn must learn their status, and hence may be involved in a disproportionate number of encounters with adults (to which they are at least initially subordinate), possibly through their failing to recognise when other birds should be avoided (Groves 1978).

The cues used by animals to assess dominance status of conspecifics may take several forms. They may be unfakeable indicators of competitive ability (such as size), badge signals of status (an example being the blackness of the throat in Harris' sparrow Zonotrichia querula (Rohwer 1975)), or the system may be based on individual recognition and the remembrance of previous relative status. No correlation was evident between dominance status and body size, and although there is variability in turnstone plumage (Ferns 1978), it does not seem to be related to dominance status (P. Whitfield, pers. comm.). However, experiments with birds on their breeding grounds have shown that turnstones recognise their neighbouring territory-holders on the basis of plumage (P. Whitfield, pers. comm.), and there seems to be no reason why such discriminatory ability should not also apply to the wintering population.

Less can be said about the social structure of wintering purple sandpipers, as comparable data on individual variability in dominance are lacking. It has been shown that individual purple sandpipers were less predictable in their movements than turnstones (Chapter 2), which may have led to greater mixing of the population, and possibly made individual-recognition dominance hierarchies less likely. This may explain why interactions between purple sandpipers were, on the whole, of greater intensity than those between turnstones, although they too were short-lived and almost always won by the initiating bird. Links between the extent of social stability or structure and

intensity of aggression have been shown in other species of wader.
Burger et al. (1979) found that under 10% of interactions between
sanderlings (which form random flocks and show little signs of
dominance structuring (Myers 1983)) were displacements (i.e.
threats), with the majority being aggressive chases. Similar ratios
were found in knots Calidris canutus, which form huge flocks (Cramp &
Simmons 1982) and therefore probably also behave as anonymous
individuals. In contrast, about 40% of turnstone intraspecific
interactions observed by Burger et al.(1979) in the same situation
were displacements, and the figure was even higher for black-bellied
(= grey) plovers; both these species have very stable social systems
with non-random associations between individuals (this study,
Townshend et al. 1984).

The evidence suggests that a proportion of the turnstone
population might suffer appreciable costs, from being victims of
kleptoparasitic attacks, if they were in close proximity to birds of
greater dominance status. Unless there are compensatory benefits for
subordinates in being close to dominants, it would be expected that
they should avoid them, and conversely, dominants should seek out
those more subordinate (Baker 1978). It has been suggested (Rohwer &
Ewald 1981) that, while subordinates pay a cost in providing food for
dominants, they may gain an advantage in avoiding aggression, as
dominants may contest with each other for the position of
kleptoparasite. The dominants and subordinates in this situation may
be envisaged as adopting two behavioural strategies of equal fitness.
However, this explanation would appear unlikely in the present
context, as there was no evidence that subordinates were involved in
less aggression than dominants (in fact the most subordinate bird in
the sample was observed in more interactions than any other).

The cost to subordinates in being near dominants may explain why dominants tend to be in smaller flocks, as there will be a tendency for birds that break away from flocks to attract fewer followers if they are dominants than if they are subordinates. Since even the most dominant birds are only obtaining a relatively small fraction of their intake through kleptoparasitism at normal flock densities, they by no means rely on the presence of subordinates to locate food. Therefore searching out subordinates is probably not the prime consideration when deciding where to forage. (The question of how birds are affected in their searching behaviour by the movements of other birds will be explored in more detail in Chapter 6.) The situation is therefore not akin to the scenario envisaged by Sibly (1984), where the population is divided into two types, "producers" and "scroungers" (i.e. those that locate and 'produce' the food, and those (the kleptoparasites) that steal it); such a rigid categorisation is perhaps more applicable to cases of interspecific kleptoparasitism. In turnstones, it would appear that all but the most subordinate birds in the population will attempt to steal profitable food from a lower-ranked neighbour if the opportunity arises, but will otherwise search for food themselves. Only in the densest aggregations will pure kleptoparasitism be a viable option; this was only approached in flocks feeding on banks of dead wrack at high water. At these times subordinates could not escape from such exploitation, as feeding patches were so reduced in number that all potential sites tended to be occupied.

The finding that the most dominant individuals are, on average, found in smaller groups would also be predicted by the group size/time-budgeting theories of Pulliam and Caraco (Pulliam 1976, Caraco 1979a, Pulliam & Caraco 1984). However, they make the assumption that dominants gain no food-finding advantage from

subordinates. Thus although small numbers of flockmates will confer anti-predatory advantages, there will come a point where the food intake rate of a dominant will start to drop as more subordinates join the group, causing depletion and interference. Therefore Pulliam and Caraco suggest that the increased aggression rate seen at higher flock densities is due to dominants attempting to drive off subordinates, so reducing both group size and the competition for resources.

Where these two functions of aggression (kleptoparasitism versus competition-reduction) differ is in the contexts of aggressive encounters, the factors which affect the rate at which they occur, and the predicted optimal group size/density for dominants. Kleptoparasitic aggression (by definition) only occurs over food, whereas aggression aimed at reducing competition may occur at any time. The latter should also occur at as high a rate as is compatible with other activities (i.e. a bird should spend all its 'free time' chasing off others) (Caraco 1979a). Thus Caraco (1979b) found that the rate of (competition-reduction) aggression increased when there was a reduction in the time required for foraging; no such change occurred in this study. In contrast, the rate of kleptoparasitism is primarily affected by the profitability of potential prey (Brockman & Barnard 1979) and the opportunities available to steal prey items (this study). It is interesting to note that gulls made virtually no kleptoparasitic attacks on either turnstones or purple sandpipers, whereas in situations where waders are handling larger prey (which are both more profitable and take longer to handle) individual gulls may adopt a purely kleptoparasitic feeding method (Barnard et al. 1982). The difference between the two types of aggression in the predicted optimal group sizes for dominants is due to the presence of

many subordinates being a cost in one situation and a benefit in the other. However, although kleptoparasitic dominants will gain from large groups (or high densities), their presence will tend to drive subordinates away, resulting in their experiencing sub-optimal group sizes. Barnard et al. (1982) obtained direct evidence of this process, when they found that the arrival of kleptoparasitic black-headed gulls Larus ridibundus led to reductions in the size of flocks of lapwings Vanellus vanellus, the parasitised species. Similarly, Harper (1982) found that subordinate mallards avoided flocks containing the most dominant individuals, and as a result a flock's size was negatively correlated with the number of dominants it contained.

It is not clear why subordinate turnstones should have a tendency to have larger home ranges than more dominant birds. It is possible that a tendency to avoid dominants and a potentially lower feeding rate might both cause birds to roam more widely in the search for alternative feeding areas (Murton et al. 1971, Monaghan 1980, Ens & Goss-Custard 1984). However, this can only remain a hypothesis in the absence of more detailed behavioural studies of foraging behaviour.

CHAPTER FIVE -- VIGILANCE

Many animals face the continual risk of being caught by a predator. One of the ways in which this threat can be reduced is by the potential victim detecting the approaching predator; this allows it to implement defensive strategies such as adopting a defensive posture, taking flight, joining a group and so on (Edmunds 1974). It is often the case, however, that animals which rely on visual detection of predators will be less able to scan for predators when engaged in activites such as feeding, as a head-down feeding posture may reduce the visual field, and the visual and neural processing required in handling food items may detract from the animal's ability to detect a distant but approaching predator (Lendrem 1984a).

As a consequence, many species have evolved forms of vigilant behaviour, where the animal periodically breaks off from a continuing activity in order to scan its environment (Dimond & Lazarus 1974, Lendrem 1982). This form of scanning is obviously incompatible with other behaviours, and so makes them less efficient in terms of the overall time required for their performance. Since time-efficiency is an important consideration for many animals, there is selection pressure for the optimal allocation of time between anti-predatory vigilance and other activities such as feeding.

In this chapter several aspects of vigilance in turnstones and purple sandpipers are examined, with special reference to how their habitat and flocking behaviour influence the level of vigilance they adopt. The chapter is divided into four sections; the first deals with the effect of habitat type, while the second looks at flock density and composition and how those affect vigilance. In the third section the trade-off the individual must make between time spent vigilant and time spent foraging is investigated by studying the

response to an increased food demand prior to migration, while in the final section the pattern of scanning within a flock and the subject of corporate vigilance are examined.

5.1 The Effect of Habitat on the Vigilance of Shorebirds: Is Visibility Important?

Many animals live in habitats which do not permit a clear view of their surroundings. There will therefore be a reduction in the distances at which predators and prey can detect one another visually. This can be investigated indirectly by measuring the vigilance of the prey (which reflects its assessment of its own vulnerability) in relation to the visibility of the habitat. Previous studies of the effects of group size, composition or position in a group on vigilance have been made in open habitats such as grass fields (e.g Lazarus 1978, Bertram 1980, Jennings & Evans 1980). However Underwood (1982) showed that antelopes increased their vigilance when in habitats he categorised as closed (i.e. with reduced visibility). In contrast Barnard (1980a) and Caraco et al. (1980b) found that birds may increase their vigilance with increasing distance from cover.

The effect of habitat complexity on vigilance was the first aspect of vigilance in turnstones and purple sandpipers to be investigated. The coastlines of the study area are composed of outcrops of rock and boulder (among which visibility may be very restricted), which are interspersed with sand or mudflats (where there are no obstructions to vision). Thus among rocks they cannot see approaching predators as easily as when on sand or mud, so may be expected to increase vigilance.

The method by which vigilance was altered was also investigated. Birds can scan more often or increase the duration of each scan; the

two processes are not mutually exclusive (McVean & Haddlesey 1980).

5.1.1 Methods

Data were collected from 3rd February to 14th April 1982 and from 7th September 1982 to the end of April 1983. This analysis omits data collected after 27th April in each spring, as the need for an increased food intake prior to spring migration affected levels of vigilance (section 5.3).

The encounter rate with potential predators was relatively high in this area. A female merlin Falco columbarius was present in the study area on numerous occasions in both winters, and peregrines F. peregrinus, kestrels F. tinnunculus, sparrowhawks Accipiter nisus and a short-eared owl Asio flammeus were also recorded. Species such as these may have considerable impacts on the survival rates of wintering waders (Page & Whitacre 1975, Kus et al. 1984, Whitfield in prep). In addition, numerous dogs were walked along the beaches and frequently chased the birds.

Observations were made with a 15-60X telescope on birds 20 to 80m from a vehicle (used as a hide) parked on the beach or promenade. My presence had no apparent effect on the birds' behaviour; they were accustomed to high levels of human activity. The efficiency of data collection was improved towards the end of the study by using a colour video camera. Close flocks were filmed (with a running commentary) in the field, and the films later played back on analysing equipment. This allowed the measuring of the same vigilance parameters as taken directly in the field. Twenty-six turnstone and 112 purple sandpiper observations were made from video film, out of the total sample sizes of 673 and 460 respectively.

A focal bird was selected and watched for exactly one minute; periods were measured with the aid of an electronic audio timer. The

number of scans during that period was recorded (using a tally counter), as was the total time spent scanning (to the nearest half-second, cumulatively recorded with a stopwatch). A scan was defined as a raising of the head, from the head-down foraging position to at least a horizontal position.

At the end of the one minute observation period the visibility experienced by the focal bird was assessed as follows. The total angle of obstructed vision (out of 360° maximum) contributed by objects (e.g. boulders, wrack banks) within one metre of the focal bird was assigned to one of four categories, scoring one to four in order of increasing visibility. Thus in Fig. 5.1 the rock on the left obstructs a sector of A° of the birds all-round vision, and that on the right obstructs B°. Summing $A + B$ produces a total of between 90 and 180°, so giving a score of 3. This scoring was carried out at three heights above the ground (Fig. 5.2). Thus a bird that scored one at 5cm and four at 10 and 15cm could see very little while in a foraging position, but experienced unrestricted vision upon raising its head (as would occur for a bird feeding in a rock pool with its head under water), whereas birds scoring two or less at all three heights had poor visibility regardless of posture (as would be the case in a habitat of large boulders). The three scores (one at each height) were then summed to give an overall Visibility Score, ranging from a theoretical minimum of three (poor visibility) to twelve (good visibility). This technique was tested for accuracy by comparing the actual Visibility Score of a location with the score estimated from the observation vehicle. This was done for a variety of habitats and distances from the vehicle. The differences between estimated and actual scores were negligible (mean difference = 0.08 $\pm$ 0.04 S.E., n=40).

The density of surrounding birds affects the vigilance of both

Fig.5.1. The method used to record the visibility score of the focal bird. The two rocks obstruct a summed angle (A + B) of between 90 and 180°, thus the visibility score is 3.

ROCK

ROCK

B

A
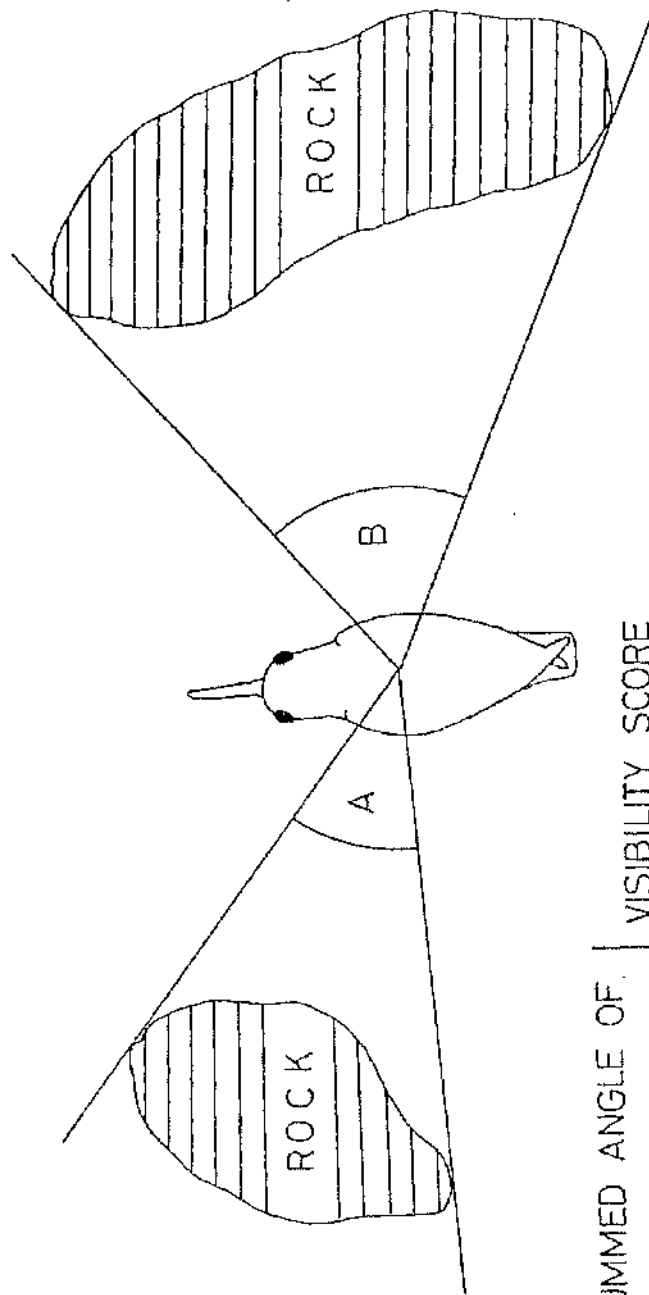
| SUMMED ANGLE OF OBSTRUCTED VISION	VISIBILITY SCORE
<90°	4
90–180°	3
180–270°	2
>270°	1

A + B = 102°

∴ VISIBILITY SCORE = 3

Fig.5.2. The three heights above ground level at which the visibility score of the focal bird was recorded, in relation to the approximate size of a turnstone or purple sandpiper. The rock on the left contributes to the scores at 5 and 10cm, while that on the right is only included in the 5cm score.

15 cm

10 cm

5 cm
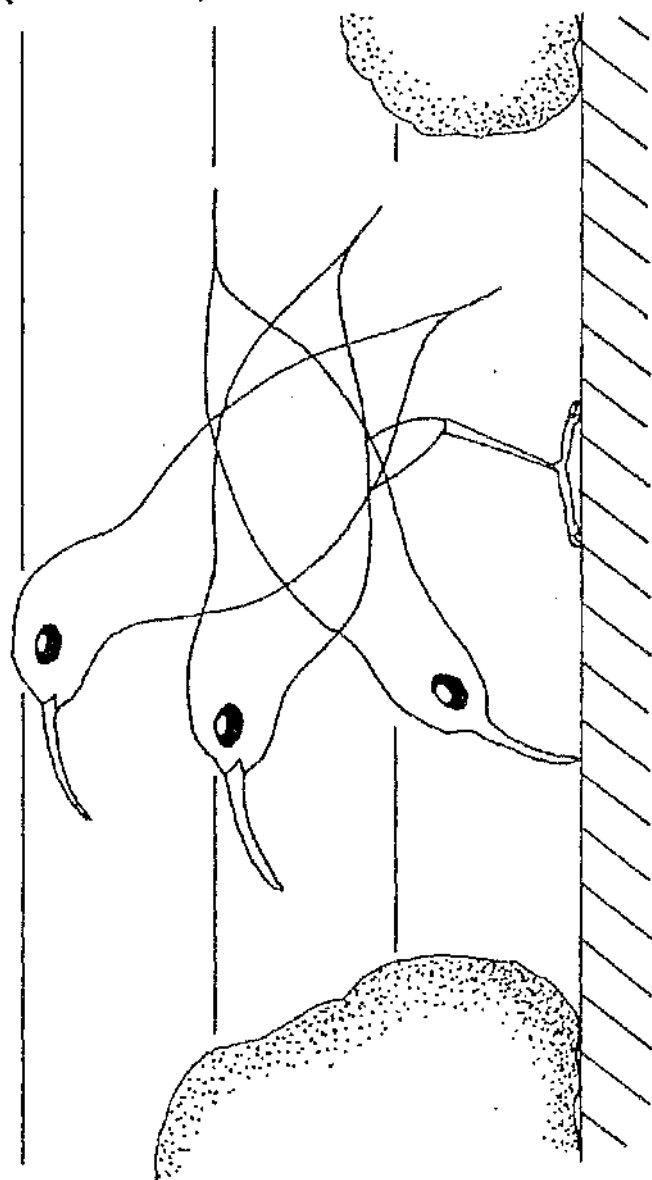
turnstone and purple sandpiper, as individuals in effect 'share' vigilance with other near neighbours they can see (section 5.2.2). Both species share vigilance with individuals of certain other wader species as well as conspecifics; for turnstone these other 'significant species' are purple sandpipers, redshanks and oystercatchers, while purple sandpipers share vigilance with turnstone as well as conspecifics (section 5.2.2). As this density effect is most marked at low densities, it could be controlled for by only using in this analysis observations in which density exceeded five birds within 10m and in sight of the focal bird, as variation in density above this level had a negligible effect on individual vigilance (Fig. 5.7).

The measurement of visibility and density required that these factors did not change appreciably during the course of the minute of observation. Therefore only relatively static birds were chosen, and records were aborted if the focal bird experienced a noticeable change of density or visibility during that minute; records were also discounted if the bird's behaviour was affected by a recognisable disturbance.

In the analyses, relationships that satisfied the conditions for the use of parametric statistics were analysed accordingly; otherwise non-parametric tests were used. Four vigilance parameters were selected for analysis:

(1) Vigilance Time, defined as the total time (in seconds) spent vigilant per minute.

(2) Scanning Rate, expressed as the number of scans per minute.

(3) Scan Duration, given by $\text{Vigilance Time}/\text{Scanning Rate}$. It is therefore the mean scan duration for that period of observation.

(4) Interscan Interval, defined as the mean time interval between the

end of one scan and the beginning of the next, and given by

$$(60 - \text{Vigilance Rate})\big/\text{Scanning Rate}$$

5.1.2 Results

The relationship between Vigilance Time and visibility is very similar in the two species, with an approximately linear increase in Vigilance Time with decreasing Visibility Score (Fig. 5.3). (Small sample sizes at low Visibility Scores are partly due to the infrequency with which birds were found in low visibility situations, and partly due to the difficulties in observing such birds once located). The variation in Scanning Rate with changing visibility is shown in Fig. 5.4. There is clearly an increase in the rate at which purple sandpipers scan as their vision becomes more obstructed, but this trend is not found in turnstones. Rather, there is an increase in Scan Duration (Fig. 5.5), far more marked than that in purple sandpipers. Therefore, turnstones increase their vigilance by making each scan longer, while purple sandpipers achieve the same level of vigilance mainly by scanning more often. In consequence, the Interscan Interval decreases markedly with decreasing visibility in purple sandpipers (Fig. 5.6), but not significantly so in turnstones, although there is a tendency for reduced intervals at the lowest recorded visibilities.

5.1.3 Discussion

Animals may adjust their vigilance according to how conspicuous they appear to predators. The brightly-coloured male mallard is more vigilant than the camouflaged female, except when in eclipse plumage, when the two sexes are the same dull colour and are equally vigilant (Lendrem 1983). The camouflaged appearance of the two waders (the turnstone being a mixture of brown, white, grey and black, while the purple sandpiper is a dark grey) makes them far more conspicuous in

Fig.5.3. The relationship between vigilance time and visibility score. Data represented as means $\pm$ 2 S.E. with sample sizes shown. Turnstone (stars and broken line): r = -0.458 (n=317), P<0.001; y = 21.1 - 1.42x.

Purple sandpiper (solid circles and solid line): r = -0.506 (n=220), P<0.001; y = 17.9 - 1.20x.

VIGILANCE TIME (sec/min)
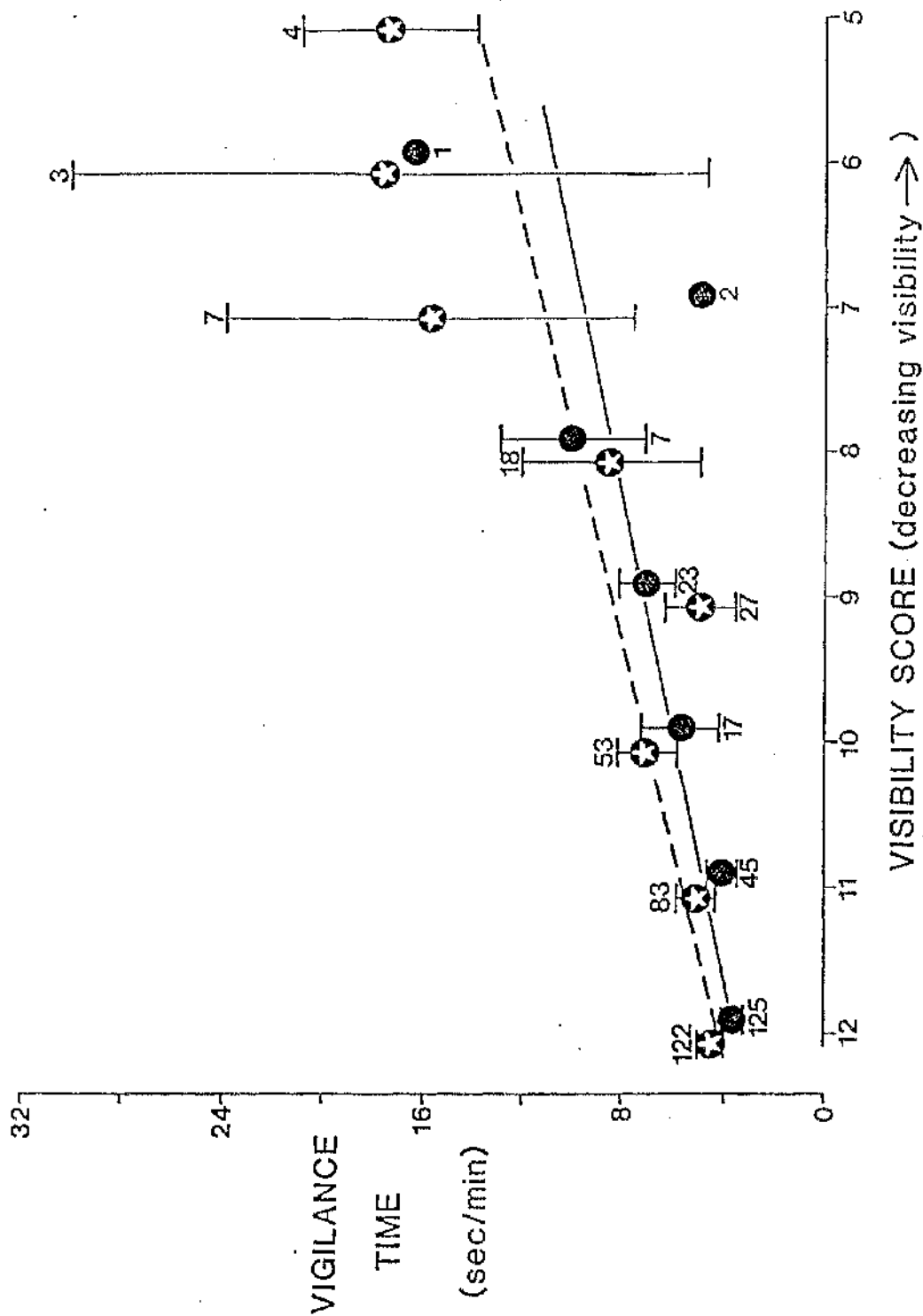
VISIBILITY SCORE (decreasing visibility →)

Fig.5.4. The relationship between scanning rate and visibility score. Data presented as in Fig.5.3. Turnstone (stars): $r_s = 0.111$ (n=317), NS. Purple sandpiper (solid circles and regression line): $r = 0.391$ (n=220), P<0.001; $y = 29.1 - 1.49x$.

SCANNING RATE (scans/min)

VISIBILITY SCORE (decreasing visibility →)
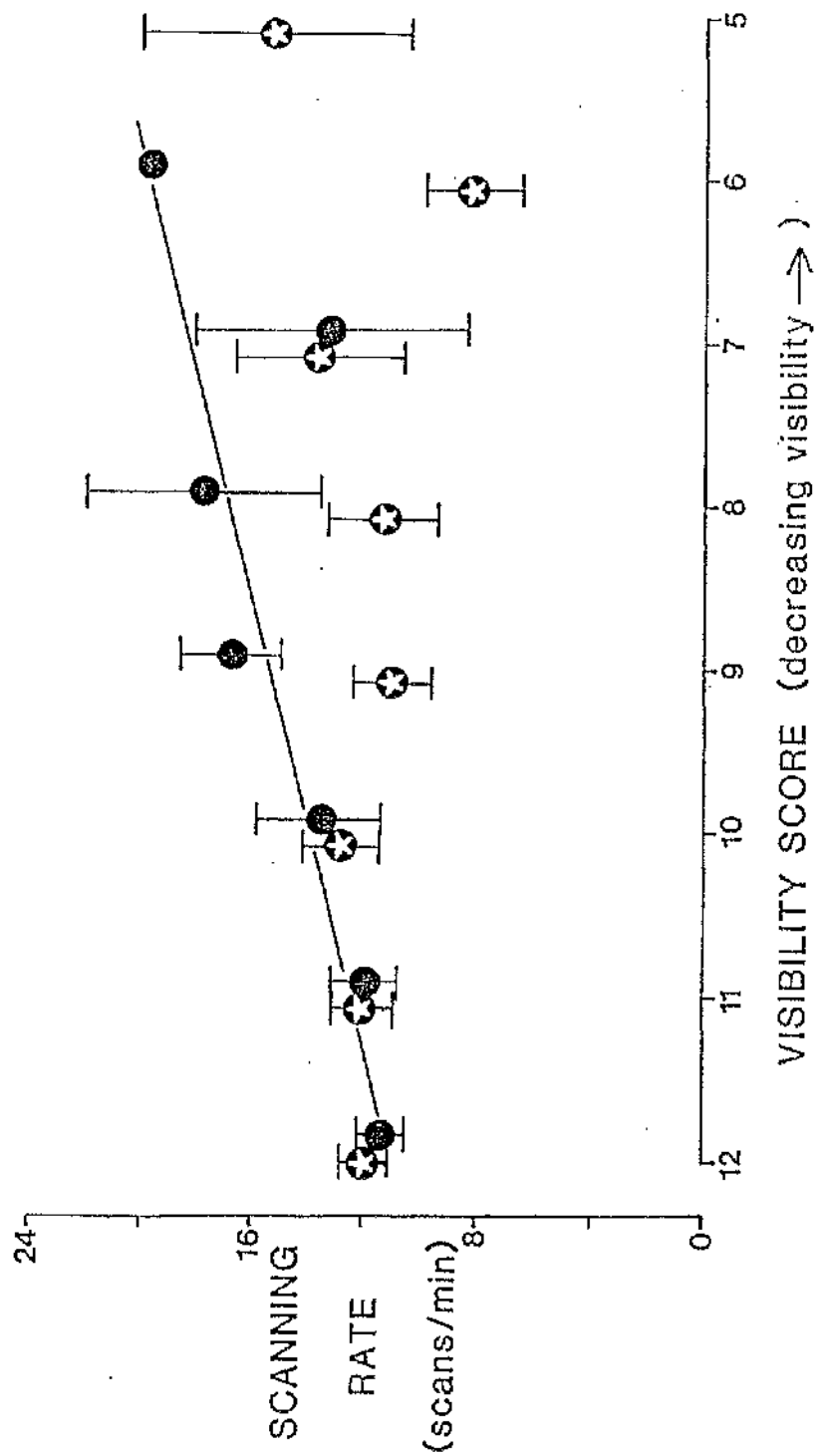
Fig.5.5. The relationship between scan duration and visibility score. Data presented as means $\pm$ S.E. Turnstone (stars): $r_s = -0.278$ (n=317), P<0.001. Purple sandpiper (solid circles): $r_s = -0.312$ (n=220), P<0.001.

SCAN DURATION (s)

3·2 2·4 1·6 0·8 0

VISIBILITY SCORE (decreasing visibility ⟶)

5 6 7 8 9 10 11 12
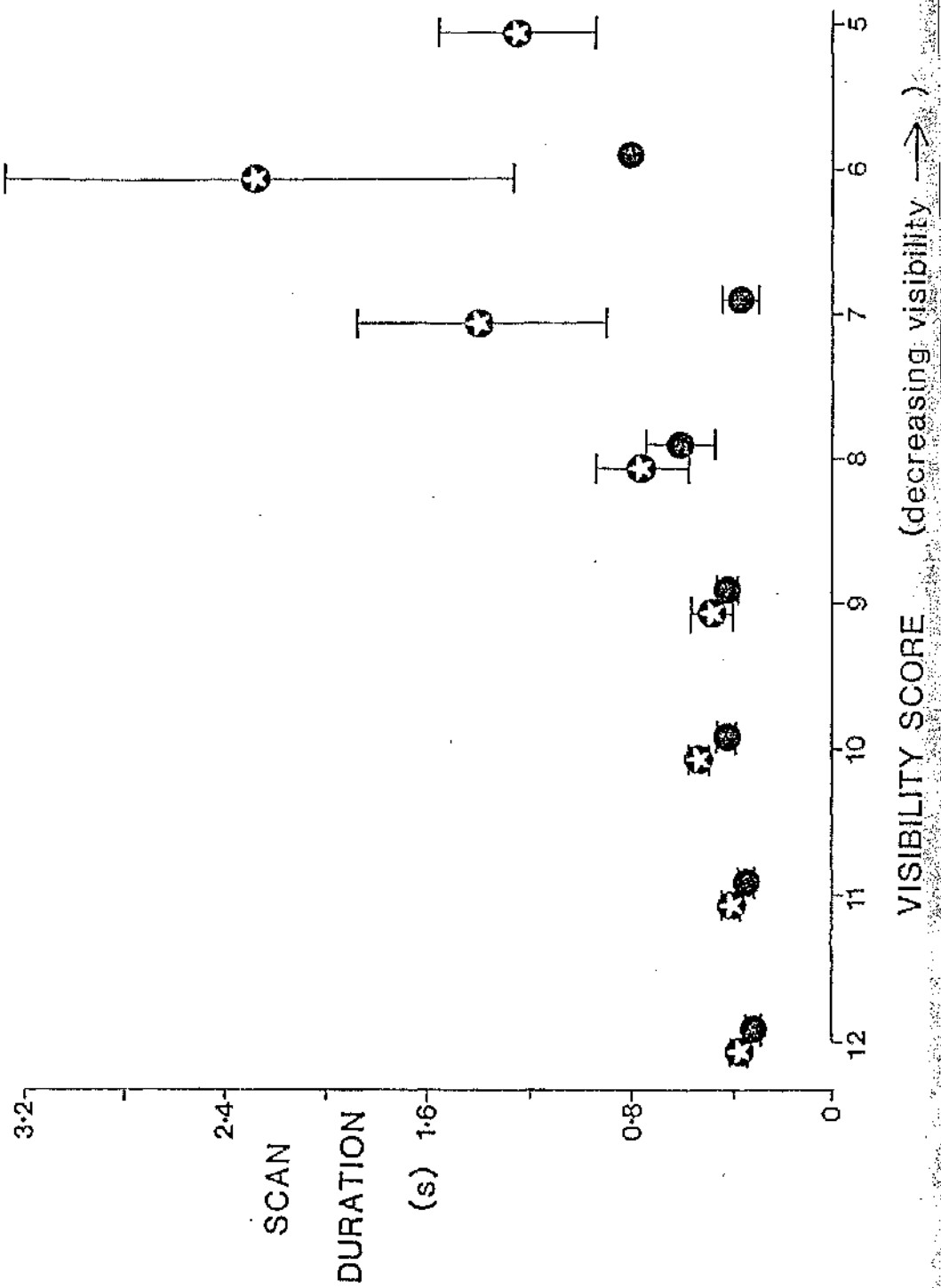
Fig.5.6. The relationship between interscan interval and visibility score. Data presented as in Fig.5.3. Turnstone (stars): $r_s = 0.101$ (n=317), P = 0.072. Purple sandpiper (solid circles and regression line): r = 0.319 (n=220), P<0.001; y = 0.76x − 3.03.

VISIBILITY SCORE (decreasing visibility ⟶)

INTERSCAN INTERVAL (s)
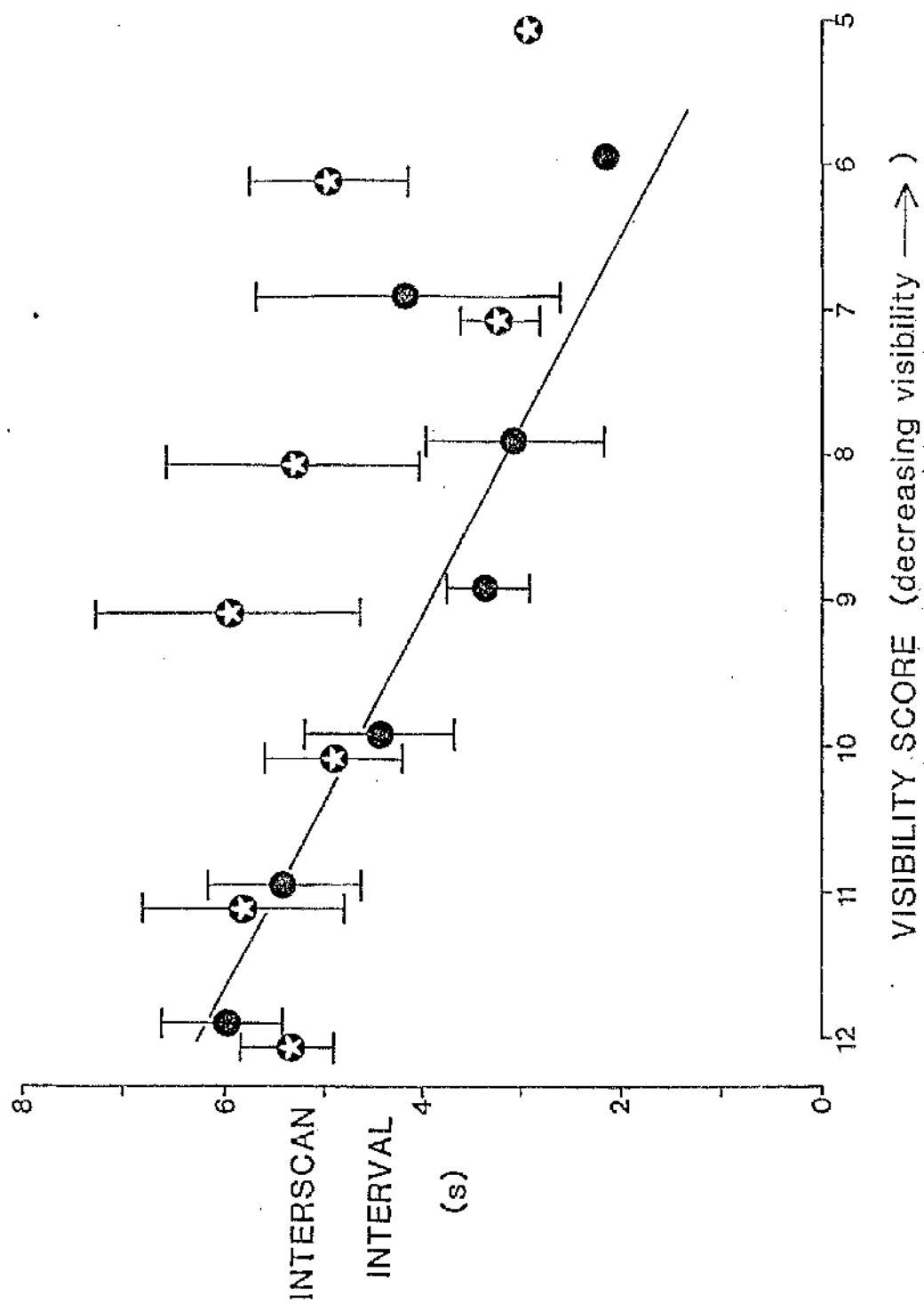
open habitats such as sandy beaches than amongst rockpools or boulders. However, this study has shown that individuals of both species clearly increase their level of anti-predator vigilance as the structural complexity of their surroundings increases, even though their conspicuousness decreases. The extent of the increase in vigilance is considerable; in good visibility areas birds spend less than one tenth of their total time vigilant, while in areas of poor visibility the proportion may be over a quarter. In the latter case much potential foraging time is therefore lost. If the time spent vigilant reflects the bird's assessment of how vulnerable it is (assuming that the time required for actual foraging is constant), then birds 'feel more at risk' as habitat complexity increases.

The presence of objects such as rocks, boulders or banks of seaweed adjacent to a foraging bird will cause complete sectors of its panoramic vision to be blocked. This will prevent it from seeing either neighbouring birds or predators behind those objects. Turnstones and purple sandpipers do not share vigilance with neighbours they cannot see (section 5.2.2), and so a decrease in visibility may produce an increase in individual vigilance due to a decrease in the number of neighbours any one bird can see. However, the effect described here is independent of neighbour density, as this was controlled for by only including in the analysis observations where the density of neighbours visible to the focal bird exceeded the level above which density has a negligible effect on vigilance.

Therefore it is the reduced ability to detect the predator that causes this increase in vigilance. The major potential predators of the birds approach prey by fast dashes either at or close to ground level (dogs and falcons respectively) (Rudebeck 1951, Page & Whitacre

1975, Blick 1980, pers.obs.), relying largely on catching the birds by surprise. Therefore even a low-lying object obstructing a shallow angle above ground level would seriously reduce the efficiency of a scan.

The objects that obstruct vision may help to hide the birds from predators, but do not hamper an attack once the prey has been spotted. This may explain a difference between this study and those of Barnard (1980) on house sparrows Passer domesticus and Caraco et al. (1980) on yellow-eyed juncos Junco phaeonotus, where both increased their vigilance with increasing distance from hedgerows or bushes (i.e. as visibility increased). In these cases the vegetation formed a refuge into which the passerines retreated if alarmed, and so vulnerability increased with increasing distance from this cover. In contrast, waders have no refuge, and so take flight and form highly manoeuvrable flocks when attacked. It therefore becomes more important to detect predators early, and so have an unrestricted view. The same is true of antelopes, as these also avoid predation by outpacing or outmanoeuvring their attackers. Underwood (1982) showed that they too increased their vigilance when in poor visibility habitats. Curlews have been observed to form flocks when feeding in fields surrounded by hedges, while maintaining a dispersed distribution on open mudflats (Abramson 1979); this, too, is probably a response to an increased predation risk, since the hedges would conceal the approach of most predators.

Turnstones and purple sandpipers face the same problem of having to increase their vigilance in areas where their vision is obstructed, but solve it in different ways. Turnstones scan at the same rate but increase the length of each scan, while purple sandpipers increase vigilance mainly by scanning more often. Of the two solutions, increasing the Scanning Rate has most effect on

decreasing the Interscan Interval, which is the period when the bird is most at risk as the probability of predator detection is lowest. Shortening this period reduces the probability that the predator will be able to move from a hidden to an attacking position undetected, as this movement is more likely to be interrupted by the bird raising its head to scan (Pulliam 1973, Lendrem 1982, 1984b). In contrast, a small increase in the length of each scan has little effect in reducing the time between scans, as Scan Duration is still short compared to Interscan Interval (c.f. Figs. 5 and 6). Therefore, for a given increase in the time invested in vigilance, the strategy of increasing Scanning Rate is more effective in reducing the risk of being caught unawares by a predator. However, this assumes that brief scans are as effective in assimilating information in poor visibility as in good visibility; perhaps this may be the case for purple sandpipers but not for turnstones.

Alternatively, the difference between the species may reflect differences in feeding behaviour. Short intervals between scans produce frequent interruptions to foraging, which could be costly in terms of efficiency when food items require long handling times and subtle manipulations. Therefore differences in diet or method of tackling prey items could explain the different strategies for the allocation of time to vigilance and foraging. Turnstones have stronger bills and are able to break open the shells of barnacles, crabs and mussels (Groves 1978, Harris 1979), processes which require coordination and timing. Frequent scanning may therefore reduce the foraging efficiency of turnstones more than that of purple sandpipers, which tend to specialize on prey (such as periwinkles) for which manipulation times are shorter (Chapter 4, Table 4.8). Turnstones did indeed have significantly shorter handling times than

purple sandpipers in rock and boulder habitats, which tend to be those in which visibility is reduced (rock: t=2.27, P<0.05; boulder: t=6.23, P<0.001; data from Table 4.8, with the addition of the mean manipulation time for purple sandpipers in boulders (0.90+0.12 secs., n=52 observations)). In open habitats of unrestricted visibility turnstones behave similarly to purple sandpipers in reducing the interval between scans as a response to decreasing neighbour density (section 5.2.2). However, food types such as barnacles, crabs and mussels that require longer handling times tend to be found only in areas (e.g rock pools) where visibility is reduced, so this does not conflict with the suggestion that prey handling time influences the method used to alter vigilance rates.

5.2 The Effects of Mixed-Species Flocking on the Vigilance of Shorebirds: Who Do They Trust?

Individuals incur a cost when scanning for approaching predators, since this is usually mutually exclusive with other important activities such as foraging. Various studies have shown that investment of time in vigilance may be reduced by associating with conspecifics (e.g. Powell 1974, Lazarus 1978, Abramson 1979, Hoogland 1979, Caraco 1979b). The theoretical explanations of such a reduction are two-fold. Individuals may benefit from the predator-detecting capabilities of fellow group-members, and so in effect 'share' vigilance (Pulliam 1973, Dimond & Lazarus 1974, Treisman 1975a,b); they may also lower their own probability of being predated simply by associating with other equally-attractive prey items (the "selfish herd" hypothesis of Hamilton 1971, Vine 1971).

Many animals feed in mixed-species groups, and there is no theoretical reason why vigilance benefits should be restricted to associations with conspecifics. However benefits from shared

vigilance require information transfer between participants (even if unintentional). This may be limited in taxonomically unrelated species dyads, unless there has been coevolution in signalling, as might occur in sympatric species or those facing similar selection pressures (Marler 1957, Moynihan 1981, Barnard 1982, Halliday 1983). Also vigilance should only be shared with neighbours that are vigilant for the same predators, while the benefit of dilution of the predator's impact by grouping requires that all members of the group are potential prey of that predator. Thus there may be constraints on the extent to which vigilance is shared between species, according to how closely related they are, and how closely matched in distribution, size and vulnerability.

A further complication is that in habitats of high structural complexity close neighbours may not be able to see each other. These birds might be predicted not to share vigilance with each other as (a) they cannot detect neighbours who 'cheat' by not scanning (Pulliam et al 1982), and (b) they may be unable to tell how many 'hidden neighbours' are present.

Interspecific sharing of vigilance and the effect of hidden neighbours have not been examined in detail by earlier workers. I therefore studied these aspects in the turnstone and purple sandpiper, which outside the breeding season often flock with each other and with other waders, while looser associations are formed with birds such as gulls, corvids, starlings and feral pigeons (Chapter 1). Thus a range of birds may be found in the vicinity of individuals of both study species, ranging from conspecifics to species of unrelated orders. The method by which birds altered vigilance in response to changes in density was investigated. Overall levels of vigilance can be increased in two ways, which are not

mutually exclusive: increasing the number of vigilant scans per unit time, or increasing the duration of each scan (McVean & Haddlesey 1980).

This section is therefore concerned with three questions:
(1) With which species do individual turnstones and purple sandpipers share vigilance (i.e. which species can be trusted)?
(2) Is vigilance shared with birds out of sight?
(3) What methods do birds use to alter vigilance levels?

5.2.1 Methods

The same data set was used as in section 5.1; the methods of data collection have thus already been described, and only additional details on the measurement of density are given here.

At the end of the one minute observation the local bird density experienced by the focal bird was recorded. Density around the focal bird, rather than flock size (as used for example by Powell (1974), Lazarus (1978) and Caraco (1979a)), was considered more likely to influence levels of vigilance for two reasons. Firstly birds often did not form discrete flocks, but were (unevenly) spread over a large area, thus producing difficulties in defining flock size. This was partly due to the presence of species (such as oystercatcher) that maintain a over-dispersed foraging distribution (Vines 1980). Secondly, when flock density is uneven, individuals are perhaps more likely to adjust their vigilance according only to the number of immediate neighbours they have (following from both Hamilton's domain of danger hypothesis and the difficulties individuals may have in monitoring the numbers and behaviour of more distant birds). This could explain the "edge effect" (Jennings & Evans 1980, Blick 1980, Inglis & Lazarus 1981, Robinson 1981), where peripheral individuals of a group may be more vigilant than those at the centre.

Bird densities were measured in two ways – the numbers of each species of bird within ten metres of the focal bird (=overall density), and the numbers of each species within ten metres which were judged to be visible to the focal bird (taking into account rocks and other objects that prevented neighbours from seeing one another) (=visible density). Therefore the two densities were equal in habitats with no obstructions to vision, but as the habitat structural complexity increased visible density became lower than overall density. Both density measures excluded the focal bird, so as to allow direct comparisons between the densities of conspecifics and of other species, in their effect on vigilance. Bird-lengths were used as a measuring unit, and the relatively close proximity of the observation vehicle to the birds and its height advantage aided the judgement of distances.

Four vigilance parameters were selected for analysis, as defined in section 5.1.1:

(1) Vigilance Time, (2) Scanning Rate, (3) Scan Duration and (4) Interscan Interval

5.2.2 Results

(a) Is Vigilance Shared With Birds Out of Sight?

A comparison was made between effects of Overall Density and visible density on vigilance, by running two parallel step-wise multiple regressions of Vigilance Time on the densities of different species, using Overall Densities in one regression and Visible Densities in the other. The relationships between Vigilance Times and density could be made linear by taking the natural logarithms of all variables (adding one to all densities so as to avoid taking the logarithm of zero). The samples for both species consisted of all observations obtained between 8th April 1982 and 26th April 1983

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where visible density differed from overall density. The effect of visibility was controlled for by entering the visibility score as a variable on the first step of the regression procedure. All species which occurred in more than one percent of observations and were recorded at at least three different densities were entered as separate variables (except that all species of gull were combined to produce a single density for gulls; these were predominantly herring gulls). The results of the parallel regressions were compared for the amount of variance in Vigilance Times explained by the two measures of density. Table I shows that for both species it is evident that the variance explained by Visible Densities is greater than that by Overall Densities, indicating that individuals adjust their rate of vigilance more according to the number of neighbours they can see than the number that are actually present. Further analyses in this chapter therefore use Visible rather than Overall as a measure of bird density.

Table 5.1. Comparison of the Importance of Overall Neighbour Density and Visible Neighbour Density in Determining Vigilance Time in Turnstone and Purple Sandpiper, After Removal of the Effects of Visibility.

Species	Sample size	Amount of Variance in Vigilance Explained* by	
		Overall Density	Visible Density
Turnstone	240	13.74%	15.31%
Purple Sandpiper	319	10.97%	14.52%

*Given by sum of R^2 values for all species whose densities significantly affected vigilance (F-test, $P<0.05$)

(b) Which Species Can Be Trusted?

Having determined that visible density was more important than Overall Density, further stepwise multiple regressions were carried out on the full sample of observations, to determine which species

did affect the vigilance of turnstones and purple sandpipers, and the relative importance of each variable. The same selection criteria for species variables and data transformations were used as before. This time, however, the order of entry of variables into the regression was not predetermined. The results are given in Table 5.2; variables found to have nonsignificant F-values (P > 0.05) are listed below the table.

Table 5.2. Variables Found to be Significantly Related to the Vigilance Time of Turnstone and Purple Sandpiper

Variable$^{\$}$	F-Value		Amount of Variance Explained	S.E. of Regression Coefficient
(a) TURNSTONE				
Turnstone density	146.4	***	14.83%	0.026
Visibility score	82.79	***	9.63%	0.138
Purple sandpiper density	55.23	***	5.84%	0.044
Redshank density	24.90	***	2.34%	0.037
Oystercatcher density	10.16	**	1.01%	0.040
		Total:	33.64%	

Sample size = 673, overall F-value = 67.63, P<0.001.
Bird densities found not to significantly affect vigilance: Ringed plover, dunlin, pigeon, gull, starling.

(B) PURPLE SANDPIPER				
Purple sandpiper density	154.7	***	34.56%	0.028
Visiblity score	49.50	***	6.17%	0.185
Turnstone density	6.80	*	0.58%	0.052
Gull density	6.39	*	0.81%	0.028
		Total:	42.11%	

Sample size = 460, overall F-value = 82.76, P<0.001.
Bird densities found not to affect vigilance: Redshank, ringed plover, oystercatcher.

$\$$ All variables (including the dependent) were transformed to natural logarithms for the regression. Significance levels: *** P<0.001, ** P<0.01, * P<0.05.

While the density of conspecifics is the most important variable

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affecting Vigilance Time in both species, it is also adjusted according to the density of several other species and the visibility score. The overall regression equations are as follows:

Turnstone:

$$\ln(\text{Vigilance Time}) = 5.32 - 0.314 \ln(T) - 0.329 \ln(P) - 0.183 \ln(R) - 0.126 \ln(O) - 1.254 \ln(\text{Visibility Score})$$

Purple Sandpiper:

$$\ln(\text{Vigilance Time}) = 5.37 - 0.348 \ln(P) - 0.136 \ln(T) + 0.072 \ln(G) - 1.305 \ln(\text{Visibility Score})$$

where T, P, R, O and G are Visible Densities of turnstones, purple sandpipers, redshanks, oystercatchers and gulls respectively.

The regression constant and coefficients for conspecific density and Visibility Score are very similar for the two species. However turnstones share vigilance with more species, while the vigilance of purple sandpipers actually increases as gull density increases. In turnstones the coefficient in the regression equation for conspecific density is significantly greater in magnitude than that for redshanks or oystercatchers (d=2.91, P<0.01 and d=3.97, P<0.001 respectively), but not significantly different from that for purple sandpiper density (d=0.29, NS). Therefore a turnstone's vigilance is reduced more in the presence of turnstones and purple sandpipers than it is by redshanks or oystercatchers. With purple sandpipers, however, the coefficient for conspecific density is greater in magnitude than that for turnstone density (d=3.60, P<0.001), indicating that turnstones have less of an effect in reducing a purple sandpiper's vigilance than do other purple sandpipers. The regression coefficient for Visibility Scores shows that vigilance increases appreciably with decreasing visibility in both species; the effect of visibility has already been investigated in more detail in section 5.1.

(c) How is the Level of Vigilance Altered?

To simplify analyses and representation of the data, densities

of the species that significantly reduced vigilance (i.e. turnstone, purple sandpiper, redshank and oystercatcher for turnstone; purple sandpiper and turnstone for purple sandpiper) were summed to produce one total density. As all species do not have equal effects on reducing an individual's vigilance, densities of species that had less effect than its own species were first converted to 'conspecific-equivalent' densities. This was done using the ratios of the respective species coefficients from the multiple regression equations given above (i.e. for a turnstone, a neighbouring redshank is equivalent to 0.183/0.314 conspecifics). The effect of visibility was removed by only considering observations where visibility was unimpaired (i.e. scored 12). Figure 5.7 shows that, for both species, Vigilance Time drops rapidly as density increases from zero (i.e. no other birds of significant species within 10m of the focal bird) to around six, but then levels off to an asymptote denoting a minimum level of vigilance. This change in vigilance rate is due to changes in both Scanning Rate (Fig. 5.8) and Scan Duration (Fig. 5.9). Scan Duration remains constant at densities greater than five, but increases sharply as density drops below this level. In contrast the Scanning Rate initially increases in both species as density drops, but this increase is not maintained as density reaches the lowest levels.

If the increase in level of vigilance with decreasing density was to be produced solely by increasing scanning rate, it can be shown that birds at a density of zero would have to scan 46.8 (turnstone) or 54.6 (purple sandpiper) times per minute (calculated as $\text{Vigilance Time at zero density} / \text{mean Scan Duration for density} > 5$). This rate of head movement would clearly reduce feeding efficiency drastically, and so there is an increase in Scan Duration

Fig.5.7. The relationship between vigilance time and surrounding visible density of birds (expressed as conspecific-equivalents, see text for details). Data are presented as grouped means $\pm$ S.E.

(a) Turnstone: $r_s = -0.395$ (n=195), P<0.001.

(b) Purple sandpiper: $r_s = -0.527$ (n=173), P<0.001.
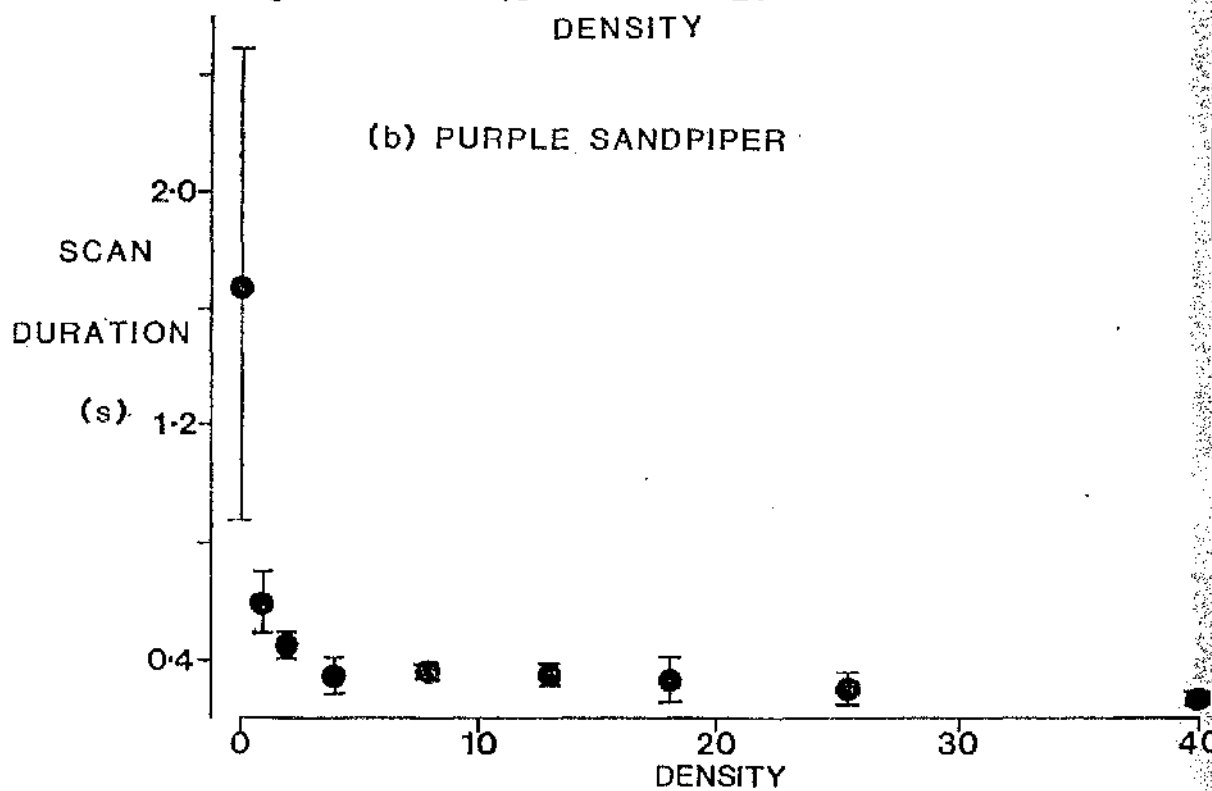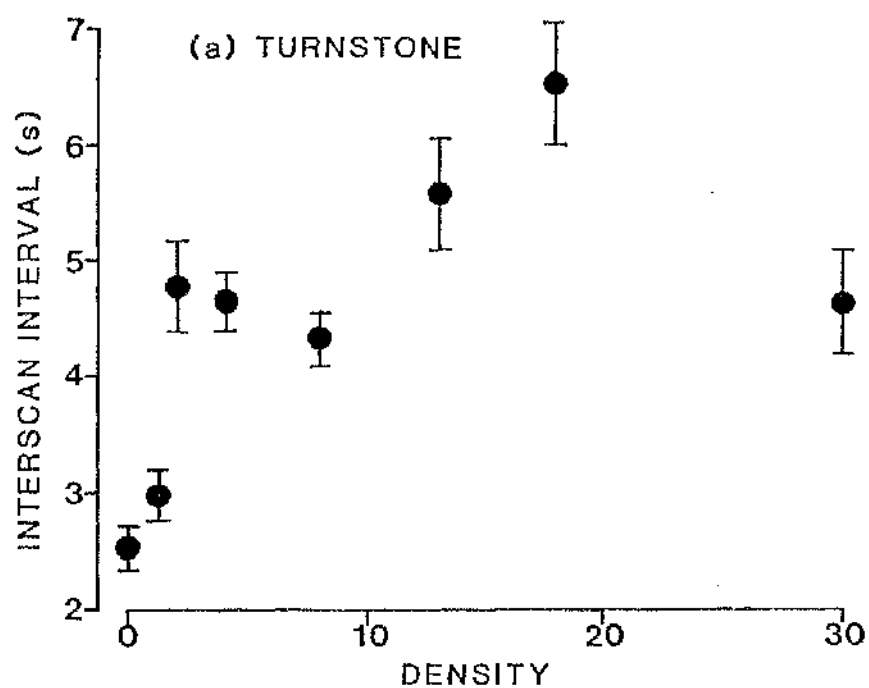
(a) TURNSTONE
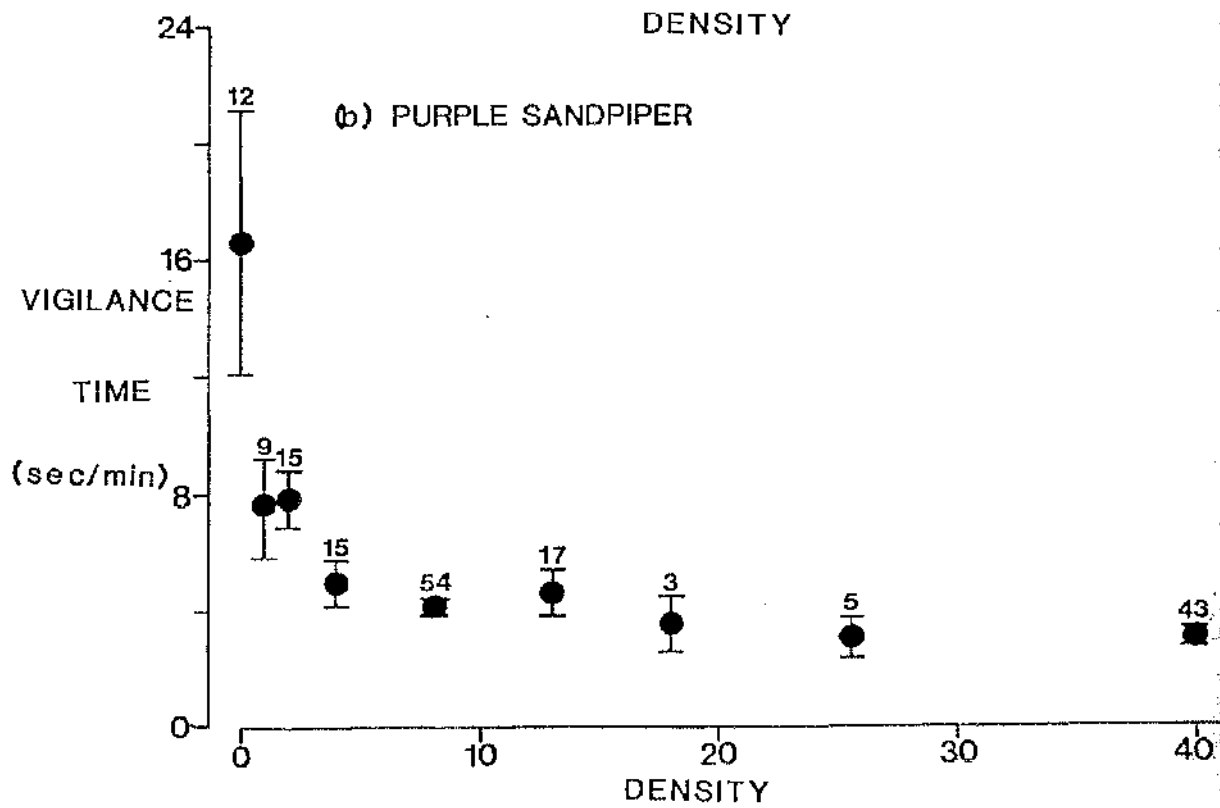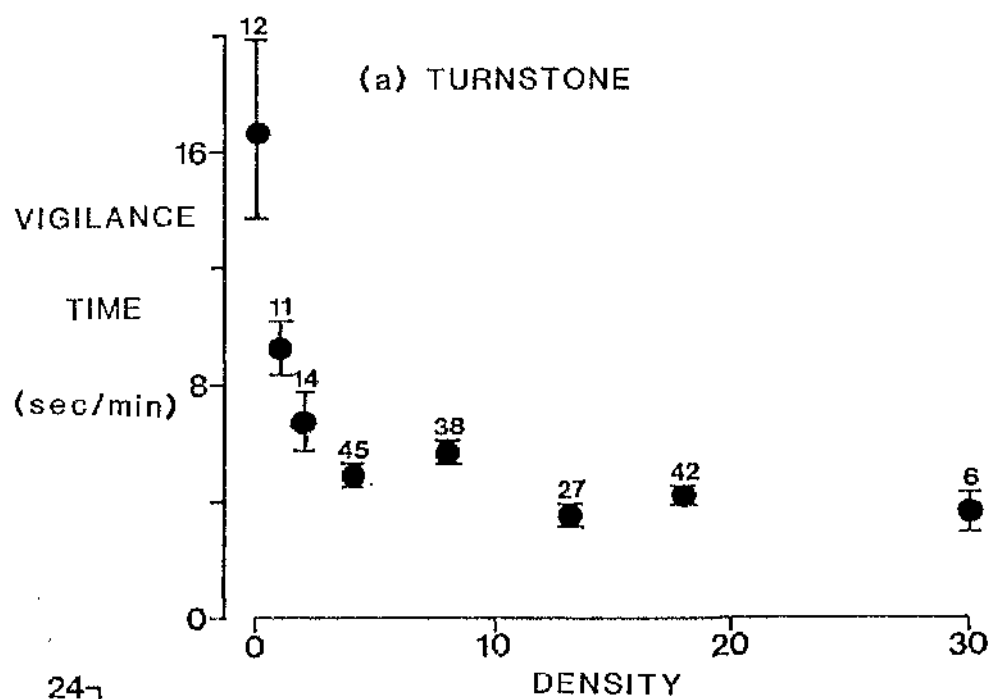
(b) PURPLE SANDPIPER

Fig.5.8. The relationship between scanning rate and visible density (expressed as conspecific-equivalents, see text for details). Data are prsented as in Fig.5.7.

(a) Turnstone: $r_s = -0.339$ (n=195), P<0.001.

(b) Purple sandpiper: $r_s = -0.389$ (n=173), P<0.001.

(a) TURNSTONE

SCANNING RATE (scans/min)

DENSITY

(b) PURPLE SANDPIPER

SCANNING RATE (scans/min)
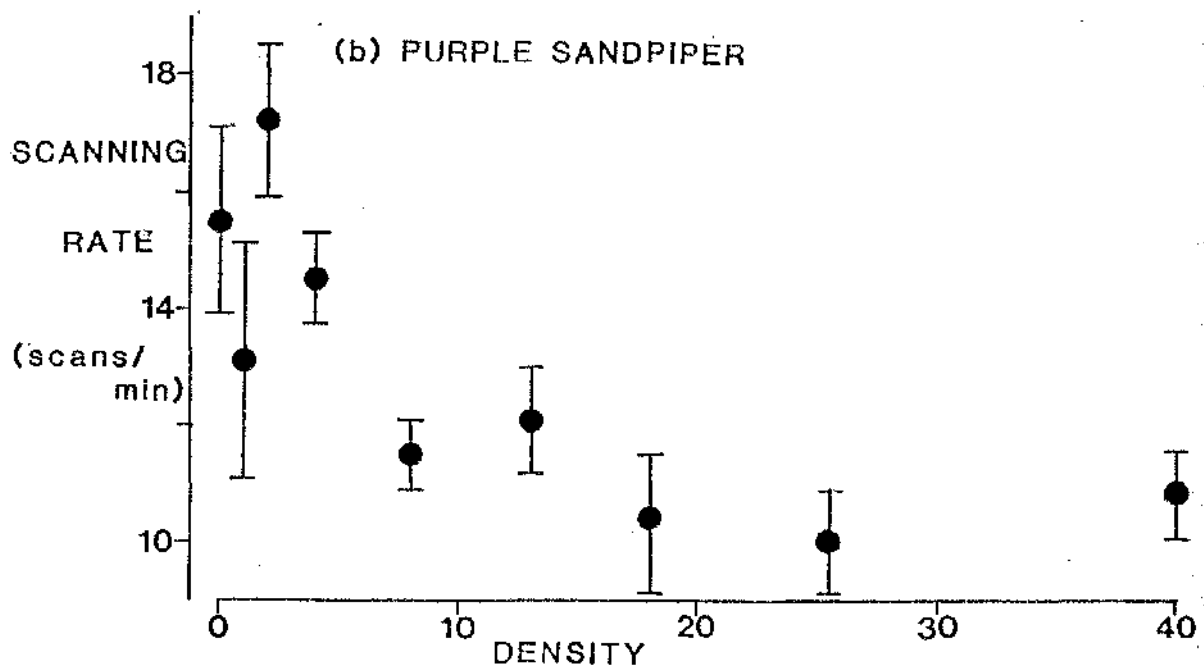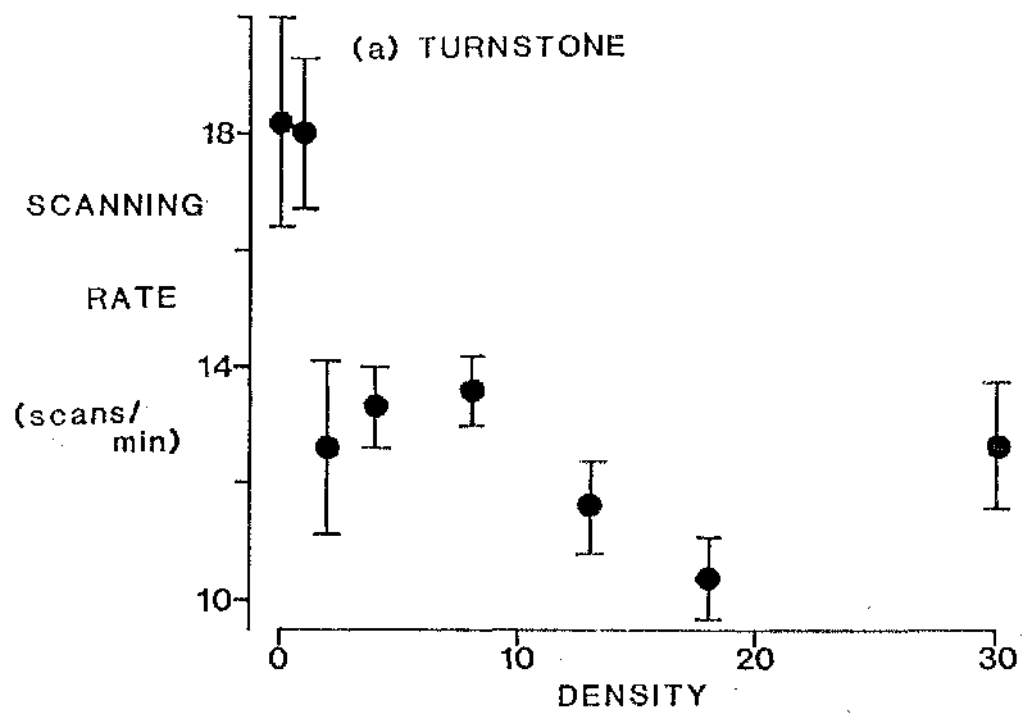
DENSITY

Fig.5.9. The relationship between scan duration and visible density (expressed as conspecific-equivalents, see text for details). Data are presented as in Fig.5.7.

(a) Turnstone: r_s = −0.208 (n=195), P<0.01.

(b) Purple sandpiper: r_s = −0.452 (n=173), P<0.001.

(a) TURNSTONE

SCAN DURATION (s)

DENSITY

(b) PURPLE SANDPIPER

SCAN DURATION (s)
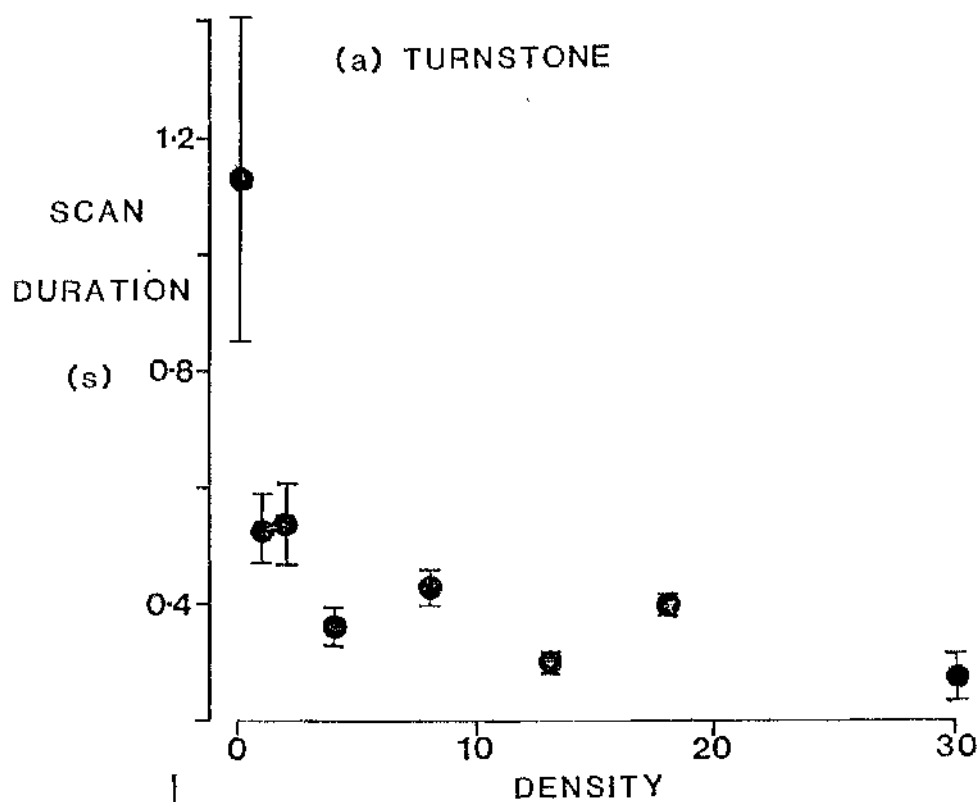
DENSITY

Fig.5.10. The relationship between interscan interval and visible

density (expressed as conspecific-equivalents, see text for details).

Data are presented as in Fig.5.7.

(a) Turnstone: r_s = 0.402 (n=195), P< 0.001.

(b) Purple sandpiper: r_s = 0.469 (n=173), P<0.001.
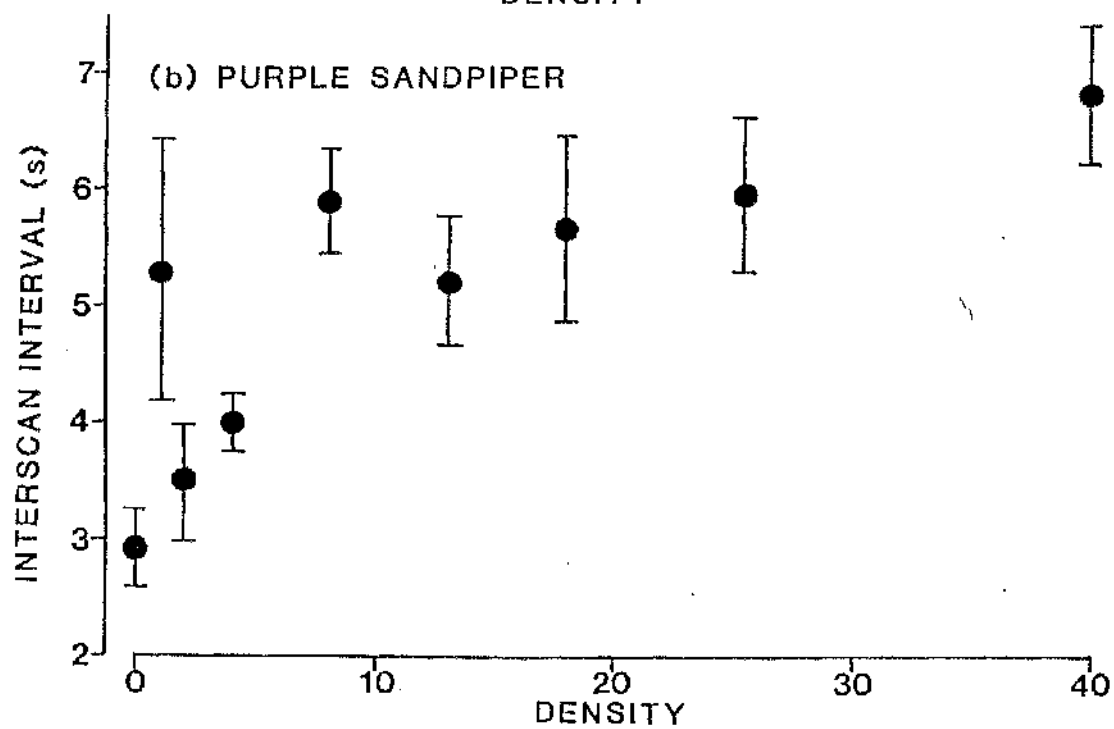
at the lowest densities, while scan rate remains relatively constant.

The Interscan Intervals increase with density in both species as a consequence of a lower scanning rate and increased time spent not vigilant (Fig. 5.10). However in turnstone the Interscan Interval then drops again for densities greater than 21 (t = 2.69, P<0.01 compared with density = 16-20). There is a tendency (although not significant) for Scanning Rate to increase over this range (t = 1.81, N.S. for the same comparison). No such effect is apparent in purple sandpipers.

5.2.3 Discussion

Both turnstones and purple sandpipers do not 'trust' neighbours that they cannot see, to be vigilant on their behalf. There are two reasons why this might be so, as mentioned earlier. Firstly birds cannot detect cheats. Pulliam et al. (1982) showed that yellow-eyed juncos scan at a rate that would be open to exploitation by cheats who do not scan themselves but rely solely on their neighbours. They hypothesised that individuals should therefore be monitoring the vigilance of their neighbours, and clearly this is impossible when neighbours are not visible. Secondly, birds may be unable to assess the Overall Density, as they are unable to tell how many hidden neighbours are present. In addition birds must be able to see the alarm-flight of their neighbours, if this is the method of signalling the approach of a predator (Davis 1975, Thompson & Barnard 1983). Therefore the decision rule on vigilance levels in the individual should be based on the number of neighbours it sees upon raising its head to scan. This would explain the greater importance of Visible Density (rather than Overall) in influencing vigilance levels.

Different species do not have equal effects in reducing vigilance levels of individuals in mixed-species aggregations. In

both turnstones and purple sandpipers conspecifics have the greatest effect in reducing vigilance, while the presence of other species may either reduce or increase vigilance, or have no effect. These differences may be expected to depend partly on the relative size of the other species. Much larger species may have fewer predators and so not show alarm at all possible predators of small waders. Indeed larger species may even in themselves constitute a threat to the small waders, so making sharing of vigilance unlikely. In addition, the evolution of information transfer between species probably depends on some degree of sympatry in habitat type, and so the communication of alarm may be limited between species that are very rarely found in the same areas. Thus the only other species found to reduce purple sandpiper vigilance is the turnstone; the other species included in the species analysis (Table 5.2) were either much larger (Table 5.3) or were rarely encountered by purple sandpipers (ringed plovers being mainly restricted to sandy habitats (Pienkowski 1981)). The turnstone is larger than the purple sandpiper, and shares vigilance with correspondingly larger wader species. The relative importance of purple sandpipers, redshanks and oystercatchers in reducing turnstone vigilance (Table 5.2) corresponds to their size compared to that of turnstones (Table 5.3), such that the similarly-sized purple sandpiper has more effect than the much larger oystercatcher. Dunlins, ringed plovers, pigeons, starlings and gulls had no significant effect on turnstone vigilance; the first two associate with turnstones less frequently than do the wader species found to have a significant effect, while pigeons and starlings are taxonomically only distantly related to waders, and have little overlap in habitat type.

The presence of gulls actually increases purple sandpiper vigilance, but has no significant effect on turnstones. The increased

vigilance is probably due to two factors: small waders must avoid being 'trodden on' by the very much larger gulls, and adjacent gulls themselves constitute obstructions to visibility – the situation can be imagined as akin to 'moving boulders' that must be avoided as well as looked over. Both of these effects are only important when the gull and wader are in close proximity. A similar result was noticed on the rare occasions when turnstones were found feeding in high density gull flocks.

Table 5.3. The Sizes (Expressed as Weights) of Bird Species Associating with Turnstones and Purple Sandpipers

Species		Mean Weight (g) *
Waders:	Dunlin	53.6
	Purple sandpiper	63.5
	Ringed plover	60.7
	Turnstone	112
	Redshank	176
	Oystercatcher	611
Non-waders:	Starling	79.5
	Domestic pigeon	249
	Herring gull	895

* Weights of waders and herring gull from Cramp & Simmons (1982), and of starling and pigeon from Greenewalt (1962)

This relationship is rather different from that involving black-headed gulls Larus ridibundus and the two waders lapwing Vanellus vanellus and golden plover Pluvialis apricaria, where the gulls appeared to provide the waders with early warning of alarm (Thompson & Barnard 1983) but were kleptoparasitic in turn and so imposed a high cost to wader foraging efficiency. This led to an increase in wader vigilance with increasing numbers of gulls (Barnard et al. 1982). Herring gulls in the present study rarely kleptoparasitised either turnstones or purple sandpipers, possibly because food items were small and therefore relatively quickly consumed and

energetically unattractive to the gulls (Brockmann & Barnard 1979).

The greatest changes in vigilance with changing density occur over the density range of zero to five birds within 10m of the focal individual, with little or no further reduction in vigilance as density increases beyond this point. However, the benefit of the dilution effect will continue to increase. In turnstones the increase in Scanning Rate (and resulting decrease in Interscan Interval) at high densities may be due to the increase in inter- and intra-specific aggression with increasing density (Chapter 4 and references therein). Much of the intra-specific aggression is concerned with food, with birds kleptoparasitising or displacing one another from sources of food. Therefore at high densities birds may become vigilant against each other (in addition to being vigilant against predators), either to spot opportunities for stealing food or conversely to avoid being the victim of a surprise attack. The difference between turnstones and purple sandpipers in this respect may be a result of the differences in rates of kleptoparasitic aggression, as turnstones have a higher rate of interaction over items of food (Chapter 4). There is also the possibility that intraspecific vigilance is for the purpose of feeding enhancement, whereby individuals improve their foraging performance by copying their neighbours (Krebs et al. 1972).

The two parameters Scan Duration and Scanning Rate alter with density but over different density ranges, with a switch from increased Scanning Rate to increased Scan Duration as density decreases below a certain level. Below this level Scan Duration is constant (approximately 0.37 seconds in both species); this is presumably the minimum time needed to take in the information required from a scan. The method of adjustment of vigilance levels by altering these two parameters is very similar in the two species.

This contrasts with the situation where visibility varies, where the species alter their vigilance in quite different ways (section 5.1.2). McVean & Haddlesey (1980) found both variables altered according to the overall vigilance rate in house sparrows , but did not directly investigate the effect of flock density or size. The fact that Scan Duration varies has implications for studies that have assumed that vigilance levels are controlled purely by scanning rate (e.g. Fleischer 1983). For this to be true, the highest vigilance levels observed in this study would require impossibly high Scanning Rates, as shown earlier. Therefore the costs of vigilance must be measured (at least in these species) in terms of time spent vigilant as well as the number of scans per unit time.

5.3 Changing Priorities: The Effect of Pre-Migratory Fattening on the Trade off Between Foraging and Vigilance

Many studies of foraging behaviour have concentrated on how animals might maximise their net rate of resource acquisition, the resource measured usually being energy (reviewed in Krebs 1978). However, recent work has shown that selection pressures other than the need to acquire resources might influence foraging behaviour (Krebs & McCleery 1984). For instance, an increase in the risk of predation might cause a shift from a strategy which maximised foraging efficiency to one less efficient but safer (Schoener 1971, Covich 1976). Therefore, while an animal's optimal strategy may not be optimal with respect to any one selection pressure, it may nonetheless represent the best compromise between conflicting selection pressures (i.e. it maximises overall survival and reproductive fitness). Spatial and temporal variations in the importance of the different parameters can lead to different solutions to such conflicts, so that optimal behaviour must be

considered as a dynamic concept, with a continual shifting of the relative costs and benefits of the different behavioral options (Pulliam 1976, McCleery 1978).

Of the various conflicts which can occur, that between the need to feed and the need to avoid predation has been studied in most detail. An increased predation risk may cause a shift in feeding location away from the area of highest net energy intake to one where risk of predation is reduced (Milinski & Heller 1978, Sih 1980, 1982a). Alternatively, there may be an increased investment in time spent vigilant for predators (Caraco et al. 1980a), which also tends to reduce food intake rate as foraging and vigilance are usually incompatible (Pulliam 1973, Powell 1974, Barnard 1980a, Goldman 1980). Although starved animals may initially optimise foraging (Sih 1982b) at the expense of predator avoidance (Heller & Milinski 1979), the risk of starvation diminishes the longer the animal feeds, so that anti-predatory strategies increase in importance as satiation is approached (McCleery 1978, Krebs 1980b).

The relative importance of foraging is not only affected by an animal's immediate needs; there are times when animals need to lay down energy reserves for anticipated future costs. An example of this is the pre-migratory period, as the migration itself may be over long distances and so impose high energetic costs due to prolonged locomotion. The individual must therefore accumulate energy stores excess to its normal requirements prior to departure, especially as feeding may not be possible en route (Page & Middleton 1972). Foraging efficiency may thus be particularly important during this period.

This section examines whether the increased importance of foraging prior to migration causes an alteration in the balance

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between foraging and avoidance of predation, by measurement of the time invested in anti-predatory vigilance in non-migratory and migratory sub-populations of turnstones, both before and during the period of pre-migratory fattening.

The north-west Palearctic population of turnstones breeds in the arctic tundra of north-east Canada and Greenland, and winters on rocky shorelines in western Europe (Branson et al. 1978). The energetic requirements of spring migration in the turnstone are considerable; for birds wintering in Britain the flight distances involved may be over 3500 km, including at least 1000 km of sea between Scotland and Iceland which must be flown non-stop, and there may be little replenishing of fat reserves once Iceland is reached (Wilson 1981). In addition, birds that arrive in the arctic having completely used up their reserves may subsequently starve to death if weather conditions deteriorate (Morrison 1975). Consequently birds do not leave Britain until they have greatly increased their fat and protein stores, as indicated by an increase in weight of over 40% (from the average winter weight of around 110g) in the three weeks preceding migration (Clapham 1979). However, there are reasons to believe that any delay in departure could seriously affect breeding success. Comparison of departure dates (Clapham 1979, Chapter 2) with dates of arrival in the arctic (Parmelee & MacDonald 1960) indicate that the migration is rapid and synchronised. All breeding birds normally arrive in the arctic within several days of each other, and pairs are established on breeding territories within a week (Parmelee & MacDonald 1960). Late arriving individuals could be at a severe disadvantage in the competition for mates and territories, and it is therefore important not only to build up enough migratory reserves prior to departure, but to do this at the correct time and rate.

Juveniles (birds in their first year of life) migrate south in

autumn to the same wintering grounds as adults; however they rarely return to the arctic to breed the following spring but instead remain in the wintering areas (Cramp & Simmons 1982, also Chapter 2). They maintain the winter weight through to the summer (Branson et al. 1979) and therefore provide a control against which the pre-migratory behaviour of the adults can be measured. As turnstones keep to small home ranges in the winter (Chapter 3), the behaviour of the same marked individuals can be followed until the moment of spring departure.

5.3.1 Methods

The data used in this analysis were Vigilance Times from the one minute focal bird observations; cases were selected where the focal bird was colour-ringed and hence of known age category. The methods of collecting the data have already been described in section 5.1.1. To simplify the analysis, only observations where the Visibility Score was recorded as 12 (i.e. the bird had unrestricted visibility) were included. All data were collected between 3rd February 1982 and 17th May 1983.

Migratory departure occurred during early- to mid-May, with only three colour-ringed adults remaining on their normal home ranges by 17th May 1983. Therefore the three-week period of weight increase in adults was taken to be from 28th April to 18th May, and the data were divided accordingly into winter and pre-migratory fattening periods.

5.3.2 Results

In adults there was a negative linear relationship between the logarithm of vigilance and the logarithm of bird density in both the winter and pre-migratory periods (Fig. 5.11), such that birds reduced the proportion of time spent scanning as surrounding shorebird

density increased (as found for the complete winter data set (including data from non-colour-ringed birds) in section 5.2.2). The relative effect of density was the same in the two periods (covariance analysis, comparing slopes of the two regression lines: $F_{128,2}=0.81$, N.S.). However, the overall level of vigilance was significantly lower in the period prior to migration compared to the rest of the winter (covariance analysis, comparing elevations: $F_{128,1}=25.74$, P<0.001).

The short duration of observations (necessary as bird density fluctuated with time) produced large variances in observed vigilance rates. This resulted in the sample sizes obtained for juveniles being too small to produce significant regressions between vigilance and density, especially as those observations from the pre-migration period were from a rather restricted range of densities. However there is no reason to suppose that density does not have a similar effect on the vigilance of juveniles as on that of adults (as their behaviour does not differ markedly in other respects). Comparing the juvenile data with those for adults shows the former to fit the adult winter relationship (rather than that for adults in the pre-migration period) in both periods of data collection (Fig. 5.12). Testing statistically (using the null hypothesis that there should be equal numbers of juvenile data points either side of the adult regression lines), juveniles were not significantly different from adults in their vigilance levels in winter (binomial P=0.49), but were more vigilant than adults in the pre-migration period (binomial P=0.01). Juvenile vigilance in the adult pre-migration period was therefore maintained at the winter level (comparing with winter adults, binomial P=0.16).

Fig.5.11. The relationship between vigilance time of adult turnstones and visible density (expressed as conspecific—equivalents, see text for details). Data are presented as in Fig.5.7.

Winter period (circles and solid regression line): $r = 0.519$, $P<0.001$; $y = -0.383x + 2.29$.

Pre-migratory period (squares and dotted regression lines): $r = -0.459$, $P<0.001$; $y = -0.495x + 1.93$.

FLOCK DENSITY (LOG SCALE)

INDIVIDUAL VIGILANCE sec/min LOG SCALE
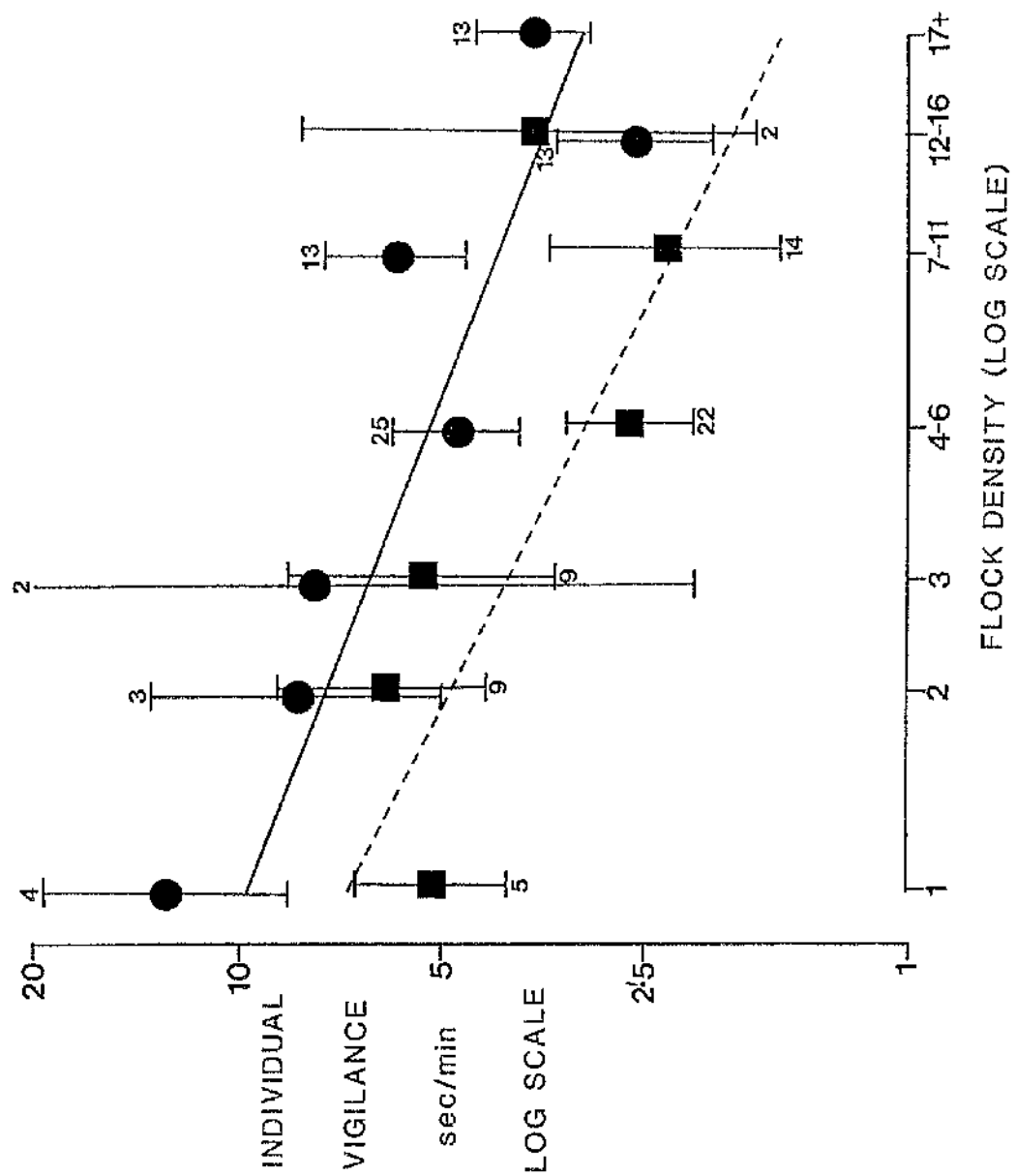
Fig.5.12. The relationship between vigilance time of juvenile turnstones and visible density (expressed as conspecific-equivalents, see text for details). Observed values for winter (circles) and adult pre-migratory periods (diamonds) are shown, together with the adult regression lines from Fig.5.11 for comparison.

INDIVIDUAL VIGILANCE sec/min LOG SCALE

FLOCK DENSITY (LOG SCALE)
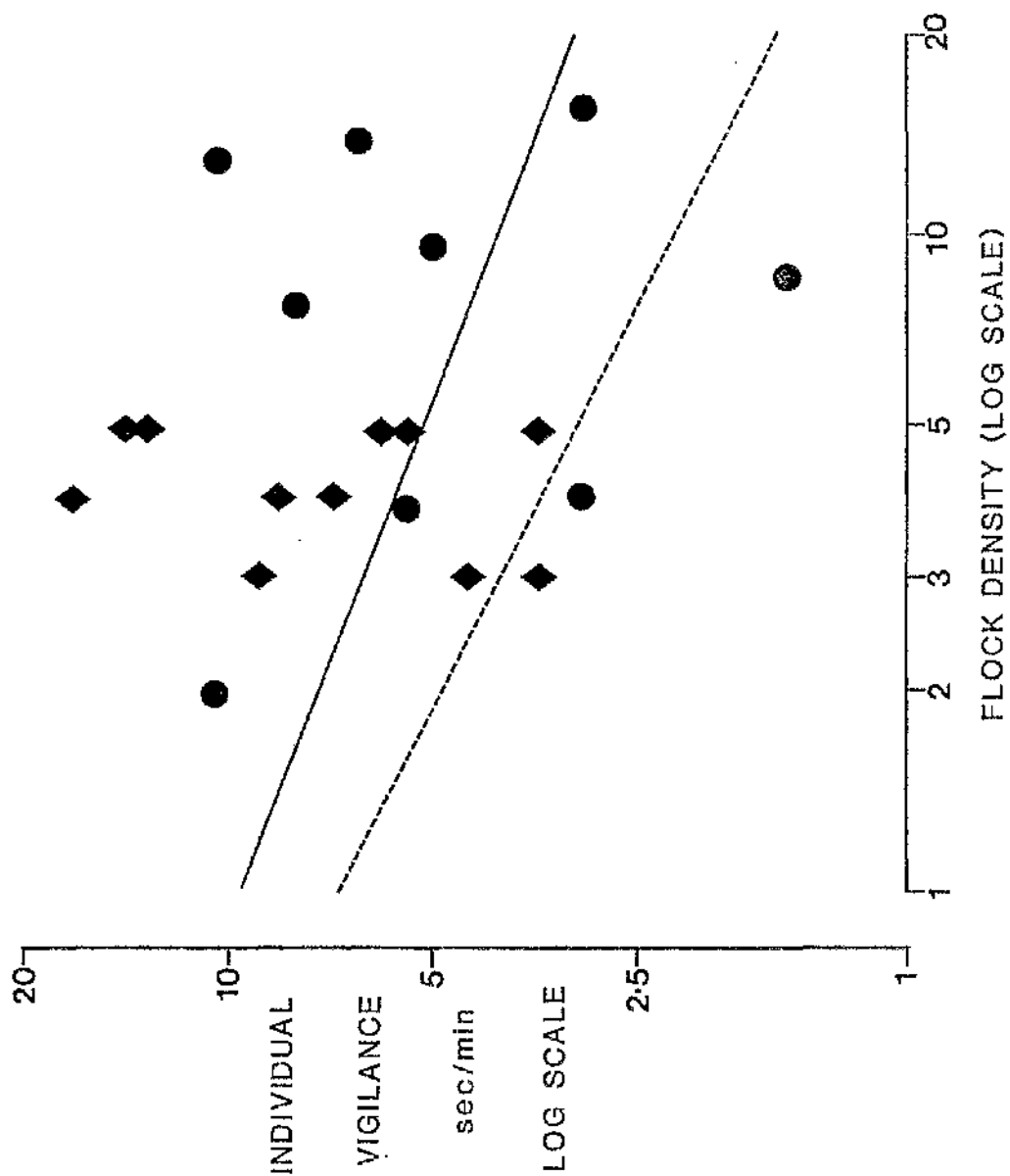
5.3.3 Discussion

The available evidence suggests that turnstones are not usually stressed during British winters; survival rates are high even in severe conditions (Chapter 2 and references therein), and, in contrast to most wintering shorebirds, there is no marked deposition of fat reserves during this period (Cramp & Simmons 1982). Therefore the relative importance of maximising energy gain can be expected to be greater in the period immediately prior to migration than during the rest of the time spent in the wintering quarters. This increased importance results in an increase in the proportion of time invested in foraging, at the expense of time spent vigilant, so producing an increased risk of predation. The period of pre-migratory fattening can thus be considered similar to one of starvation, during which resource accumulation acquires a higher priority, at the expense of other behaviours (Heller & Milinski 1979, Krebs 1980b). The lack of a reduction of vigilance in juveniles confirms that it is the factor of migration that causes this change in adults.

Since individual vigilance decreases with increasing flock density, adult turnstones might be expected to compensate for their need to reduce vigilance in the pre-migratory fattening period by forming denser flocks. Caraco et al.(1980a) found that yellow-eyed juncos formed larger flocks when the risk of predation was increased by there being a predator in the area. However, the situation in the ruddy turnstone is more complicated, as the numbers of all species of wader present in the study area declines during this period (as birds migrate), so reducing the potential for formation of larger flocks (Chapter 6). The costs of being in larger or denser flocks, such as higher levels of aggression or feeding interference (Chapter 4), and the possible requirement of an alteration in home ranges to encompass such flocks, may inhibit their formation. Adults reduced their

vigilance by as much in high density flocks as in low, so that increased risk-taking was not restricted to situations where investment in vigilance would normally be at a high level.

A second strategy for adults might be to preferentially seek out juveniles (as these are more vigilant). However, as juveniles form only approximately 15% of the population, and as (by the same reasoning) they should perhaps avoid adults, the effect is unlikely to be great, and indeed was not noticeable in this study.

5.4 Corporate Vigilance and the Pattern of Scanning Within a Flock

By sharing vigilance with neighbours, birds are in effect producing a group "corporate vigilance" (Vendrem 1984b), which can be defined as the proportion of time that one or more members of the group are vigilant. It has already been shown (section 5.2.2) that individuals reduce their investment of time in vigilance as flock density increases; this does not, however, preclude the possibility that there is a simultaneous increase in corporate vigilance (Pulliam 1973). Thus, joining dense flocks may produce two benefits associated with anti-predatory behaviour: firstly a reduction in time lost to foraging through being vigilant, and secondly an increase in the likelihood of detecting an approaching predator.

Corporate vigilance would be most effective if within the flock there was a temporal spacing of scans, so that neighbours scanned alternately rather than simultaneously. In this situation, corporate vigilance would be the sum of the vigilance of the group members, no scanning time being "lost" through the simultaneous vigilance of several birds. However, this would require high levels of co-ordination and hence communication between neighbours, and a more likely pattern would be for birds to scan independently of one another. In this case there would be a degree of overlap in the

scanning periods of individuals, and corporate vigilance would be a function of the probability that one or more birds were vigilant.

Distinction can be made between these two situations by examining the proportions of time that 0,1,2,3... individuals in a flock are vigilant. If birds make scans independently of each other, these proportions will tend towards the binomial distribution (Elcavage & Caraco 1983). If, however, they are able to alternate periods of vigilance with each other, there will be fewer occasions when more than one bird is vigilant than would be predicted from the binomial distribution.

Therefore the inter-relationship of corporate vigilance and flock density was examined by (1) determining the pattern of scanning, and then (2) using the result to calculate estimated corporate vigilance for different flock densities.

5.4.1 Do Birds Coordinate Scanning with their Neighbours?

Methods

It was reasoned that birds would be best able to coordinate scanning when in tight monospecific flocks, and so a conservative approach was adopted wherby the test of the ability to coordinate was made on birds in this situation. Video film was made of relatively static and dense flocks (21 turnstones feeding on dead wrack, 35 purple sandpipers feeding on rock). The temporal distribution of scans by members of the flock was found by determining the proportion of birds vigilant at half-second intervals, using slow-motion and freeze-frame analysing equipment. The observations could be considered independent of each other, as the interval between them was significantly greater than the mean duration of scans made by an individual in either flock (mean scan duration of turnstones = 0.353 $\pm$ 0.027 sec (n=50), purple sandpipers = 0.377 $\pm$ 0.035 s (n=50)). As

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the entire flocks could not be kept in the field of view at the magnification required to monitor individual behaviour, the counts were made of a subset of the flocks – the ten birds at the "left-hand end" of both flocks. The number of birds out of the ten was recorded for each observation. The frequency distribution of scores was then compared to the expected binomial distribution for independent random scanning.

Results

The mean proportions of birds scanning per frame, and hence the probabilities of an individual being vigilant, are shown in Table 5.4. These values were then used to generate expected probabilities that from zero to seven birds out of ten (the observed range) would be simultaneously vigilant.

Table 5.4. The mean proportions of time turnstones and purple sandpipers, in monospecific flocks of 21 and 35 respectively, spent vigilant (as determined by video frame analysis).

Species	No.frames examined	Mean no. birds out of 10 vigilant	Proportion of time individual is vigilant
Turnstone	240	0.979	0.0979
Purple Sandpiper	120	1.425	0.1425

The distributions of observed and expected scores are shown in Fig.5.13. In neither species is there any departure from the expected distributions (turnstone: $X^2 = 3.40$, 4df., NS; purple sandpiper: $X^2 = 8.60$, 4df., NS). Therefore even in ideal situations neither species showed a tendency for neighbouring birds to coordinate their scanning so that individual scanning bouts did not overlap. Indeed, the trend was in the other direction, towards a temporal clumping of scans rather than regular spacing. This tendency could be due to either (1) occasional environmental stimuli (such as moving objects) that prompt

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Fig.5.13. Frequency distributions of the number of birds, out of a group of ten, which were vigilant at any one time. Thin lines = observed; thick lines = expected from binomial distribution.

(a) Turnstone (240 observations). (b) Purple sandpiper (120 observations).

(a)

FREQUENCY

No. OF BIRDS VIGILANT

(b)

FREQUENCY

No. OF BIRDS VIGILANT
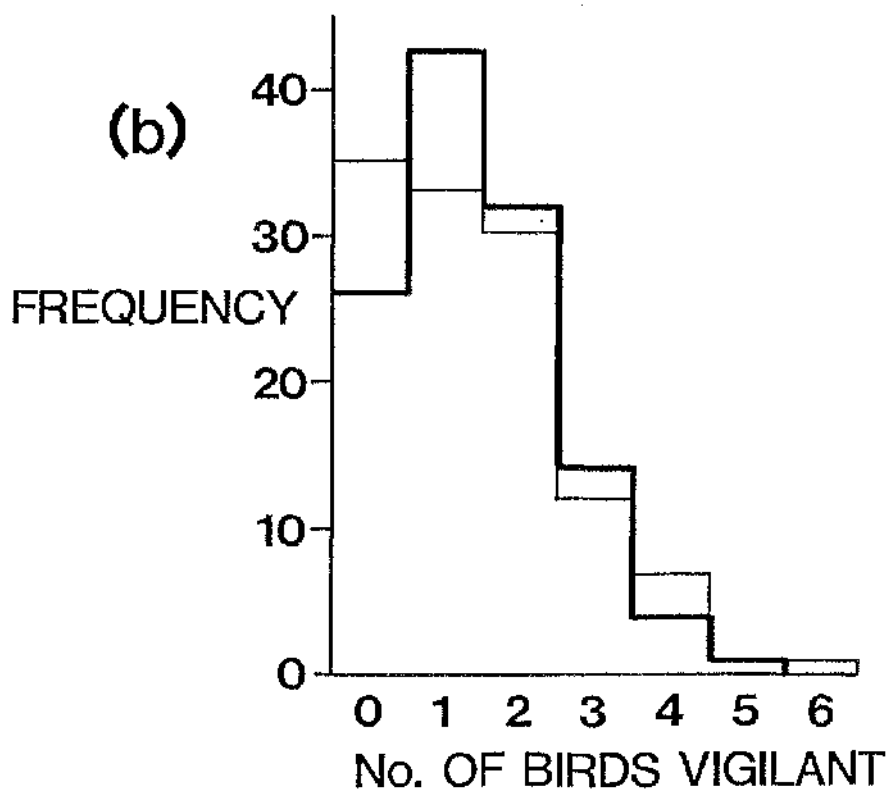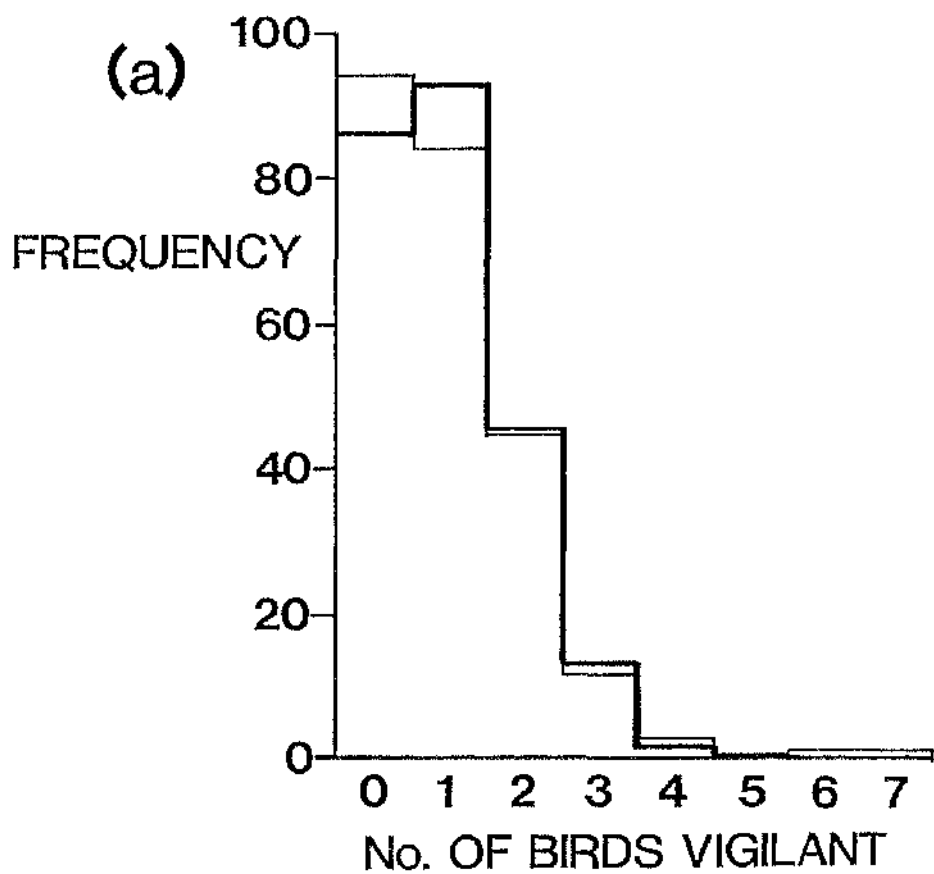
vigilant behaviour, or (2) social facilitation (Crawford 1939), in which scanning by one bird (possibly for a greater-than-average duration) prompts similar behaviour in neighbours.

However, as these trends towards a temporal clumping of scans were not statistically significant, it can be assumed that although birds adjust the amount of time they spend vigilant according to the density of birds around them (section 5.2.2), their decision on when to scan is made independently of the vigilance behaviour of neighbours.

5.4.2 Does Corporate Vigilance Increase with Flock Density?

Methods

Given that birds in a group initiate scans independently of each other, corporate vigilance (the proportion of time that one or more birds is vigilant) can be estimated as:

$$V_c = 1 - \text{(Probability that no bird is vigilant)}$$

$$= 1 - (1 - V_i)^n \tag{1}$$

where V_i is the proportion of time an individual in that group is vigilant, and n is the group size (modified from Rubenstein 1978). However, in the situation studied flock size was often indeterminate (as explained earlier). As birds were found to adjust their vigilance according to the number of birds they could see (i.e. their visible density), it was felt that this same unit of measurement could be used to substitute for group size. Visible density (being either equal to or less than overall density) was therefore a minimum estimate of group size. There will therefore be a tendency towards underestimating corporate vigilance as density increases. This will lead to Type II errors (failure to reject the null hypothesis of flock size/density having no effect on corporate vigilance), rather

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than production of spurious relationships where none exist (Sokal & Rohlf 1981).

Estimates of corporate vigilance were obtained by substituting values for V_i and n from the one minute focal bird observations into equation (1) (V_i being equal to $Vigilance\ Time/_{60}$, and n taken as visible density). An assumption of the estimation is that all birds in the group are equally vigilant; this is less likely to be true in a mixed-species flock, and so the analyses were restricted to cases where the only visible birds within 10m were conspecifics. Habitat visibility was ruled out as a confounding variable by only including cases where the focal bird had an unrestricted view of its surroundings.

Results

In both species the overall trend is for an increase in corporate vigilance with visible density (Fig. 5.14). Single birds spend less than 30% of their time vigilant, whereas when surrounded by over thirty conspecifics there is at least one of the group vigilant for over 75% of the time. This trend is evident even over the range of from zero to ten birds within 10m. It is therefore unlikely to be due to the presumed increase in intraspecific vigilance which may possibly occur at higher densities (section 5.2.3).

The statistical significance of the trends cannot be tested, as the two axes are not truly independent (the value for visible density being used in the equation to generate the estimate of corporate vigilance). However, the trends observed are not due purely to this interdependence of x and y; if individual vigilance (the other variable used in the estimation of corporate vigilance) was held constant, corporate vigilance would increase far more swiftly as

Fig.5.14. The calculated corporate vigilance (i.e. the percentage of time at least one bird was vigilant) of (a) turnstones and (b) purple sandpipers in conspecific flocks (represented as means $\pm$ S.E. with sample sizes). Also shown are the relationships expected if individual vigilance remained constant at the level of a solitary bird (curves), and if corporate vigilance remained constant (dashed lines).

(a)

(b)
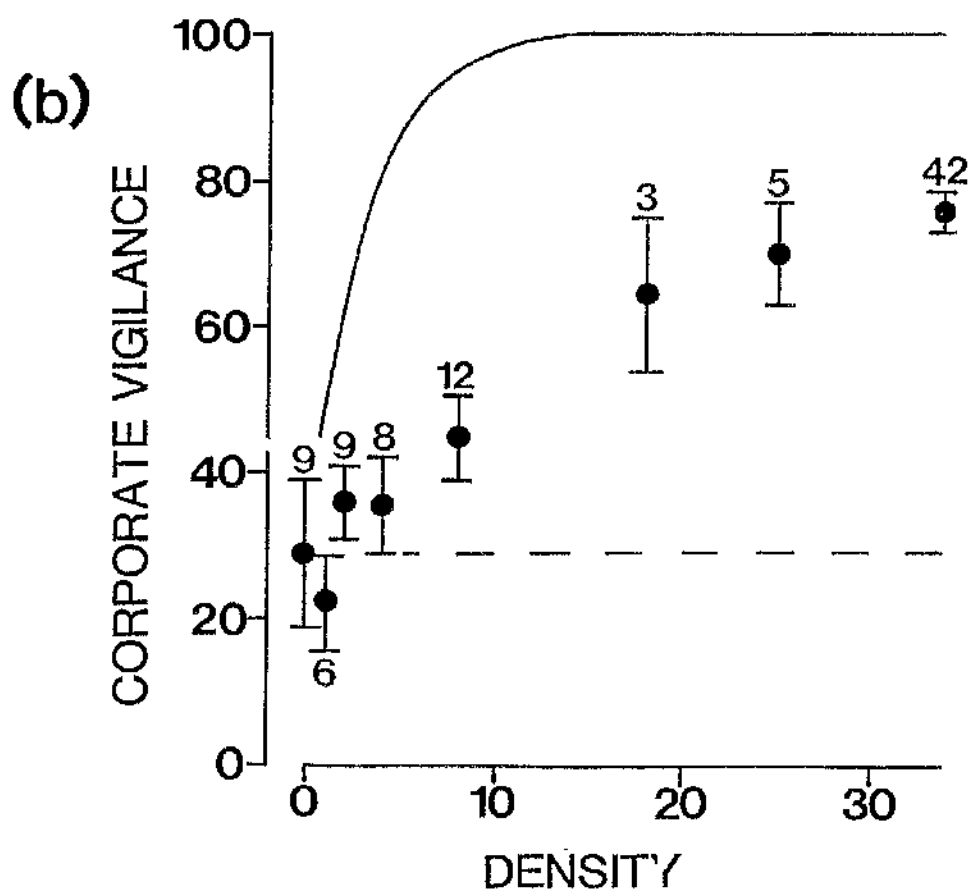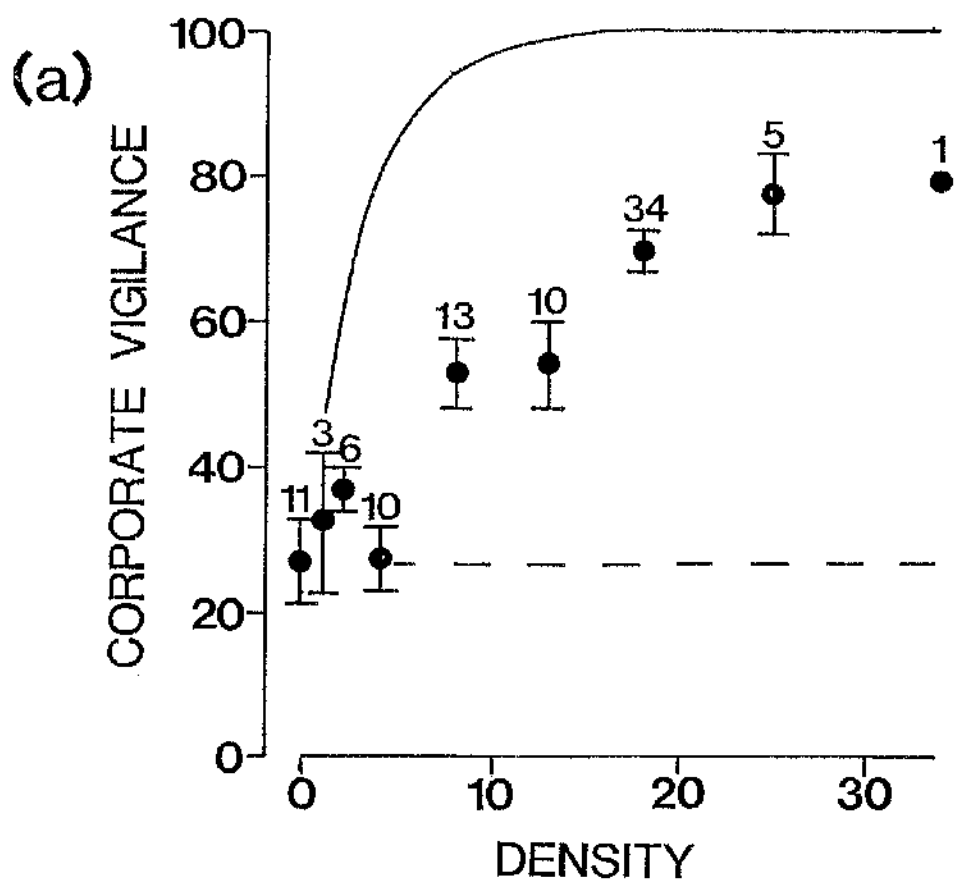
visible density increased (Fig. 5.14). Thus the observed relationships between visible density and vigilance are intermediate between the extremes of (1) individual vigilance held constant regardless of flock density (the curves in Fig. 5.14), and (2) individual vigilance reduced with increasing density to the extent that corporate (flock) vigilance remains constant (Fig. 5.14, dashed lines).

Discussion

As flock density increases, turnstones and purple sandpipers adjust their vigilance so as to gain two advantages: an increase in the proportion of time available for feeding (section 5.2.2), and an increase in the combined vigilance of the flock. Increased corporate vigilance will lead to an increased probability of an approaching predator being detected by a member of the flock, an idea first theoretically stated by Pulliam (1973) and later developed by Pulliam et al. (1982) and Lendrem (1982,1984b). Although there are differences between the models of Pulliam et al. and Lendrem (the former making the rather restricting assumption that scan duration is unaffected by group size), both show that the increased probability of detection arises from the increased likelihood that a flock member will commence scanning before the predator has time to make an undetected approach. Studies both in laboratory (Powell 1974, Lazarus 1979) and semi-natural (Kenward 1978) conditions have shown that large flocks detect predators earlier (or at greater distances) than do small flocks or solitary birds; the latter study also showed that it was largely the element of surprise that determined whether a goshawk's (Accipiter gentilis) attack on a woodpigeon (Columba palumbus) flock was successful. The resulting inverse relationship between attacked flock size and success rate was similar to that

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found by Page & Whitacre (1975), who found that a female merlin was more successful in attacks on solitary birds than on flocks of up to fifty. Although the possibility cannot be ruled out that solitary birds were more likely to be those that were sick (and hence more vulnerable), the hunting method employed by the predator makes it likely that the detection distance was crucial in deciding the outcome of an attack. As discussed earlier (section 5.1.3), merlins use a fast low glide to approach targets on the ground, aiming to reach prey before they have time to react. The observations of Page & Whitacre (1975) suggest that once shorebirds have taken to the air, their chances of surviving a merlin attack are great (the raptor failing in all 82 attacks on sandpipers in flight, compared to success rates of between 6.9 and 25.6% (depending on flock size) when initiating attacks at birds of the same species on the ground). It therefore becomes imperative for ground-feeding shorebirds to detect an approaching predator as soon as possible.

CHAPTER SIX - FLOCKING AND ITS REGULATION

The previous two chapters have demonstrated that the magnitude
of both the costs and benefits of flocking in turnstones and purple
sandpipers changes with flock density. By increasing their density,
both species gain time from a reduced commitment to vigilance
(Chapter 5); however, this benefit to each individual may be offset
by the cost of aggression, which increases with flock density
(Chapter 4). Therefore the optimal density is likely to be a
compromise between these conflicting trends. Birds at very low
densities incur the cost of excessively high rates of vigilance;
however, by only increasing their density a little, this allocation
of time to vigilance is much reduced. Further increases in density
cause little further change in vigilance, whereas the costs of
aggression continue to rise.

Caraco & Pulliam (1980) have suggested that flock size should
increase as long as the time gained from reduced vigilance is greater
than the time lost through aggression. In other words, the only cost
of being in a large flock, or at high densities (the two being
closely related), is the time spent in actual aggression. While this
approach produces quantifiable predictions about optimal group sizes,
it makes the somewhat unrealistic assumption that the rate of intake
per unit time spent in actual feeding is constant, regardless of
flock size or density. Thus no allowance is made for the phenomenon
of interference, where high flock densities can reduce the feeding
efficiency of an individual even if no actual aggression takes place.
As interference has been found to be an important factor in
influencing the feeding rates of many wader species (see references
in Chapter 4), it can be assumed that, while the time spent in
aggression is an indicator of the extent to which the presence of

neighbouring birds may influence foraging efficiency, the true cost is likely to be higher, and so high densities will lead to substantial reductions in foraging efficiency.

For instance, the average bird in a good visibility habitat should seek to remain at densities of not less than four visible conspecifics within a 10 m radius (so as to minimise its vigilance rate), while at the same time it should be attempting to remain in areas of minimal density (to reduce the costs of aggression and interference). This would suggest that the optimal flock density in this situation should lie in the region of four visible conspecifics within 10 m. This may not be the case, however, in poor visibility habitats, as individual vigilance must be greater (Chapter 5), and a greater proportion of neighbouring flockmates will not be visible, so necessitating a higher overall density for a given visible density.

It should therefore be the case that turnstones and purple sandpipers attempt to regulate their flocking behaviour so as to approach the predicted optimum. A factor which could prevent densities from stabilising at an optimum is the tidal cycle, which enforces an increase in flock densities over the high tide period. A second complication is that a significant proportion of the total wader density around purple sandpipers and turnstones is typically composed of other species, which may have an optimum dispersion different to that of the study species. This could also therefore affect the likelihood of birds of any species attaining an optimal density. However, since interspecific aggression (and hence probably competition) was lower than intraspecific (Chapter 4), it might be expected that both species should seek out those heterospecifics with which they share vigilance (Chapter 5) in preference to conspecifics, as they would thus gain the anti-predator advantages of flocking with reduced foraging costs (Powell 1974, Morse 1977).

Such polyspecific associations may of course arise by chance, through the mutual selection by different species for the same habitat or food patch (Waser 1982). Hence, although Stinson (1980) showed that many species of wader (including turnstones) tended to be found in polyspecific groups, this alone proved nothing about the functional basis for such aggregations. However, more direct evidence for positive associations would be obtained if it could be shown that one species modified its dispersion in response to changes in the dispersion of another. Thus the situation here may be one of flux, with the prediction that both turnstones and purple sandpipers should be continually altering their dispersion in an adaptive manner, to compensate for changes in the density of other species (or for changes in the extent of available foraging area). This is therefore analogous to the Equilibrium Flock Size (EFS) of Krebs (1974), which is postulated to be the size at which a flock may be maintained by dynamic equilibrium; the equilibrium results from the decisions of individual members on whether to join or leave the flock, made on the basis of their foraging success. Although flocks have indeed been found to stabilise at an equilibrium size in species as diverse as great blue herons <u>Ardea</u> <u>herodias</u> (Krebs 1974), house sparrows (Barnard 1980b) and lapwings (Barnard <u>et</u> <u>al</u>. 1982), there are theoretical reasons to suggest that the EFS may be larger than the size which maximises individual net benefit (i.e. the optimum), since incoming individuals will tend to gain more from joining a flock already at (or slightly above) the optimum size than from feeding alone; thus the flock will always tend to increase away from its optimal size (Sibly 1983, see also Pulliam & Caraco 1984). However, the maintaining by purple sandpipers and turnstones of an optimal density is more plausible, as each individual has a greater ability

to alter its surrounding density than it has to alter its group size.

This chapter will therefore examine the extent of flocking in turnstones and purple sandpipers, in order to test whether there was any evidence that the birds attempted to regulate the density and composition of flocks. As suggested above, in open habitats flock density should tend towards the predicted optimal density of four visible conspecifics within 10 m. A further aspect to be studied is the mechanism of how flock density is maintained. Most turnstone and purple sandpiper flocks are mobile, and so for birds to maintain a given flock density requires that their patterns of movement are influenced by the position and movement of their neighbours. While in many situations animals adopt a movement strategy that maximises the efficiency of searching for food (e.g. Smith 1974a,b, Metcalfe 1985), and while the same approach can be applied to the movement of a bird flock as a whole (Cody 1971), the searching strategies of birds within that flock must in addition be sensitive to the behaviour of other flock members. Previous work on the search paths of birds within flocks (e.g. Goss-Custard 1970, Smith 1977) has concentrated on the turning rate of individuals, with a tendency to ignore the influence of the position of neighbouring birds on the direction in which turns are made. Thus birds that stray towards the the edges of a flock must show a tendency to turn back if they are to remain within it, and the strength of this tendency will govern the cohesiveness of the flock. It can therefore be predicted that the position of neighbouring birds should have a greater influence on individual search paths in areas of low visiblity, where the benefits of flock cohesion are greatest.

One final aspect to be considered in this chapter is the effect of social rank on the search paths of individuals. Other studies of group-living species have found that an individual's spatial location

within a group may in part be determined by dominance rank. The most commonly found situation is that subordinates tend to be located on the periphery (as found, for instance, in wood pigeons Columba palumbus (Murton et al. 1971), feral pigeons (Murton et al. 1972), wedge-capped Capuchin monkeys Cebus nigrivittatus (Robinson 1981) and toque monkeys Macaca s. sinica (Dittus 1977). An animal's spatial position within a group may have important fitness consequences, as peripheral individuals may be forced to be more vigilant (Lazarus 1978, Jennings & Evans 1980), possibly suffering a higher predation risk through an increased domain of danger (Hamilton 1971). They may also be denied access to a localised food source, or suffer a reduced foraging efficiency through being forced to keep out of the way of dominants (Murton et al. 1971). The position of individuals within a group was difficult to measure in turnstones and purple sandpipers, due to the frequent lack of a distinct group boundary (as discussed in Chapter 1). However, it was possible to measure the movement patterns within flocks of birds of different rank, which would shed light on whether the dominance hierarchy had any effect on the general spatial structure of flocks.

6.1 Methods

Feeding flocks were located opportunistically, as described in Chapter 1. Measurements were made of flock density and of the visibility of the habitat in which each flock was feeding, with at least one hour between successive measurements in the same area. The density (both overall and visible, as defined in Section 4.1) of each species was recorded as one of the following categories: 0, 1, 2, 3-5, 6-10, 11-15, 16-20, 21-30, 31-40, 41+ birds estimated to be within 10 m of a single turnstone or purple sandpiper selected at random from each flock. The visibility experienced by this representative

for the flock was also noted, using the same scoring method as described in 5.1.1. The state of the tide was recorded as the time (in minutes) since the previous high water. The cyclical nature of the tide produced changes in flocking behaviour that were virtually symmetrical either side of high and low water. Therefore for certain analyses data collected on the falling and the rising tide were combined, by converting tide time to a new variable, time from (i.e. before or since) low water.

One section of the study area was selected for more detailed analyses of the dynamics of turnstone flocking. The musselbeds and pools of Coalruffie (see Chapter 1, Fig.1.1) are a relatively small and discrete area of habitat with good observer access and no regions of poor visibility, so allowing complete censusing. Coalruffie supported a stable population of turnstones, although the number of purple sandpipers fluctuated greatly from day to day (Chapter 2, Fig.2.8). The effect of tidal state on the populations of turnstones and other waders at Coalruffie was assessed by making complete counts of the area during the exposure period. These counts were made on numerous days during the winter, with never more than four counts (separated by at least 30 mins) made per day.

In the spring, redshanks and oystercatchers (the most abundant of the other wader species) migrated to their breeding grounds before the turnstones or purple sandpipers. This resulted in a period of about a month when the turnstones and purple sandpipers were still present but the redshank and oystercatcher densities were much reduced. Therefore, when analysing flock densities, the field season was divided into winter- and spring-density periods, with the dividing date being selected arbitrarily: observations and counts made on or after April 16th each spring were included in the spring-

density period, when redshank and oystercatcher densities were on average much lower. A similar situation did not arise in the autumn observations, as field work did not commence until after the great majority of birds were established in their wintering quarters, and there is also no period when turnstones are present but not redshanks or oystercachers.

The earlier spring departure of redshanks and oystercatchers provided a natural experiment to test the effect of reducing heterospecific densities on the flocking behaviour of turnstones. A second experiment, with a more manipulative approach, was designed to test whether turnstones would respond over the short term to sudden alterations in the densities of these other species. Both oystercatchers and redshanks are more wary than turnstones, and so tend to take flight more readily when approached by a person on foot. The birds at Coalruffie were quite often disturbed by people digging for bait or examining rock pools, and would quickly resume feeding once the disturbance had passed. Walking over the musselbeds of Coalruffie would cause birds to fly, at first usually to another part of the musselbed; if approached again, they would often leave the area completely. By carefully controlling the distances to which I approached mixed-species feeding flocks, it was thus possible to either (a) disturb all birds, causing them to fly but not leave Coalruffie, or (b) disturb them, causing a proportion of the redshanks and oystercatchers to leave Coalruffie. The first alternative thereby constituted a control for the second, removal, experiment, to check the possibility that any alterations in turnstone flocking behaviour were caused by the disturbance per se rather than by the resulting alterations in species densities.

The removal and control disturbance experiments were carried out as follows. Firstly, pre-disturbance counts were made of all

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turnstones, purple sandpipers, redshanks and oystercatchers at Coalruffie. (The only other waders present were occasional single curlews.) Then both overall and visible densities were measured, as above, for each turnstone. Ten minutes later, I walked from the observation vehicle down onto the musselbed, and disturbed birds (by walking towards them) until they had all been caused to fly, and, in the case of removal experiments, at least half of the oystercatchers and redshanks had completely left Coalruffie. This would take approximately ten minutes. I would then return to the vehicle, count the number of birds remaining, and again measure densities around each turnstone 10, 20, 30 and 40 minutes after the end of the disturbance. A second complete count of the four species was made approximately 35 minutes after the disturbance, to check that the populations were remaining stable. All experiments were carried out on the falling tide, commencing between 215 and 310 minutes after the previous high water. Several experiments failed, either because my disturbance succeeded in removing turnstones as well as other species, or because the birds were disturbed for a second time by some other cause partway through the experiment. A total of seven trials were completed successfully; four removals (on 6th March, 29th October, 1st and 15th December 1983) and three controls (on 1st, 16th and 17th November 1983).

The cohesiveness of turnstone flocks was investigated by studying the search paths of individual birds on the flock periphery. The bird's position was monitored at 3-second intervals (timed with an electronic audio timer), and its path simplified by assuming it had moved directly between these 3-second loci (Fig.6.1a). Thus the path was visualised as a sequence of straight lines, along which the turnstone moved, taking three seconds to cover each section. Changes

in direction could thus be related to the general direction of movement three seconds earlier. The 360° around the bird was divided into six 60° sectors, so that at the end of each 3-second period the bird was recorded as having moved either Forward, Left, Right, Back-Left, Back-Right or Backward with respect to its previous direction of movement (Fig.6.1b). In summary, a bird's movement was recorded as a series of direction headings (e.g. F-L-R-BL-F-, where F stands for Forward etc.), each with respect to the bird's direction of movement during the previous three seconds.

This was then related to the sectors which contained other birds. A note was made every three seconds of the sectors within which was found another turnstone less than 10 m from the focal bird. Thus the complete record would be: F(L3)-L(F3)-R(L4)-BL(R3)-F(R4)- etc., where the sector and distance (in metres) of neighbouring turnstones are indicated in parentheses. Thus, in the example given above, the focal turnstone moves forward, with its only neighbour 3 m to its left; the focal bird then moves left, resulting in the neighbour now being 3 m in front of it, and so on. To simplify both data collection and analysis, focal birds were selected that were on the periphery of flocks, so that only one sector was occupied by neighbours at any one time.

Three situations were compared:

(1) Turnstones feeding in monospecific flocks in habitats with reduced visibility;

(2) Turnstones feeding in monospecific flocks in habitats with good visibility;

(3) Turnstones feeding in mixed-species flocks in habitats with good visibility, with at least one other sector occupied by another species (i.e. purple sandpiper, redshank or oystercatcher) in addition to the sector occupied by a neighbouring turnstone.

Fig.6.1. The method used to record search paths.

(a) The path of the bird (dotted line) is simplified to its position at three second intervals (dots) linked by straight lines.

(b) The movement between the three-second markers is ascribed to one of six possible directions (Forward, Left, Right, Back–left, Back–right or Back), with respect to the previous direction of movement (indicated by the arrows). In this example, the bird moved Forward, then Left, then Forward.

(a)
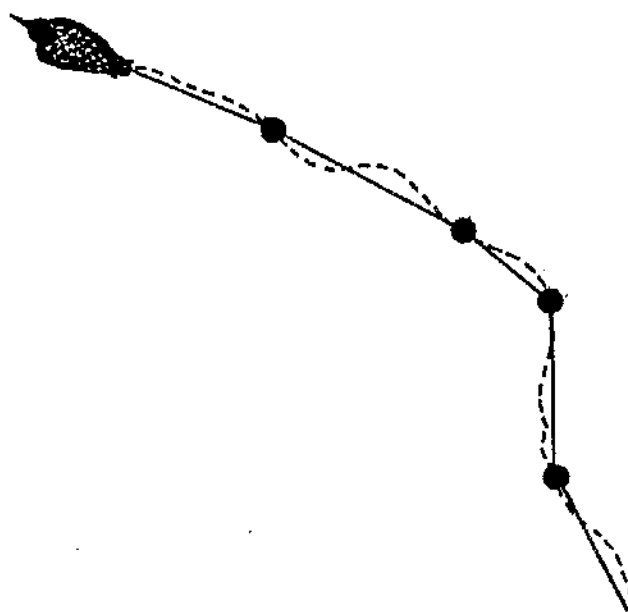
(b)
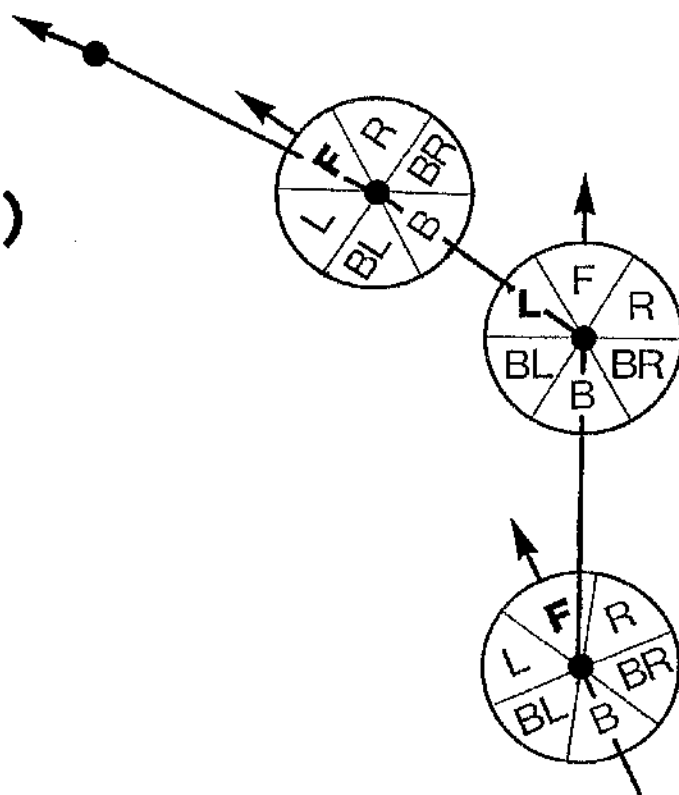
The aim was to determine whether the tendency to move towards other turnstones (and so maintain flock cohesion) was correlated with the vigilance benefits that would be gained from greater cohesion. Thus it was predicted that turnstones in poor visibility areas should have a greater tendency to move back towards other birds than those in good visibility areas, and in the latter situation should show even less of a tendency to move towards other turnstones if surrounded by potential flockmates of other species.

Data were collected by dictation into a tape recorder, either in the field or during playback of video film of foraging birds. Periods when the focal bird did not move further than its own body length during the 3-second intervals were discarded from subsequent analyses.

A second series of observations was designed to test whether dominance status affected the search path of a bird when in situations where the opportunities of potential kleptoparasitism were great. Video films were made of dense turnstone flocks with high aggression rates, and the search paths of individual birds recorded upon playback of the film. Colour-rings could not be read from the film, and so it was not possible to ascribe an independent ranking of dominance status through knowledge of a bird's identity. Instead, birds were picked at random from the film, and their behaviour monitored for as long as they remained within the field of view. Those birds seen to supplant others were classified as dominants, those seen to be supplanted were termed subordinates, while those that were not involved in any interactions during the period of observation were classified as birds of unknown status. Any birds seen both to supplant and also be supplanted were omitted from the analyses. These classifications, although rather crude, would tend to

select the most and least dominant birds in the flocks, as there were consistent and major differences between individuals in the proportions of encounters won (Chapter 4). The sequence of turns made by the focal birds was recorded as above; the only difference being the recording of the positions of neighbouring birds. In the dense flocks filmed for this analysis, there was almost always more than one sector occupied by other turnstones. However, the only sector that was noted was the one containing the nearest turnstone seen to peck at a food item or the substrate (i.e. the 'nearest feeding neighbour')during each three second interval. The recording of such detailed information was made possible by the use of slow-motion and freeze-frame video analysing equipment.

6.2 Results

6.2.1 Species Composition of Flocks

The overall species-compositions of all exposure-period feeding flocks are shown in Figure 6.2. The data were obtained from the density measurements, taking the mid-point of each density category. They have been weighted according to the number of turnstones (or purple sandpipers, as appropriate) in the flock. Thus an observation of the species-density experienced by a flock of ten turnstones was given ten times the weighting of an observation of the species-density experienced by a single turnstone. Figure 6.2a thus represents the species composition of feeding flocks experienced by the average turnstone, rather than the average species composition of flocks in which turnstones were found.

Although the range of species with which turnstones and purple sandpipers were seen to occur was quite broad (13 species for turnstones, 11 for purple sandpipers), few species were recorded regularly. On average, approximately one half of the birds with which

Fig.6.2. The overall species composition (expressed as a percentage of the total) of (a) turnstone and (b) purple sandpiper exposure-period feeding flocks, weighted according to the number of turnstones or purple sandpipers present in each flock.

Key to species:

T = turnstone; P = purple sandpiper; O = oystercatcher; R = redshank; Rp = ringed plover; Gp = golden plover; D = dunlin; C = curlew; B = bar-tailed godwit; G = gulls; S = starling; E = eider; Cr = crow.

The distributions are based on 415 turnstone and 205 purple sandpiper flocks respectively.

(a)

(b)
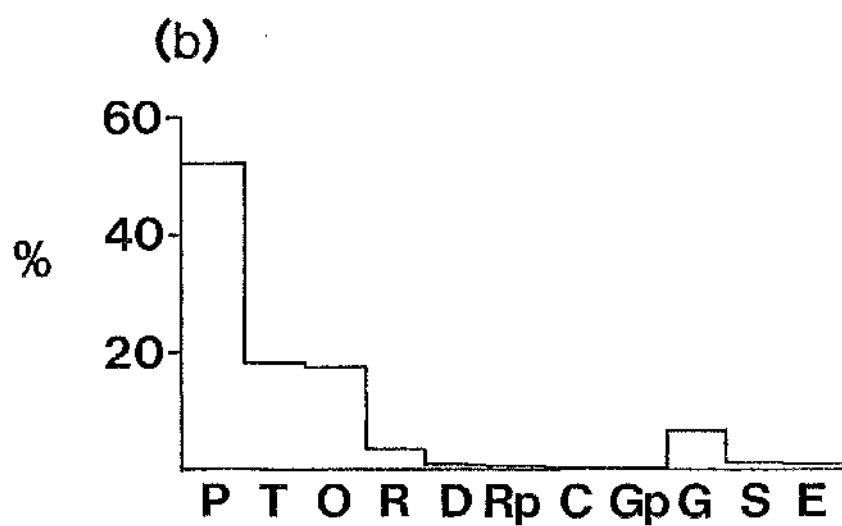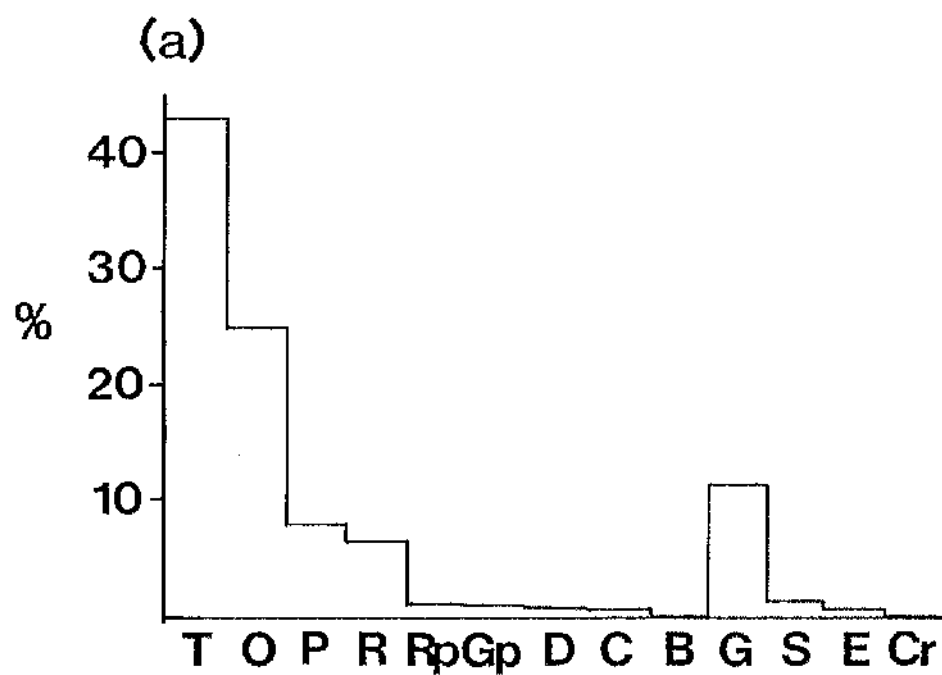
both turnstones and purple sandpipers flocked while feeding were conspecifics. The proportion of neighbouring birds being of a species which they 'trusted' to be vigilant on their behalf (see Chapter 5) was therefore high: 83% for turnstones and 70% for purple sandpipers.

6.2.2 The Effect of Visibility on Tidal Changes in Flock Density

The relationship between tidal state and the density of exposure period feeding flocks was found to be affected by the visibility of the habitat in which they were feeding. In areas of good visibility, the increased foraging area produced by the falling tide resulted in decreases in flock density. In turnstones, the decrease was principally caused by changes in conspecific density (Fig.6.3a). In contrast, in purple sandpipers the trend of lower conspecific densities towards low water was not significant (Fig.6.3d), and instead it was mainly reductions in the densities of other species that caused the drop in general wader densities. However, these changes in flock densities with tidal state did not occur in poor visibility habitats; here the overall densities remained at a high level irrespective of the state of the tide.

As would be expected, the visible wader densities in good visibility areas were, on average, only slightly lower than the overall densities. However, in poor visibility areas (i.e. where the visibility score was less than 10) they were much lower, averaging 70% of the overall densities for purple sandpipers (Fig.6.3 e & f) and only 44% for turnstones (Fig.6.3 b & c). Thus, had overall flock densities in low visibility areas dropped with the tide as in other areas, the corresponding visible densities at low tide would have been extremely low. Instead, by maintaining high overall wader densities throughout the tidal cycle, flocks in low visibility habitats experienced visible densities similar to the lowest ones

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Fig.6.3. Regression lines of the relationships between time from low water and the exposure period winter flock densities, in poor visibility (dashed lines) and good visibility (solid lines) habitats. Observations either side of low water have been combined to calculate each regression; regression lines have, however, been mirrored to ease interpretation (see text for details). The mean value is plotted where the regression line is not statistically significant.

(a) - (c) Densities around focal turnstones (poor visibility n=84 observations, good visibility n=331 observations).

    (a) Overall density of turnstones.
        Good visibility:$r=0.290$, $P<0.001$.
        Poor visibility: $r=-0.048$,NS.

    (b) Overall wader density (exressed as turnstone equivalents - see text for details).
        Good visibility: $r=0.192$, $P<0.001$.
        Poor visibility: $r=-0.033$, NS.

    (c) Visible wader density (expressed as turnstone equivalents - see text for details).
        Good visibility: $r=0.221$, $P<0.001$.
        Poor visibility: $r=-0.034$, NS.

Dots indicate corrected levels after weighting for flock sizes - see text for details. Mean ratio of weighted : unweighted densities is 1.36:1 for good visibility and 1.52:1 for poor visibility

(d) - (f) Densities around focal purple sandpipers (poor visibility n=33 observations, good visibility n=172 observations).

    (d) Overall density of purple sandpipers.
        Good visibility: $r=0.111$, NS.
        Poorvisibility: $r=-0.214$, NS.

    (e) Overall wader density (expressed as purple sandpiper equivalents - see text for details).
        Good visibility: $r=0.127$, $P<0.05$.
        Poor visibility: $r=-0.125$, NS.

    (f) Visible wader density (expressed as purple sandpiper equivalents - see text for details).
        Good visibility: $r=0.126$, $P<0.05$.
        Poor visibility: $r=-0.134$, NS.

Dots indicate corrected levels after weighting for flock sizes - see text. Mean ratio of weighted : unweighted visible wader densities is 1.62:1 for good visibility and 1.52:1 for poor visibility.

(a)

DENSITY

4
2

-300   0   300

(b)

DENSITY

6
4
2

-300   0   300

(c)

DENSITY

6
4
2

-300   0   300

MINUTES FROM LOW WATER

(d)

DENSITY

4

2

-300   0   300

(e)

DENSITY

6

4

2

-300   0   300

(f)

DENSITY

6

4

2

-300   0   300

MINUTES FROM LOW WATER
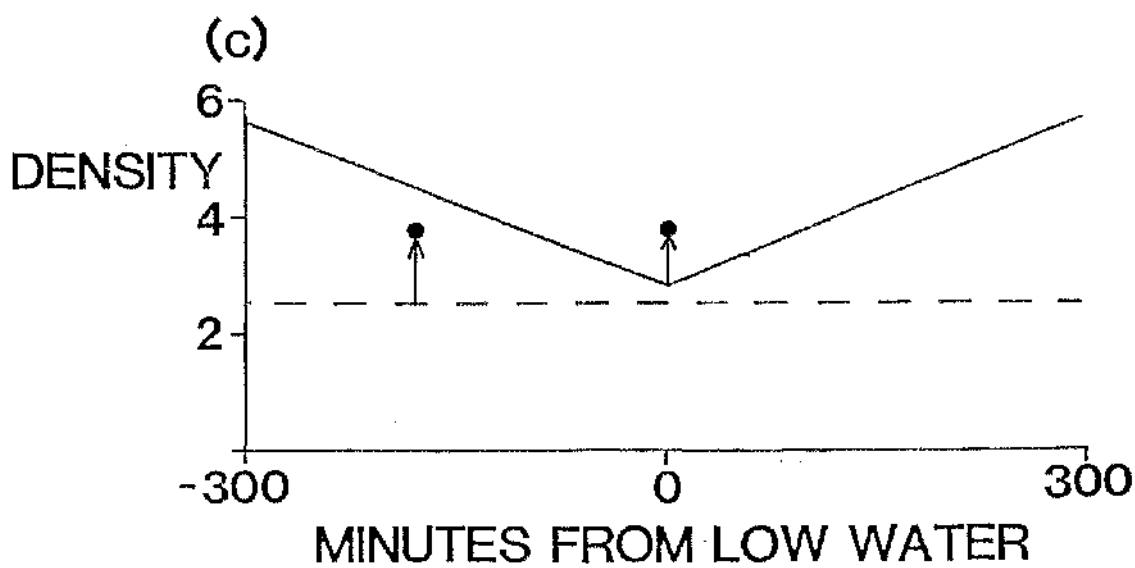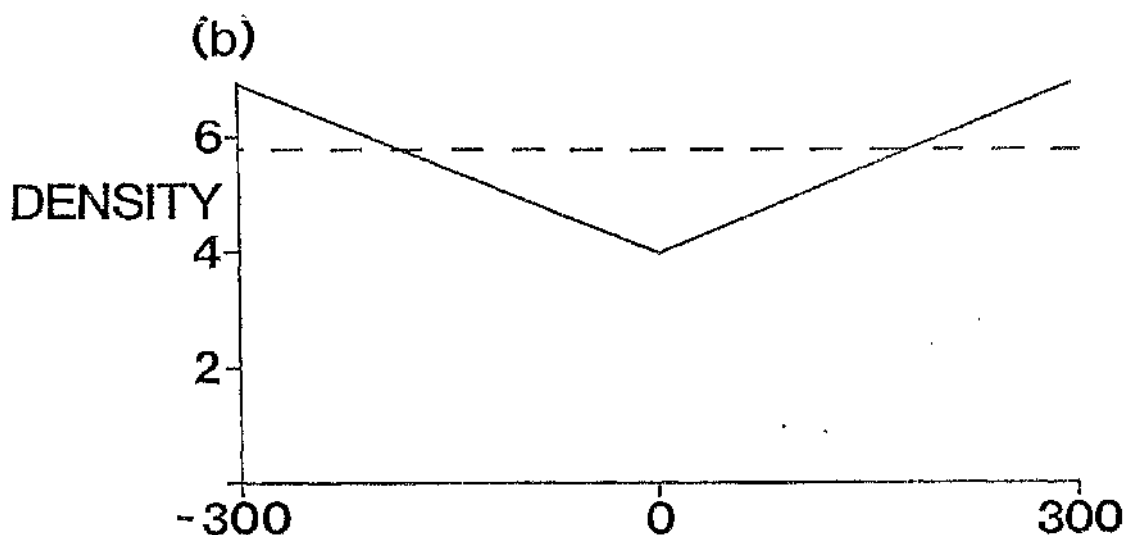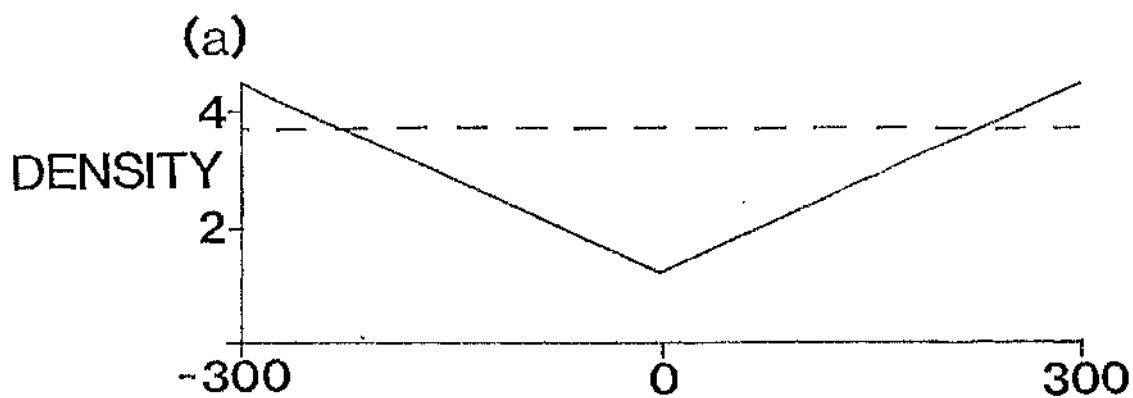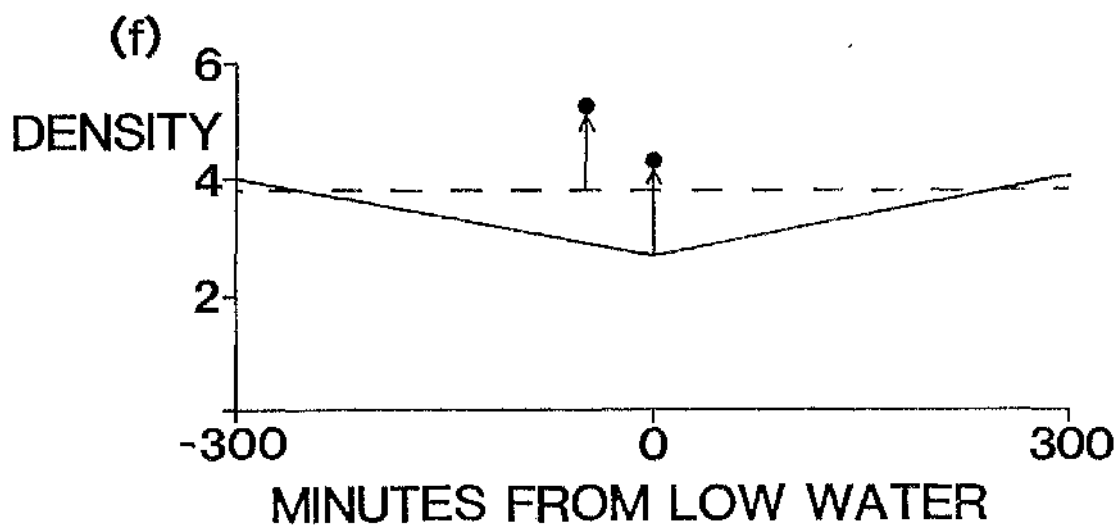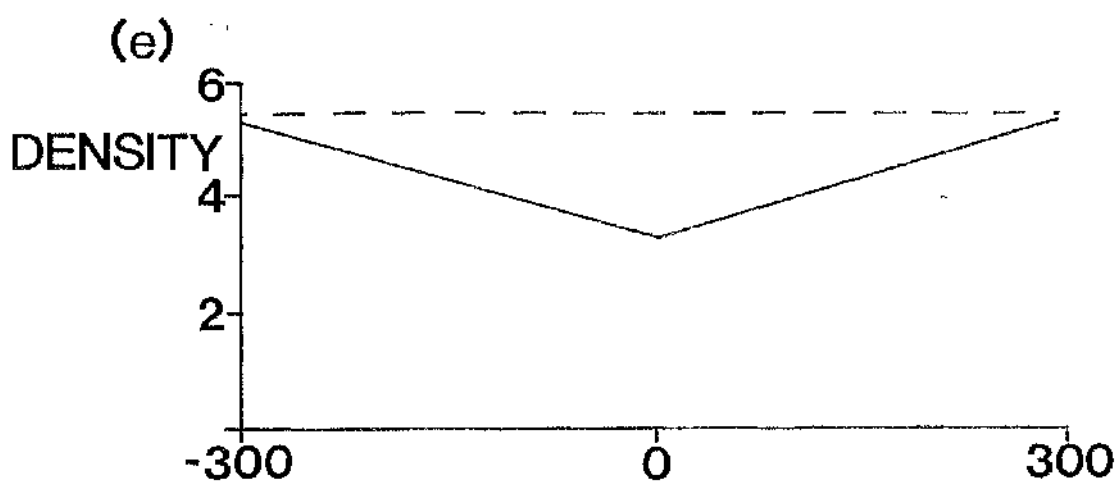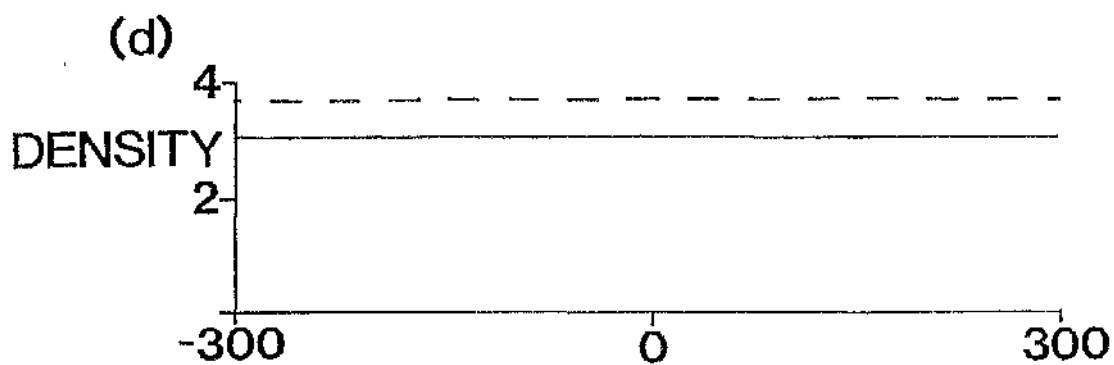
experienced by flocks in good visibility areas.

The regressions shown in Figure 6.3 are based on observations which were not weighted for flock size (i.e. each flock was given an equal weighting, regardless of the number of turnstones or purple sandpipers it contained). Regressions could not be calculated using weighted data, as data points would not then be independent. However, a crude correction factor can be applied by calculating the ratios of weighted mean density : unweighted mean density. In neither species did these ratios change with tide time (taken as minutes from low water) in either visibility category; this was true for conspecific densities, overall wader densities and visible wader densities (Spearman's rank correlation; in all cases P>0.1). Therefore the mean values of these ratios have been used in Figure 6.3 c and e to indicate the approximate minimum wader density experienced by the average turnstone or purple sandpiper (as opposed to that experienced by the average flock in which one of those species was found). These corrections show that, regardless of habitat visibility or tidal state, the average turnstone or purple sandpiper never experienced flock densities lower than approximately four visible conspecifics (or their equivalent) within ten metres.

6.2.3 Tidal Changes in the Number and Density of Birds at Coalruffie

Figure 6.4 shows the number of oystercatchers and redshanks at Coalruffie over the tidal cycle during the winter. The area was completely under water for approximately 2.5 - 3 hours over the high tide period, and so the first birds did not arrive until at least 100 minutes after high tide. Numbers of both species then increased rapidly as the musselbeds and rock pools became exposed by the falling water level. Both species would begin to leave the area once the tide had turned, although some redshanks would often remain and

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begin to roost on the rocks until these were covered by the incoming tide.

In contrast, the turnstones that foraged at Coalruffie tended to arrive and depart as one flock. Consequently the number of turnstones present did not vary with tidal state from the time that the flock arrived until it left (Fig.6.5; Rank correlation between the minutes from low water and the number of turnstones present, $r_{sp}=0.22$, n=59, NS). After arrival, the flock of 15-25 birds would gradually break up, as the birds began to spread out and move amongst the other species that were present. Thus the density of conspecifics around each turnstone dropped towards low water (Fig.6.6b), whereas the densities of redshanks and oystercatchers remained the same, due to the continuing arrival of these species counteracting the increasing area available for foraging (Fig.6.6a). Therefore the redshanks and oystercatchers became an increasingly important component of the wader density around each turnstone towards low water. As mentioned earlier, the number of purple sandpipers present at Coalruffie fluctuated greatly from day to day, and consequently showed no tidal trend.

6.2.4 The Effect of the Removal of Redshanks and Oystercatchers on the Flocking Behaviour of Turnstones

(a) Long-Term (Seasonal) Removal

The apparent shift by turnstones to a stronger association with other species as they increased in numbers at Coalruffie could have been a spurious coincidence rather than a beneficial adaptation to a changing environment. However, evidence for the latter interpretation came in the spring, when the numbers of oystercatchers and redshanks were much reduced (Fig.6.4). This led to a significant drop in the densities of redshanks and oystercatchers around turnstones (Fig.6.6a). The turnstones responded to this reduction in the

Fig.6.4. The mean numbers (± S.E.) of (a) oystercatchers and (b) redshanks present at Coalruffie in relation to the state of the tide. Winter counts (September to 15th April) represented as circles and solid lines. Spring counts (16 April to end of May) represented as squares and dashed lines.

Sample sizes: oystercatcher – 68 winter and 16 spring counts
              redshank   – 65 winter and 16 spring counts

(a)

NUMBER OF BIRDS — MINUTES AFTER HIGH WATER

(b)

No. OF BIRDS — MINUTES AFTER HIGH WATER
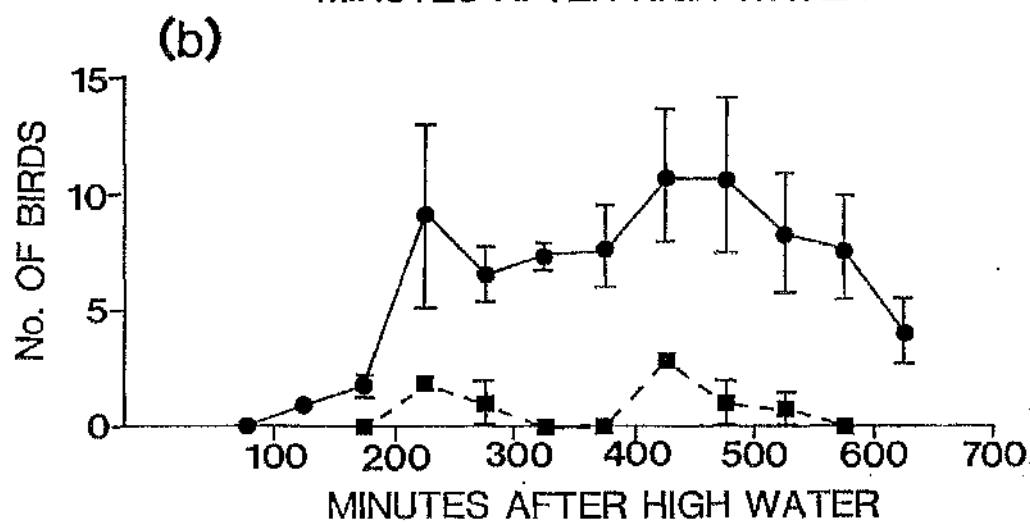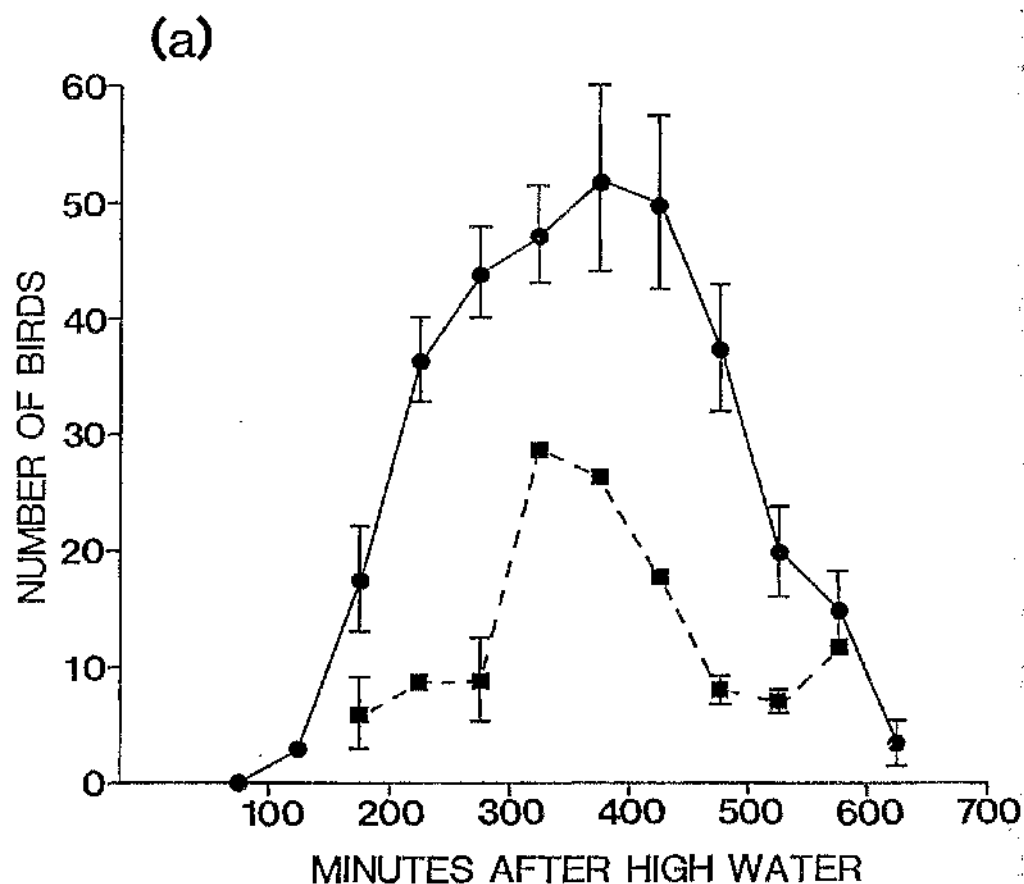
Fig.6.5. The mean number ($\pm$ S.E.) of turnstones present at Coalruffie in winter (September – 15 April) in relation to the state of the tide (n=59 counts; zero counts excluded). Also shown (squares) are counts made in spring (16th April to end of May, n=24).
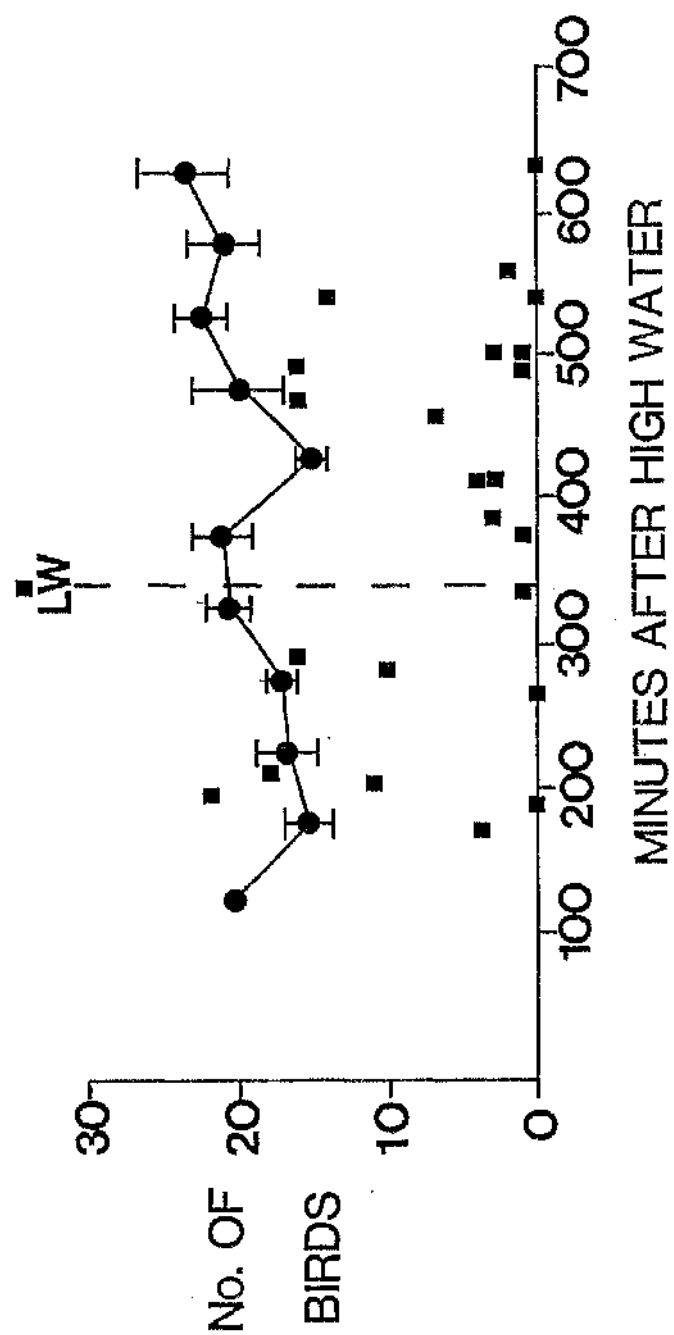
availability of alternative flockmates by aggregating more closely, so increasing their own density (Fig.6.6b). This resulted in their maintaining the visible wader density at the same level in spring as in winter (Fig.6.6c).

This can be contrasted with the flocking behaviour of purple sandpipers. As stated earlier, this species did not utilise Coalruffie as regularly as did the turnstones, and so the comparison must be made using data from the entire study area, rather than just Coalruffie. However, the same reductions in redshank and oystercatcher numbers were undoubtedly occurring throughout the study area. Purple sandpipers did not share vigilance with either redshanks or oystercatchers, but only with turnstones. Therefore the spring reduction in numbers of the former two species would not be expected to have had the same effect on their flocking behaviour as it had on turnstones. Figure 6.7 demonstrates that this prediction was upheld; there were no differences between winter and spring in the densities around purple sandpipers of either turnstones or conspecifics, and consequently no difference in visible wader densities.

Thus the spring drop in the numbers of redshanks and oystercatchers coincided with changes in the flocking behaviour of turnstones (which had previously derived vigilance benefits from associating with them); in contrast, purple sandpipers (which did not share vigilance with either redshanks or oystercatchers) showed no change in flocking behaviour when these two species departed.

(b) Short-term (Disturbance) Removal

The results of the short-term removal experiments at Coalruffie corroborated the findings of the winter-spring comparison. On average, my disturbance succeeded in removing 42% of the oystercatchers and 57% of the redshanks present at Coalruffie,
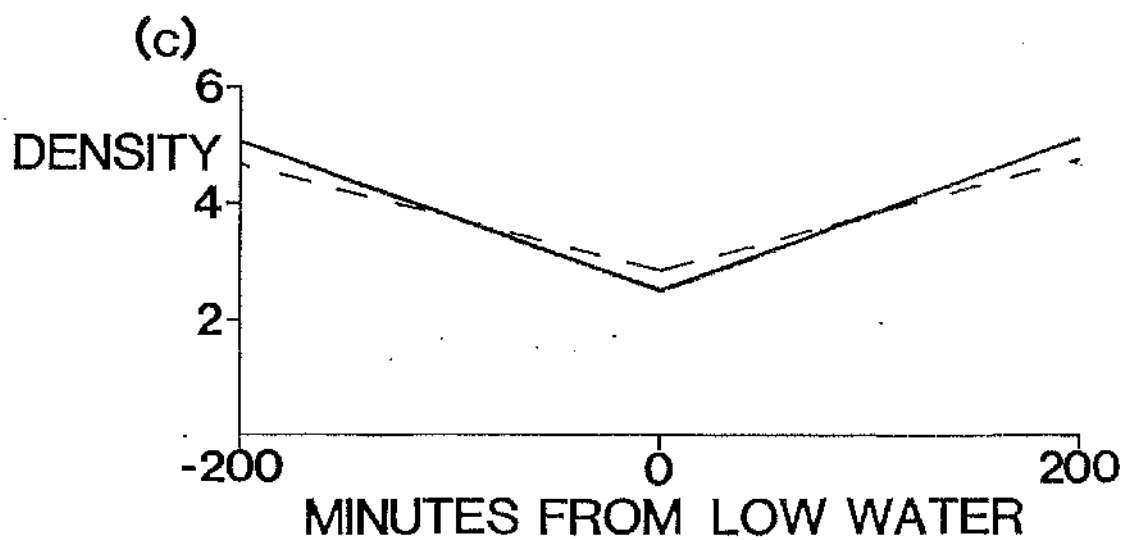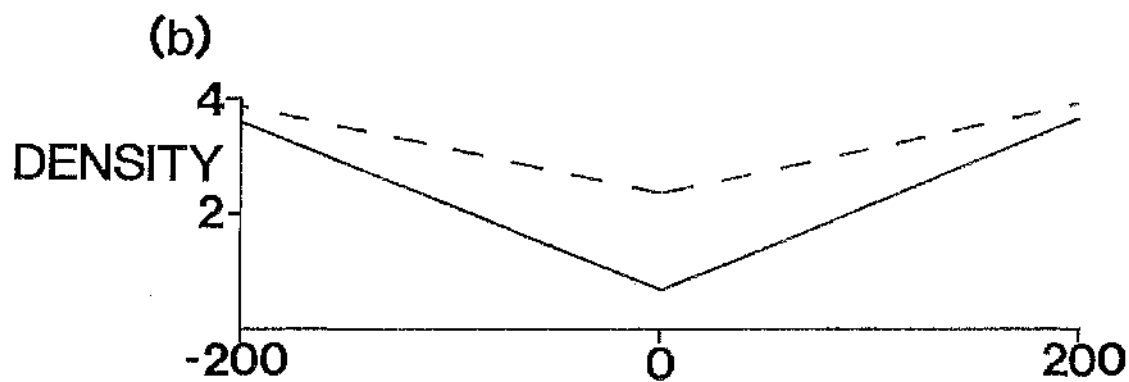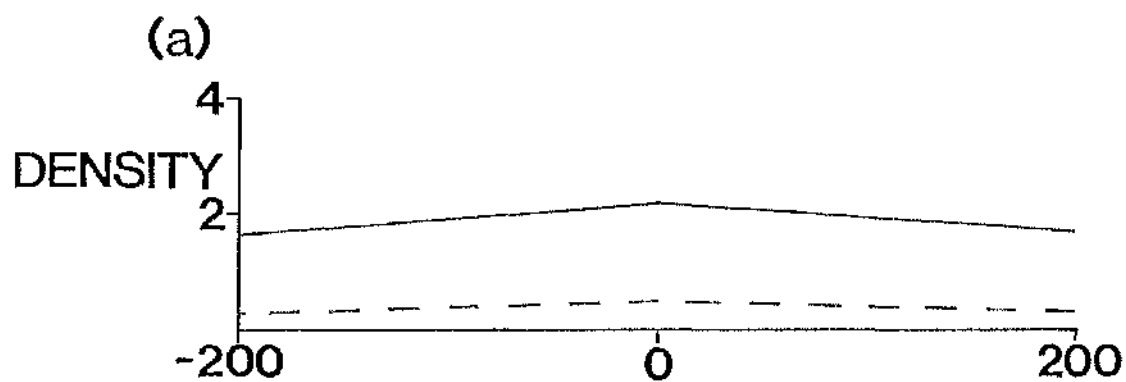
Fig.6.6. Regression lines of the relationships between the state of the tide and flock densities around focal turnstones in winter (solid lines, n=136 observations) and in spring (broken lines, n=29 observations). Regression lines are drawn mirrored either side of low water, as described for Fig.6.3.

(a) Overall density of redshanks + oystercatchers (expressed as turnstone equivalents − see text for details).

Covariance analysis comparing regression line slopes of winter and spring data: $F_{159,2} = 0.03$, NS. Comparing elevations: $F_{162,1} = 25.12$, P<0.001.

(b) Overall density of turnstones.

Covariance analysis comparing regression line slopes: $F_{159,2} = 0.15$, NS. Comparing elevations: $F_{162,1} = 4.98$, P<0.05.

(c) Visible wader density (expressed as turnstone equivalents − see text for details).

Covariance analysis comapring slopes: $F_{159,2} = 0.02$, NS. Comparing elevations: $F_{162,1} = 0.001$, NS.

(a)

DENSITY

4

2

-200   0   200

(b)

DENSITY

4

2

-200   0   200

(c)

DENSITY

6

4

2

-200   0   200

MINUTES FROM LOW WATER

Fig.6.7. Regression lines of relationships between time since low water and flock densities around focal purple sandpipers in winter (solid lines, n=151 observations) and spring (dashed lines, n=49 observations). Regression lines are drawn mirrored either side of low water, as described for Fig.6.3.

(a) Overall density of turnstones.

Covariance analysis comparing regression line slopes: $F_{194,2} = 0.09$, NS. Comparing elevations: $F_{197,1} = 1.50$, NS.

(b) Overall density of purple sandpipers.

Covariance analysis comparing slopes: $F_{194,2} = 0.03$, NS. Comparing elevations: $F_{197,1} = 0.01$, NS.

(c) Visible wader density (expressed as purple sandpiper equivalents – see text for details).

Covariance analysis comparing slopes: $F_{194,2} = 0.63$, NS.

Comparing elevations: $F_{197,1} = 0.07$, NS.

(a)

DENSITY

-200   0   200

(b)

DENSITY

-200   0   200

(c)

DENSITY

-200   0   200

MINUTES FROM LOW WATER
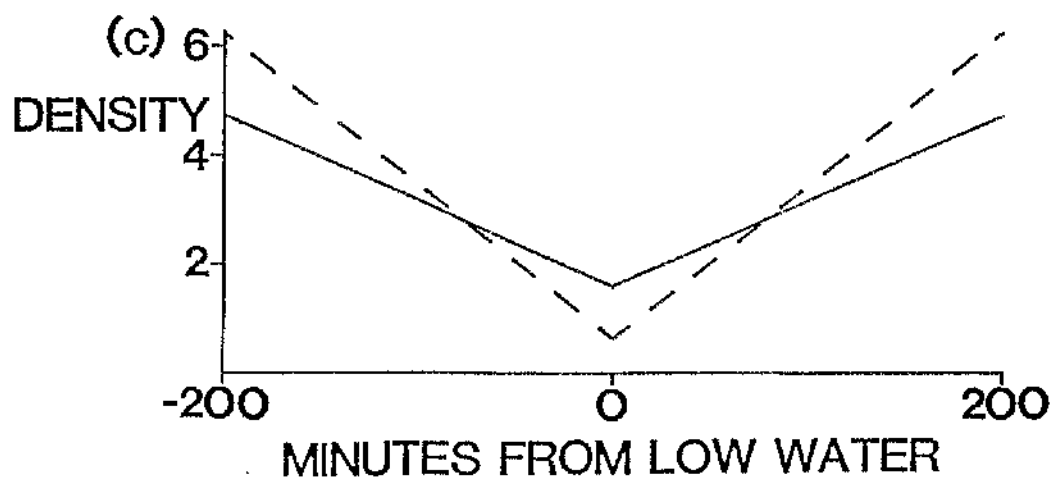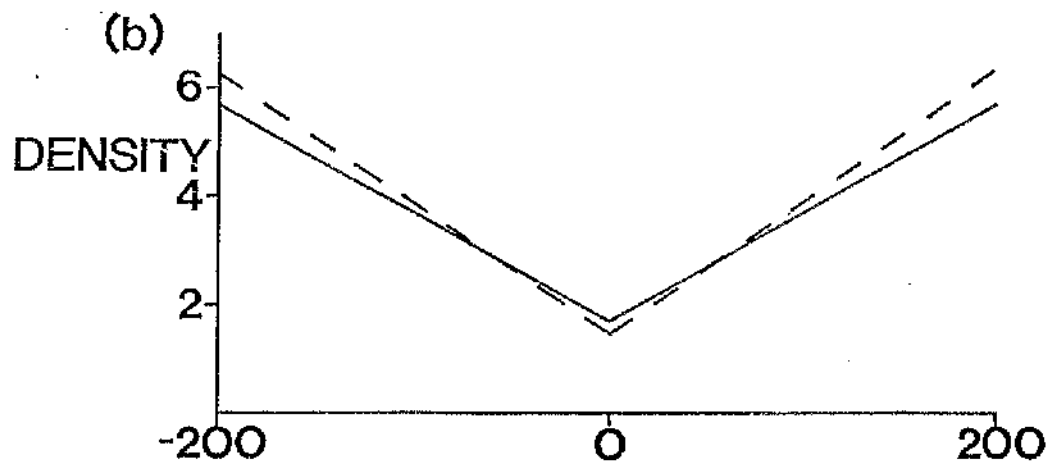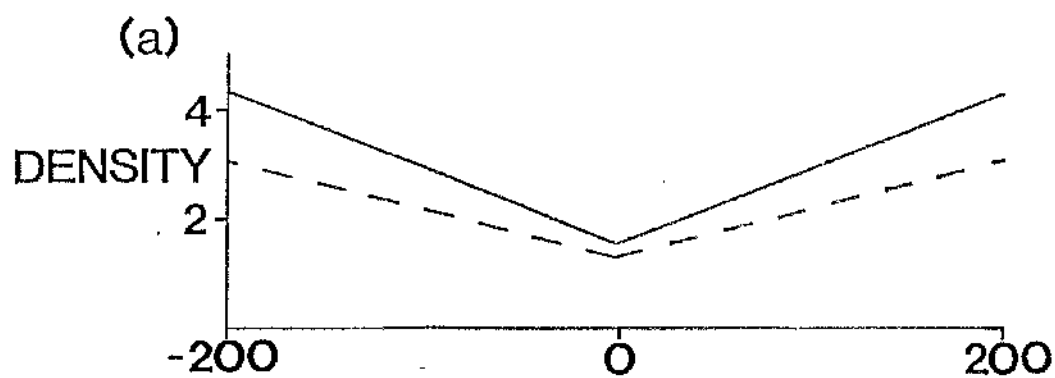
without appreciably altering turnstone numbers (Fig.6.8). Purple sandpipers were only present in small numbers in all trials, and so were a minor component in turnstone flock densities.

The removal of many of the oystercatchers and redshanks caused a significant reduction in their density around each turnstone. This was counteracted, however, by an increase in the clumping of turnstones, so that their visible wader density did not drop despite the reduction in wader numbers. The birds resumed feeding within several minutes of my leaving the musselbeds, and moved into the same areas of musselbed they had been feeding in prior to my appearance. Nonetheless, the local densities of turnstones were maintained at a high level for at least 40 minutes after the disturbance, over a period of the tidal cycle where they would normally be dropping (see Figure 6.6b).

That my disturbance did not in itself cause the birds to change their dispersion is also demonstrated by the results of the three control experiments (Fig.6.9). The post-disturbance counts in these control trials showed that virtually no birds were caused to leave the area, and in fact the number of oystercatchers slightly increased (as would normally be expected at this period of the tide). The density measurements show that there were no changes in density after the disturbance, indicating that those changes that occurred in the removal trials resulted from the changes in the number of birds present, rather than from my appearance on the musselbeds.

Thus both these experiments and the seasonal comparisons indicate that turnstones disperse so as to reduce their own density if other species (with which they share vigilance) are present. If, however, these other species are removed, then the turnstones are forced to choose between either aggregating more, or feeding in lower density flocks (with the cost of either spending more time vigilant

Fig.6.8. The flock densities (expressed as means $\pm$ S.E.) around focal turnstones at Coalruffie before and after periods of disturbance (marked by the black bars). Also shown are the significance levels of t-tests comparing post-disturbance densities with those 10mins prior to the disturbance (* P<0.05, ** P<0.001). Sample sizes for means vary between 42 and 61 observations from 4 disturbance trials. The variation results from failures in locating all birds within each 10min. period.

(a) Overall density of oystercatchers.

(b) Overall density of turnsones.

(c) Visible wader density (expressed as turnstone equivalents - see text for details).

The changes in the numbers of birds present in response to the disturbance are given below.

	Mean no. before	Mean no. after [*]	% change
Turnstone	19.3	19.8	+ 2.6
Purple sandpiper	3.3	2.3	-30.8
Redshank	12.8	5.5	-56.9
Oystercatcher	49.5	28.5	-42.4

* Mean of one count made immediately after disturbance and another 30mins later in each trial.

(a)

(b)

(c)

MINUTES FROM DISTURBANCE
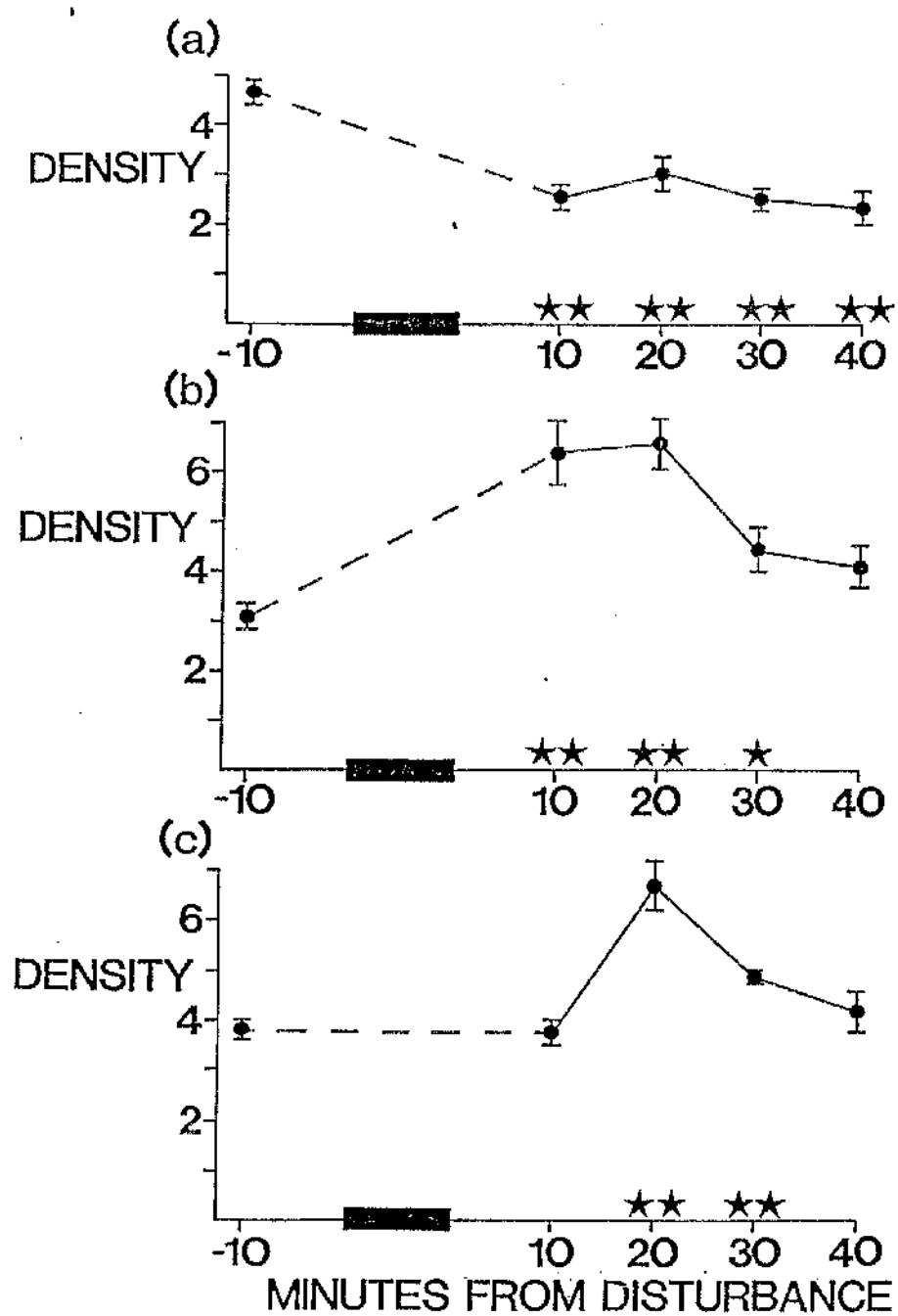
Fig.6.9. Flock densities around turnstones at Coalruffie in control disturbance trials; data represented as in Fig.6.8; 3 trials were carried out, and sample sizes range from 29 to 40 for each point.

(a) Overall density of oystercatchers.

(b) Overall density of turnstones.

(c) Visible wader density (expressed as turnstone equivalents – see text for details).

The changes in the number of birds in response to the control disturbance are given below:

	Mean no. before	Mean no. after[*]	% change
Turnstone	17.7	17.7	0
Purple sandpiper	10.7	10.7	0
Redshank	6.0	5.2	−13.9
Oystercatcher	48.7	54.0	+10.9

[*] Mean of one count made immediately after disturbance and another 30mins later in each trial.

(a)

DENSITY

(b)

DENSITY

(c)

DENSITY

MINUTES FROM DISTURBANCE
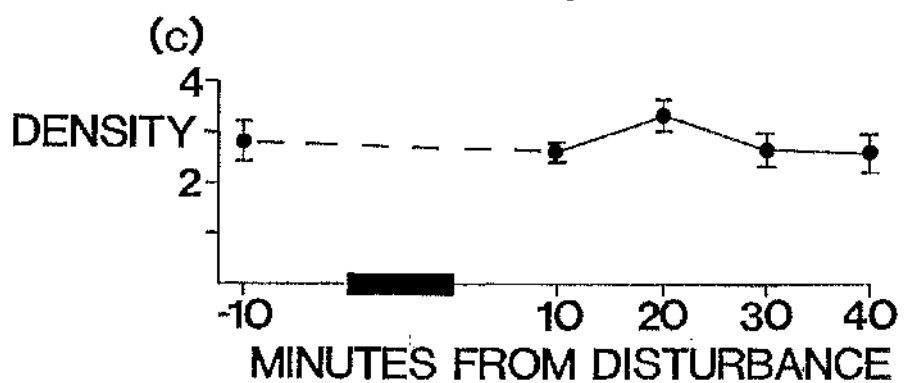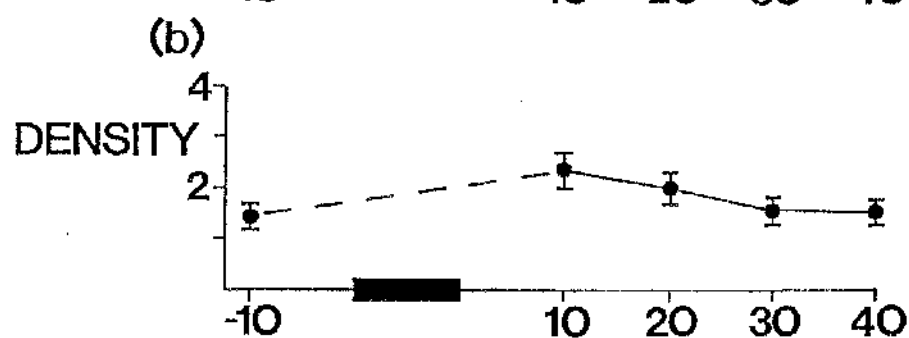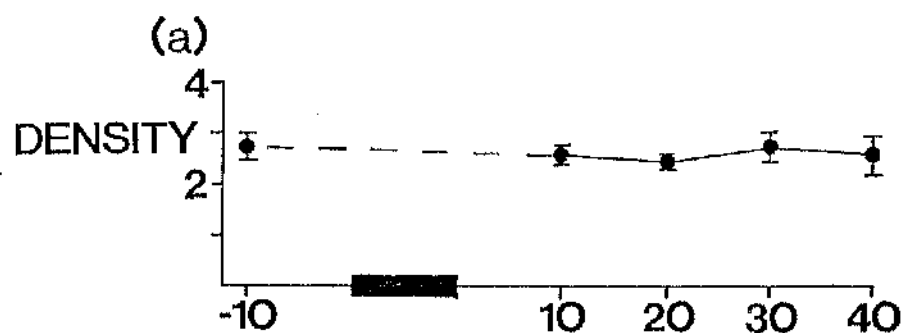
or running a high risk of predation). The evidence shows that they opt to feed at higher conspecific densities.

6.2.5 The Mechanisms of Flock Cohesion: Turnstone Search Paths

(a) The Effects of Visibility and the Presence of Other Birds

Turnstones do not move randomly while foraging; instead there is a strong directional component to their movement. Therefore in all situations there was a high probability that a bird would continue to move in the same general direction in which it had been recorded moving three seconds earlier. In other words, Forward was the most commonly recorded of the six directions of movement in the analyses of search paths. However, the probabilities of moving in any one direction were found to be affected by the presence of other birds, and this factor in turn was affected by habitat visibility.

Figure 6.10a illustrates that for turnstones in low visibility habitats (i.e. mean visibility score not greater than 10), there was a strong tendency to turn in the direction of the only neighbouring conspecific in addition to the high probability of continuing the previous direction of movement. A bird was always more likely to turn towards a sector when it was occupied by another turnstone than when it was not, and this was especially marked when the nearest conspecific was more than two metres distant (Fig.6.11a). For instance, a turnstone was four times more likely to make a complete 180° turn and move Backwards if the Back sector was occupied than if it was not. These findings are unlikely to have been the result of birds moving back towards food patches, as in all cases the flocks as a whole showed a directional trend, moving steadily across the boulder habitat.

This tendency to move towards other turnstones was not so marked when birds were feeding in monospecific flocks in good visibility
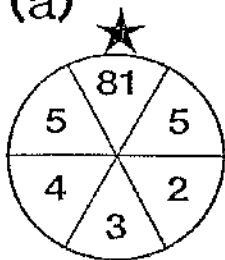
Fig 6.10. The percentages of turns made in each of six directions by foraging turnstones, in relation to the location of the only other turnstone within 10m (indicated by a star). The top sector in each circle indicates the percentage of moves made into the Forward sector; the bottom sector indicates the percentage made into the backward sector etc.

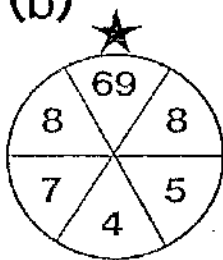(a) Birds in monospecific flocks in poor visibility habitats (n=525 moves, made by 37 birds).

(b) Birds in monospecific flocks in good visibility habitats (n=440 moves, made by 19 birds).

(c) Birds in mixed species flocks (i.e. with other species within 10m) in good visibility habitats (n=525 moves, made by 15 birds).

(a)

Row 1 (★ top): 81, 5, 5, 4, 3, 2

Row 2 (★ left): 49, 36, 8, 3, 0, 5

Row 3 (★ right): 44, 6, 47, 3, 0, 0

Row 4 (★ left): 56, 18, 3, 18, 3, 3

Row 5 (★ right): 61, 11, 11, 3, 3, 11

Row 6 (★ bottom): 75, 4, 5, 2, 12, 2

(b)

Row 1 (★ top): 69, 8, 8, 7, 4, 5

Row 2 (★ left): 41, 25, 22, 0, 0, 13

Row 3 (★ right): 30, 23, 37, 10, 0, 0

Row 4 (★ left): 59, 17, 11, 4, 2, 7

Row 5 (★ right): 57, 16, 19, 2, 2, 5

Row 6 (★ bottom): 73, 6, 11, 3, 5, 3

(c)

Row 1 (★ top): 58, 14, 16, 6, 3, 3

Row 2 (★ left): 63, 20, 12, 2, 4, 0

Row 3 (★ right): 40, 32, 17, 7, 2, 3

Row 4 (★ left): 60, 8, 23, 2, 4, 2

Row 5 (★ right): 56, 18, 15, 1, 2, 8
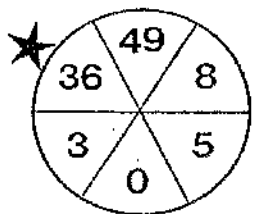
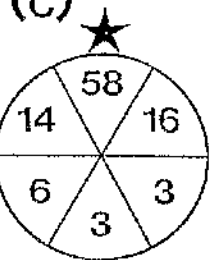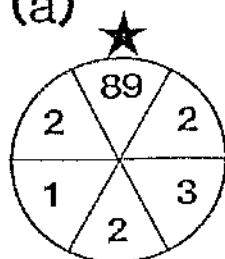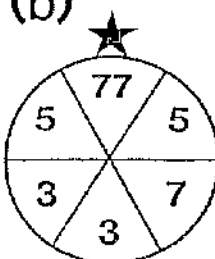Row 6 (★ bottom): 65, 10, 15, 2, 3, 5

Fig.6.11. The percentages of turns made in each of six directions by foraging turnstones as in Fig.6.10, except that observations are restricted to situations in which the nearest turnstone was more than 2m from the focal bird. Sample sizes (a) n=64 moves, (b) n=66 moves, (c) n=129 moves.

(a) (b) (c)

Row 1:
(a) ★ 89, 2, 2, 1, 3, 2
(b) ★ 77, 5, 5, 3, 7, 3
(c) ★ 61, 10, 18, 4, 4, 3

Row 2:
(a) ★ 17, 83, 0, 0, 0, 0
(b) ★ 38, 25, 31, 0, 6, 0
(c) ★ 58, 24, 11, 3, 0, 5

Row 3:
(a) 30, 10, 60 ★, 0, 0, 0
(b) 27, 18, 36 ★, 18, 0, 0
(c) 46, 28, 12 ★, 8, 4, 2

Row 4:
(a) 46, 18, 0, 27 ★, 0, 9
(b) 56, 22, 15, 4 ★, 4, 0
(c) 58, 8, 24, 3 ★, 3, 5

Row 5:
(a) 68, 0, 0, 0, 33 ★, 0
(b) 58, 15, 12, 4, 8 ★, 4
(c) 53, 22, 16, 1, 5 ★, 3

Row 6:
(a) 63, 8, 5, 3, 2, 20 ★
(b) 68, 8, 12, 3, 2, 8 ★
(c) 67, 9, 15, 2, 5, 2 ★
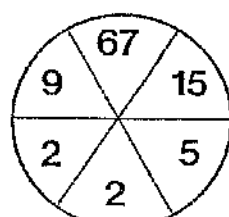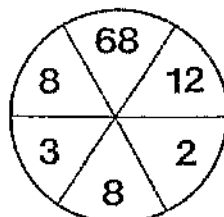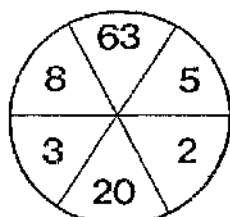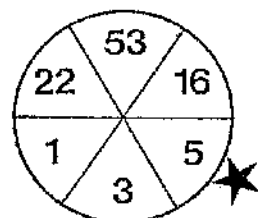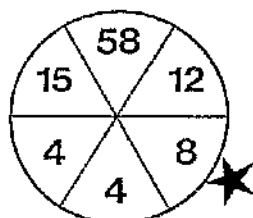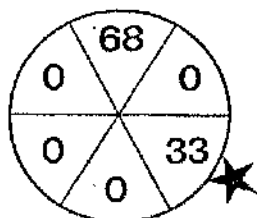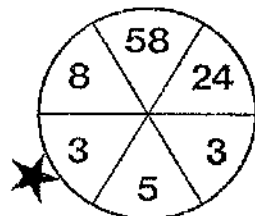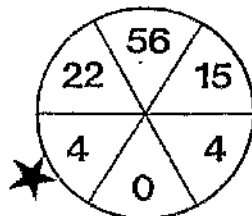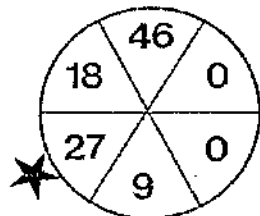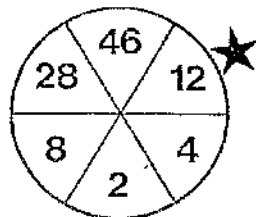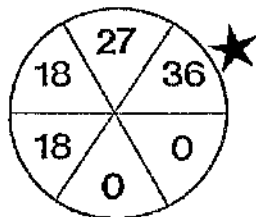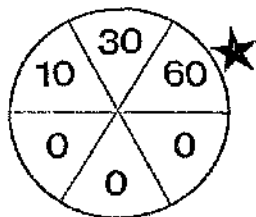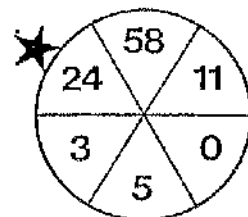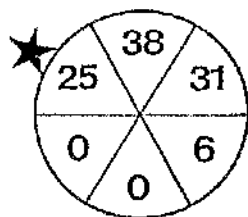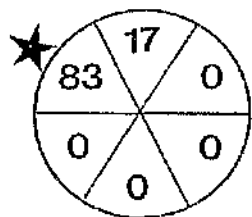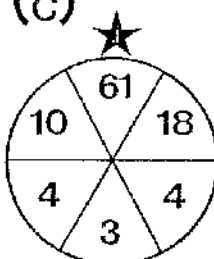
areas (Fig.6.10b). A turnstone was less likely to move in the direction of other turnstones (regardless of which direction that was) when in good visibility habitats than when the visibility was reduced (Wilcoxon's paired signed-ranks test; $T_s = 0$, n = 6, P < 0.05).

Turnstones in good visibility habitats were even less likely to turn towards other conspecifics if other species were present. (Fig.6.10c). When purple sandpipers, redshanks or oystercatchers were within ten metres of the focal bird, it had a significantly reduced tendency to move towards the nearest conspecific, especially if this was more than two metres away (Fig.6.10b & c; Wilcoxon's paired signed-ranks test, $T_s = 0$, n = 6, P < 0.05). In fact, when other species were present, the location of conspecifics appeared to have no effect on the direction in which a turnstone moved.

(b) The Effect of Dominance Rank in High-Density Flocks

Data were gathered from flocks of between 12 and 44 turnstones, feeding on shingle, loose rock and dead wrack; in all cases the visible density was at least ten birds within 10m of a focal bird. Individuals were followed on the video film for between 20 and 380 seconds, and were seen to interact up to nine times within that period. A total of 13 birds were only seen winning encounters (these were defined as the more dominant birds), 26 were defined as subordinate, having been seen only to lose encounters, and 33 were not seen to interact at all. Seven birds were seen to both win and lose interactions during the period that they were observed; these birds are omitted from the analysis.

Table 6.1 The proportion of moves different categories of turnstones made towards their nearest feeding neighbour. Samples are broken down according to the position of the neighbour. Data were obtained from dense flocks, and in all cases the neighbour was less than 3m from the focal bird

Direction of Neighbour	(A) % Moves	(A) (n)	(B) % Moves	(B) (n)	(C) % Moves	(C) (n)
Forwards	62.1	(29)	57.9	(57)	52.0	(25)
Left	45.0	(20)	30.3	(33)	13.3	(30)
Right	50.0	(22)	24.1	(54)	24.0	(25)
Backleft	50.0	(10)	17.1	(41)	8.0	(25)
Backright	33.3	(6)	13.0	(23)	14.3	(21)
Backwards	15.4	(13)	13.3	(15)	6.3	(16)

A = more dominant birds
B = birds of unknown rank
C = more subordinate birds

Comparing the search paths of the more dominant and more subordinate birds, it is evident that the more dominant birds were more likely to turn towards their nearest feeding neighbour than were the more subordinate individuals (Table 6.1; Wilcoxon's paired signed ranks $T_s = 0$, n = 6, P < 0.05). Thus, if all sectors are combined, the dominant birds moved towards their nearest feeding neighbour on 47% of occasions, whereas the proportion was 20% for more subordinate individuals. The sample of birds not seen to interact would be expected to exhibit behaviour which, on average, was intermediate between the other two groups, as it undoubtedly contained birds of a broader spectrum of dominance ranks than either extreme. This was confirmed, as the proportion of turns made towards the nearest feeding neighbour was significantly lower than that of the more dominant birds (Wilcoxon's paired signed ranks, $T_s = 0$, n = 6, P < 0.05), but was generally higher (although not significantly so) than the more subordinate birds (Wilcoxon's $T_s = 2$, n = 6, NS).

6.3 Discussion

In common with many other studies (e.g. Recher 1966, Burger et al. 1977, Brearey 1982, Fleischer 1983), this chapter has shown that

the oscillations of the tide induce cyclical changes in the densities of shorebird flocks. Over the high water period, feeding flocks are necessarily at high densities due to the limited area available for foraging. Densities then decrease as the dropping tide exposes a far greater potential foraging area; however, in neither turnstones nor purple sandpipers does the tendency to flock break down. As a consequence, at low water neither species is evenly dispersed over the intertidal zone, but is distributed in the form of fluctuating aggregations that move amongst the birds of other species. Thus, even though there are, for instance, only approximately 230 turnstones feeding in an area of some 1,500,000m^2 of suitable habitat (Chapter 1), each will have on average a minimum of 1.3 conspecifics within 10 m of it, and considerably more in regions of low visibility.

Individual turnstones and purple sandpipers will therefore tend to be close to other members of the same species; these conspecifics will nonetheless be only one component in a multi-species flock assemblage. When visible densities of the other species are converted to conspecific-equivalents (the currency which measures the vigilance benefits of flocking), it is evident that both turnstones and purple sandpipers derive considerable benefits from the natural densities of these other birds. As a result, on average both turnstones and purple sandpipers tend towards optimal flock densities, by avoiding those extremes of densities which result in their incurring high costs of either vigilance or aggression and interference. This is true even in low visibility areas, where overall densities must be maintained at high levels in order to produce the optimal intermediate visible densities. The two sets of removal experiments provide good evidence that this was not coincidental, as birds were shown to make adaptive responses to compensate for changes in flock density. It should not

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be thought surprising that such fine-level compensatory changes in dispersion may occur, as other studies have also found adaptive shifts in flocking behaviour in response to changing conditions. For instance, a situation analogous to an increase in aggression and interference was observed by Barnard et al. (1982) in their study of plover and gull foraging flocks. The movement of black-headed gulls (which kleptoparasitise plovers) into a lapwing flock resulted in a reduction in the flock size through a proportion of the lapwings immediately leaving; the same effect was noted upon the arrival of large numbers of golden plovers (which tend to cause interference to foraging lapwings, so reducing their feeding efficiency). In contrast, an increased predation risk may have the opposite effect. Caraco et al. (1980a) found that yellow-eyed juncos fed in larger flocks when a predator was present in the study area; removal of the bushes used by the birds as protective cover apparently produced a similar response (Caraco et al. 1980b) (although the latter analysis suffers from the inclusion of 'flocks' of zero birds in the calculation of the mean flock size).

These two studies have dealt with flock size, rather than density. The two parameters are closely linked where flocks are small; however flock size will tend to become less relevant to the behaviour of individuals as it increases, as local variations in the density of birds on one side of the flock will tend to exert a greater influence on their behaviour than any fluctuations in the number of birds at the other side. Thus Myers' (1980) observation of buff-breasted sandpipers *Tryngites subruficollis* leaving their feeding territories to form flocks on the appearance of a predator can also be viewed as the response of birds in what is, in fact, an over-dispersed and low density flock, to increase their local density within the flock by greater aggregation. It is valid to consider the

sandpipers' dispersion as being equivalent to a flock, since there was a cohesive response by the group as soon as any one bird detected a predator.

Such low density flocking is only possible in habitats with unrestricted visibility. A reduction in visibility will reduce the visual contact between members of the flock unless nearest neighbour distances are small. Thus one consequence of feeding in reduced visibility areas may be the necessity of increased flock densities, as found for turnstones and purple sandpipers on rocky shores in this study and for willets Catoptrophorus semipalmatus feeding in a salt marsh by Blick (1980).

One of the mechanisms of maintaining such densities is likely to be the tendency for moving birds to turn towards their neighbours. In turnstones this appears to be most pronounced when the individual has strayed some distance from the rest of the flock. In contrast, a turnstone within a mixed-species flock appears to be uninfluenced in its chosen direction of movement by the positions of conspecifics, as it can move in other directions yet still remain within the flock. Having lost the flock-cohesion constraints of moving, the bird should therefore adopt a movement strategy that maximises the efficiency of searching. Cody (1971) calculated, through computer simulations, that an animal would maximise the searching coverage of a limited area if it apportioned its time spent moving in the four directions Forward, Left, Right and Backward according to the following approximate ratios: 0.65F : 0.15L : 0.15R : 0.05B. If the equivalent proportions are calculated for the complete sample of moves made by turnstones feeding in mixed species flocks (i.e. Fig.6. c), converting the six 60° sectors to four 90° sectors by interpolation, the result is 0.653F : 0.152L : 0.148R : 0.047B. This is remarkably close to the

simulated optimum, which indicates that turnstones are able to achieve an extremely high efficiency of searching coverage over the limited extent of the intertidal area when unconstrained by the limitation to remain close to other conspecifics.

Vines (1980) found that, on average, oystercatchers tended to turn away from their nearest neighbour if they approached too closely. This tended to maintain an overdispersed distribution, rather than create flocks; a possible benefit of this behaviour was that individuals stood a reduced risk of being caught by surprise in a kleptoparasitic attack by another bird. Turnstones appear to behave in a similar manner when feeding in high density flocks in good visibility areas; however, the movement pattern adopted seems to depend on dominance status. The tendency for more dominant birds to move towards feeding neighbours not only enables them to kleptoparasitise more easily, it will also increase the likelihood that they move towards the centre of flocks. Conversely, the trend for subordinates not to move towards their neighbours may result in their gradually moving towards the flock periphery. While being on the flock periphery may reduce the risk of losing food to more dominant birds, it may also increase the risk of predation; the tendency of subordinates to avoid other birds may therefore not be so pronounced in habitats with a low risk of kleptoparasitism. This will be discussed further in the chapter that follows.

CHAPTER SEVEN - DISCUSSION

A key component of the dynamics of animal populations is the density at which the animals live. While in part controlled by population size, the spacing behaviour of the animals concerned is an important determinant of population density. Outside of the breeding season, foraging turnstones and purple sandpipers are clearly gregarious, and it has been shown that turnstones are attracted to other conspecifics, orientating their search paths such that they move with them, rather than turn away. This tendency to form groups affects other aspects of their behaviour such as the amount of time devoted to anti-predator vigilance, aggression, and kleptoparasitism, and their foraging efficiency. These effects in turn have consequences for the adaptive significance of the spacing behaviour, and thus influence its nature.

It is a generally accepted consequence of the theory of evolution by natural selection that those animals which live in groups do so because the benefits to the individual of this form of sociality outweigh the costs. The aim of this study has been to determine the costs and benefits of flocking, and the factors which influence these, in turnstones and purple sandpipers, in an attempt to investigate the extent to which flocking is an integral part of the social organisation and population ecology of these species.

Numerous costs and benefits which animals might acrue from feeding in groups outside of the breeding season have been suggested. These are briefly described below; more complete reviews of this topic can be found in Morse (1977), Bertram (1978), Blick (1980) and Pulliam and Millikan (1982). Possible benefits to the individual from such group living are:

(1) Improved probability of finding food through local enhancement,

copying, or an increase in the availability of prey items due to the prey being made more conspicuous by the disturbance effect of the group.

(2) An increased probability of capturing food items through the co-operative hunting efforts of the group.

(3) The capacity to capture and handle larger prey.

(4) More efficient utilisation of food resources, due to greater control over the spatial pattern of resource depletion and hence improved ability of the individual to estimate current resource distribution.

(5) Improved opportunities for more dominant and aggressive animals to kleptoparasitise other individuals.

(6) A decrease in the proportion of time that must be invested in anti-predator vigilance (and consequent increase in time available for other activities such as foraging), due to the sharing of vigilance with other members of the group.

(7) A reduction in the risk of being caught by a predator due to

    a) the presence of "many eyes" increasing the likelihood of the approaching predator being detected;

    b) a potential reduction in the predator's efficiency due to its being confused by the movement of the group;

    c) the predator being deterred by the group's united defence;

    d) a reduced probability of being the victim, due to the "dilution" effect.

Potential costs of living in goups outside of the breeding season are:

(1) A reduced probability of finding food items due to

    a) local depletion;

    b) the presence of the group causing a temporary reduction in food availabiliy due to a withdrawal response by the prey;

    c) the close proximity of other members of the group interfering

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with the searching efficiency of the individual.

(2) A greater loss of food items to other individuals through kleptoparasitism.

(3) A higher rate of aggression, which is costly in terms of lost time and energy, and the risk of injury.

(4) An increased conspicuousness to predators.

(5) A greater risk of disease and parasite transmission.

As most of these costs and benefits vary according to the size, and often density, of groups, questions concerned with the adaptive significance of groups relate not only to whether or not an animal should live in groups, but also to how large and of what form these groups should be.

A number of factors affect the cost benefit ratio of group living; some of these variables, listed below, remain constant for each species, while others vary both between individual members of a species and between different habitats. Thus the animal's optimal social environment may show temporal and spatial variation, ranging from living alone to living in a large group. Such variables are:

(1) The status of the individual. Subordinates and dominants may differ in their competitive abilities.

(2) Food abundance. There will be a greater tendency for groups to form at food patches when food is limited, as the intruder pressure will be higher and it will be more costly for one individual to defend the patch.

(3) Food distribution. Increased patchiness of food supplies may lead to the adoption of territorial defence rather than grouping.

(4) Prey type or behaviour. The possible costs of prey withdrawal as a response to the predators will only apply to certain prey types, while the incidence of kleptoparasitism will depend on the

opportunities and profitability of so doing.

(5) Conspicuousness of the group. This will partly depend on the appearance of the species concerned, and partly on the habitat. Cryptic species may stand a far greater chance of avoiding detection if solitary than if in a group.

(6) The abundance of predators.

(7) The nature of the habitat.

(8) The priorities of the individual. The food intake requirement of an individual is not constant throughout its life, and variation may cause shifts between risk-prone and risk-averse foraging strategies. Thus animals nearing starvation, preparing for migration or breeding may behave in a manner that potentially increases their food intake, but also exposes them to a higher predation risk.

(9) The long term requirements of the individual. Animals may optimize their behaviour in the long rather than the short term.

(10) The composition of the group. The attractiveness of the group to incoming individuals will depend upon the individuals and species of which the group is composed.

Both turnstones and purple sandpipers clearly benefit from foraging in groups in terms of an increased overall anti-predator vigilance at a reduced time cost to the individual. Thus predators will be more readily detected by groups, and the flight response of a highly manouverable flock may confuse the predator and reduce its success rate as has been found in other studies (Neill & Cullen 1974, Page & Whitacre 1975, Kus quoted in Myers 1984). The individuals presumably also benefit in that, when in a group, their chances of being the victim are reduced due to dilution of the predator's effects (Hamilton 1971). Unfortunately, it was not possible to study foraging benefits directly, due to the difficulties in quantifying feeding rates and prey types, as discussed in Chapter 4. However,

when foraging in a group, dominant turnstones appear to have benefited from an increased opportunity to kleptoparasitise subordinates. This clearly represents a cost to subordinates of group foraging. Moreover, the level of aggression (predominantly food related) increased substantially with flock density in both species. This suggests that local competition, a potential cost of flocking, was also increasing at higher densities. Other studies of foraging shorebirds have shown that loss of food and time in aggression are only two components of the reduction in efficiency which occurs at high flock densities; time devoted to avoiding encounters with other birds may also increase, and there may be a reduction in searching efficiency (e.g. Ens & Goss-Custard 1984).

These costs and benefits of foraging in groups were found to vary in relation to both social and environmental factors. Time devoted to vigilance did not only vary in relation to group size, but also in relation to habitat type. Both species were more vigilant in low visibility habitats, depite the fact that they were probably less conspicuous to predators. This may explain why they tended to occur at higher flock densities in these low visibility habitats, since this would to some extent offset the increased vigilance level required in these habitats. In turnstones, an alternative explanation for the higher flock densities in low visibility habitats is that, since rates of kleptoparsitism tended to be lower in these predominantly rock and boulder areas, this cost of high density was reduced. However, in purple sandpipers there were no habitat differences in kleptoparasitism rates, yet flock density was still higher in low visibility habitats. This suggests that the higher densities in these habitats were probably necessitated by vigilance requirements in both species.

A further variable that influences flock density is the state of the tide. Flock densities increased towards high tide. While this may in part be due to compression of the available foraging habitat, it is possible that increased predation risk in the upper shore area is a contributory factor. The structural complexity of the upper shore area facilitates ambush predation by raptors and mammals, and the threat from human disturbance is greater in this area. Other studies have also suggested that flock dynamics are influenced by predation risk. For example Willis (1972) suggested that the absence of flocking behaviour in the birds of Hawaii might be related to the lack of avian predators, while Caraco et al. (1980a) found that dark-eyed juncos formed larger flocks when a predator was present in the area. Hitherto territorial wintering sanderlings were found to abandon their territories and join flocks in years in which a merlin frequented their foraging areas; moreover, foraging flocks increased in both size and density with this higher risk of predation (Myers 1984).

Since the wader groups studied were clearly not made up of identically behaving units, these costs and benefits of flocking applied differentially to individuals in relation to their status, age and species, and possibly also sex (although the latter was not examined due to the difficulties of sexing birds in the field). It has been demonstrated (Chapter 3) that individual turnstones tended to associate with only a limited subset of the turnstone population in the study area. This permitted the development of dominance hierarchies, presumably based on individual recognition. Subordinate individuals suffered higher rates of kleptoparasitism, and conversely, dominant individuals were able to obtain both food items and feeding positions from other birds. The aggression-related costs and benefits of group foraging were therefore different for different

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individuals. The costs of increasing flock density were greater for subordinates, leading to differences in the optimum flock density for individuals of different status. Search paths differed in relation to status when turnstones were feeding in dense flocks. Subordinates were less likely to move towards near neighbours than were dominants, presumably because of the risk of being kleptoparasitised. However, since the regulation of flock density is not wholly within the control of each individual, it is likely that some individuals had to forage under sub-optimal conditions.

One consequence of the movement patterns of subordinates as compared with dominants is that subordinates may tend to end up on the periphery of flocks, where they are presumably more vulnerable to predation (Vine 1971, Kus quoted in Myers 1984). There is evidence to suggest that juvenile turnstones tend on the whole to be subordinate to adults (Groves 1978, P. Whitfield pers. comm.). There was an insufficient number of marked juveniles in this study to examine their status in detail. However, overall, juveniles were found to disappear from the study area at a higher rate than adults, presumably due to a combination of higher mortality and higher vagility, as has been shown in other studies (Kus et al. 1984, Myers 1984, P.Whitfield pers. comm.). In general, survival of dominants is likely to be greater than that of subordinates (due to greater access to available food resources and a reduced risk of predation), which has clear implications for the dynamics of the population.

Although both turnstones and purple sandpipers were found in the same multi-species flocks, the relative costs and benefits of flocking differed between the two. It was established that, in comparison with turnstones, purple sandpipers do not appear to benefit as much, in terms of reduced time spent vigilant, from the

presence of other species in the flock. In contrast to turnstones, the number of purple sandpipers in particular localities varied greatly from day to day. This may have been a consequence of the greater need for individual purple sandpipers to remain associated with a conspecific flock in order to obtain the vigilance benefits of flocking. Thus the use of a particular feeding site is more likely to be dependent upon the presence of conspecifics in purple sandpipers than in turnstones. In turnstones, one benefit of "trusting" heterospecifics is that conspecific density can be reduced, so reducing local competition and interference, while maintaining the vigilance benefits of higher flock densities. That this is not the case for purple sandpipers means that, to obtain a given vigilance level, they must tolerate higher conspecific densities than do turnstones. Presumably, they are able to do this because, being tactile rather than visual feeders, they actually suffer less interference from conspecifics when searching for food. Similar tolerances of high conspecific densities have been reported for tactile foraging waders in other studies (Goss-Custard 1976, 1980).

In turnstones and purple sandpipers the anti-predator benefits of mixed species flocking appear to apply mainly to predator detection. The characteristic response of such flocks in the study area to the approach of a raptor was that the flight flocks were composed of species of similar sizes. Thus turnstones and small sandpipers departed together, becoming separated from the larger waders such as redshank, oystercatchers and curlews, with which they had previously been foraging. This tendency to take flight with birds of a similar size may, in part, be due to the difficulties of maintaining the flock cohesion necessary to confuse a predator when the flock is composed of individuals of very disparate size and flying performance. A further possible disadvantage of mixed species

flight flocks is that it may be easier for the pursuing predator to select a victim, due to the increased conspicuousness of individuals of species which comprise the minority of the flock (i.e. the so-called "oddity" effect (Curio 1976)).

Not only were the groups not composed of identically behaving units, but the behaviour of the individuals themselves was not constant, varying in space and time. Some of the ways in which environmental heterogeneity affected spacing behaviour have been discussed above. Temporal variation in vagility, flock dynamics and individual time budgets were also found to occur in this study. In spring, turnstones were found to increase the size of their home ranges. This occurred at the same time as (a) an overall reduction in the numbers of both turnstones and (especially) other species in the study area, due to the departure of some birds for their breeding grounds, and (b) an increased aggregation of the remaining turnstones, leading to higher turnstone flock densities. There are a number of possible explanations of these changes. As suggested in the previous chapter, the increase in conspecific density in the turnstone may have been to compensate for reduced heterospecific density. The disturbance experiments at other times of year demonstrated that, in the absence of heterospecifics, turnstones increased their local flock density. This hypothesis is further supported by the fact that purple sandpipers (which do not benefit from the presence of these other species) did not alter their conspecific flock density between winter and spring. Thus the increase in home range size observed in the turnstone probably reflects the increased movement necessary for the formation of flocks due to the overall decrease in the number of birds in the area.

Alternatively, the increased range size may have been due to

prey depletion necessitating an expansion of foraging range, or reflect a movement of subordinates into preferred areas on the departure of dominants. These explanations are less likely for the following reasons. Prey abundance may in fact be increasing rather than decreasing by the time turnstones and purple sandpipers migrate; furthermore, if prey depletion had occurred, it would be expected that flock densities would decrease rather than increase, in order to reduce local competition. The remaining turnstones were not consistently found in particular localities, but rather wandered over the entire study area, which implies that they were not occupying preferred areas. Moreover, since there was no correlation between the size of a bird's winter home range and the extent of its spring vagrancy, and since home range size was correlated with dominance status, the implication is that dominants wandered as much as subordinates, which would also run counter to the hypothesis that movements were caused by subordinates invading those areas previously occupied by more dominant birds.

The situation is further complicated by the fact that, in spring, the priorities of the adult turnstone have altered due to the need to build up fat reserves prior to the migration to their breeding grounds. The time budgets of adults, but not juveniles, were found to alter in spring such that they devoted more time to foraging. The overall level of adult vigilance decreased at this time independent of flock density. This undoubtedly leads to an increased risk of predation, especially at the lowered flock densities which would have occurred after the departure of the other birds, had the remaining turnstones not aggregated.

This study has therefore shown that the spacing behaviour of individual shorebirds in the non-breeding season represents a trade off between the costs and benefits of living in groups, and that the

relative levels of these costs and benefits vary with season, habitat and individual status. Such differences affect the flocking behaviour, dispersion and ultimately the survival of individuals, and hence their population dynamics.

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