WINTERING RAPTORS AND THEIR AVIAN PREY: A STUDY OF THE BEHAVIOURAL AND ECOLOGICAL EFFECTS OF PREDATOR-PREY INTERACTIONS.

Will Cresswell

This thesis has been composed by myself and represents my own work except where acknowledged.

Thesis submitted for the degree of Doctor of Philosophy
University of Edinburgh
1993

ABSTRACT

Sparrowhawks, peregrines, and merlins were observed hunting known prey populations (mainly redshank, dunlin and skylarks) at the Tyninghame estuary (East Lothian, Scotland). Raptor predation was shown to be the most significant cause of mortality in some wader species. Kleptoparasitism of raptors carrying prey, by carrion crows, significantly increased the over winter mortality of some waders. Redshank populations were most affected by raptor predation. No selection for body size in redshank was found, but juveniles were more likely to be killed by raptors. This was a consequence of adult redshank risk-averse foraging, and excluding juveniles from low-risk,and low-feeding profitability areas. Juveniles, even though feeding in a relatively profitable area compared to adults, still showed risk-prone foraging within that area.

Flocking reduced an individual redshank's probability of being killed by a raptor. Larger flocks were preferentially attacked, but an attack was significantly more likely to succeed on a smaller flock. Within a larger flock a redshank was less at risk through the "dilution" effect, vigilance effects (which were shown to be a direct consequence of flock size) and probably also the "confusion" effect. Redshank did not gain any foraging benefits within larger flocks. Redshank responded differently when attacked in a similar way by the three species of raptor. The response that was most likely to lead to escape from a sparrowhawk was most likely to lead to capture on peregrine attack, showing that raptor discrimination was important.

Skylarks used song as a pursuit-deterrent signal on attack by merlins. Other anti-predation responses also influenced the probability of capture, and their use probably depended on the condition of the skylark.

All three raptors were generalist avian predators with overlapping diets, although merlins specialised on skylark and dunlin. Interspecific raptor size differences and intraspecific sexual size dimorphism were reflected in differences in the size of prey chosen. The three raptor species differed in their attack characteristics, but prey capture success rates were similar and generally low. Attack success rate was determined mainly by prey behaviour, condition of the prey, and time since the previous hunt. Attack rates depended on availability of prey, temperature and time of day. Prey was chosen according to size, numerical availability and vulnerability of a species (which was shown to consist of attack rate, success rate, conspicuousness of the prey, and association with vulnerable species). The three raptor species were probably energy-intake minimisers during the winter: most of the daily time budget was spent inactive, and much time was available for the usually very brief hunts.

Most mobbing of raptors was probably kleptoparasitism. Kleptoparasitism risk between raptors and from crows was high: much of sparrowhawk feeding behaviour reflected this risk. Interactions between raptors appeared to be based on the relative risk each species represented as a kleptoparasite.

ABSTRACT

Raptor predation was studied by direct observation of sparrowhawks, peregrines, and merlins, hunting a known prey population, and subsequent recovery of kills. Raptor predation was shown to be the most significant cause of mortality in most wader species. Kleptoparasitism of raptors carrying prey, by carrion crows, significantly increased the over winter mortality of some waders. Redshank populations were most affected by raptor predation; over 50% of the total population and over 90% of the juvenile population were taken in two winters. No selection for body size in redshank was found, but juveniles were more likely to be killed by raptors. This was a consequence of adult redshank risk-averse foraging, and excluding juveniles from low-risk,and low-feeding profitability areas. Juveniles, even though feeding in a relatively profitable area compared to adults, still showed risk-prone foraging within that area. Flocking reduced an individual redshank's probability of being killed by a raptór. Larger flocks were preferentially attacked, but an attack was significantly more likely to succeed on a smaller flock. Within a larger flock a redshank was less at risk through the "dilution" effect, vigilance effects (which were shown to be a direct consequence of flock size) and probably also the "confusion" effect. Redshank did not gain any foraging benefits within larger flocks. Reduced individual risk of predation appeared to be the main reason for flocking. Redshank responded differently when attacked in a similar way by the three species of raptor. During an attack the probability of capture depended on the escape response. The response that was most likely to lead to escape from a sparrowhawk was most likely to lead to capture on peregrine attack, showing that raptor discrimination was an important determinant of over-winter survival. Alarm calls were relatively unimportant as an anti-predation behaviour in redshank. Skylark, in contrast, used song as a pursuit-deterrent signal on attack by merlins. A merlin was more likely to give up sooner and to be unsuccessful if the skylark being chased had sung at the beginning of the attack. Skylarks used other anti-predation responses on merlin attack, which also influenced the probability of capture. All three raptors were generalist avian predators with overlapping diets, although merlins specialised on skylark and dunlin. Interspecific raptor size differences and intraspecific sexual size dimorphism were reflected in differences in the size of prey chosen. Sparrowhawks mainly made single attacks per hunt, at prey on the ground; peregrines made several attacks per hunt, at prey in flight; merlins were intermediate. Chase lengths were mostly very short except for some merlin attacks on skylark. Prey capture success rates were low and depended mainly on prey behaviour, condition of the prey, and time since the previous hunt. Attack rates depended on availability of prey, temperature and time of day. Prey was chosen according to size, numerical availability and vulnerability of a species (which was shown to consist of attack rate, success rate, conspicuousness of the prey, and association with vulnerable species). Most mobbing of raptors could be interpreted as kleptoparasitism. Kleptoparasitism risk between raptors and from crows was high: much of sparrowhawk feeding behaviour reflected this risk. Raptor-raptor interactions appeared to be based on the relative risk each species represented as a kleptoparasite. The three raptor species were probably energy-intake minimisers during the winter: most of the daily time budget was spent inactive, and much time was available for the usually very brief hunts.

TABLE OF CONTENTS

Chapter 2: Methods

2.5 Prey of Raptors

2.6 Redshank Data

Chapter 3: Raptor Predation on Wintering Wader Populations at the Tyninghame Estuary, East Lothian

Chapter 5: Choice of Redshank Feeding Location: Profitability or Risk?

5.2 Results

Chapter 6: Sparrowhawk Winter Hunting Behaviour

6.2 Results

6.2.3 Attack Rate

6.3 Discussion

Chapter 7: Peregrine and Merlin Winter Hunting Behaviour

7.2 Results

7.2.3 Diet

7.3 Discussion

Chapter 8 Interactions Between Merlins and Skylarks

8.2 Results

10 Appendices

ACKNOWLEDGMENTS

This work was carried out while I was in receipt of a NERC studentship at Edinburgh University. During my Ph.D research I was fortunate to have three excellent supervisors, with different strengths and areas of experience. I am very grateful to them for helping and teaching me so much during the past thee years. I would like to thank Philip Whitfield for initiating the project, and teaching me much about raptors and waders, and the practicalities involved in long-term field work. I would like to thank Linda Partridge and Philip Ashmole for their advice, enthusiasm and editorial comments. Thanks to Graham Appleton, Ian Bainbridge, Jeremy Wilson, Graham Scott, Colin Davison, Chris Thomas, Karen Rose, Adrian Carter, Susie Cresswell and all others who helped with cannon-netting and kill searching. Thanks to Bobby Anderson for his cooperation and help with work carried out at the John Muir Country Park, Tyninghame. Thanks to John and Eddy, and the factor, Mr. Milligan, of the Tyninghame Estate for giving me much practical help and access to the estate. Thanks to Mike McGrady for teaching me to handle and radio-tag sparrowhawks, and for his enthusiasm. Thanks to Pete Gordon for his help confirming wader counts at Tyninghame. Thanks to John Deag and Dennis Holt for computing advice and help. Thanks to Peter Whelpdale and Dave McKenzie for their logistical support. Thanks to my parents for their support and enthusiasm. In particular, I would like to thank Sue Holt for her contributions to every aspect of this study, from kill-searching to editorial criticism, and for her constant support and understanding.

CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Interactions between predators and prey have been responsible for the evolution of much of the morphology and behaviour observed in animals (Edmunds 1974, Curio 1976, Bertram 1978, Harvey & Greenwood 1978, Pulliam & Caraco 1984, Endler 1991). Natural selection will favour those predators that detect and capture prey most efficiently, and will favour those prey that are able to detect and escape from predators most efficiently. The result is an evolutionary arms-race, in which predators continually improve hunting abilities while prey continually improve escape abilities (Dawkins & Krebs 1979, Futuyma & Slatkin 1983, Endler 1986, Vermeij 1987). Predator-prey interactions are to be discussed within this thesis in the context of this continuous selection.

Predator-prey interactions affect instantaneous behavioural decisions by the prey (Lima & Dill 1990), and the predator (Endler 1991). Instantaneous behavioural decisions, such as aggregation by the prey, or choice of prey species by the predator, may affect local population dynamics of both predators and prey (Hassell & May 1974, May 1978, Hildrew & Townsend 1982, Heads & Lawton 1983, Hassell & May 1985, Partridge & Green 1985, Whitfield 1985a). If behavioural differences which lead to some subset of the prey population being killed by predators are genetically based (Taylor 1984), then the long term selection pattern will be affected. This thesis will study the evolutionary consequences of predator-prey interactions by exploring the effects that decisions by the predator or prey may have:

1. How predation affects a local prey population.
2. How a prey population affects a local predator population.
3. How the relative abundance of different prey species affects predator behaviour.
4. How prey behaviour affects predator behaviour.
5. How predator behaviour affects prey behaviour.

The effects are all interlinked, particularly 1 to 3, and 4 and 5: responses by the predator will be met by responses by the prey, instantly in the form of behavioural decisions, seasonally in the form of population dynamics, and over generations through evolution. Because of the dynamic nature of the interaction it is most meaningfully studied as a complete system.

Studying the predator, without knowledge of the prey, or *vice-versa* will give little idea of the relative importance of the selective pressures acting on the animals. In order to understand real biological systems a wide study is needed, particularly in the case of avian predators, which are to some extent generalists (Rudebeck 1950,1951, Baker 1967, Newton 1979, Ratcliffe 1980, Newton 1986). The population levels, and vulnerabilities of each prey species will affect the vulnerabilities and populations of other prey species. The degree of predation on a species at any one time may be determined entirely by the availability and behaviour of another prey species (Tinbergen 1946, in Newton 1986, Holt 1984). Similarly, generalist predators compete with each other and so the type and level of predation on a species may be determined by the presence or absence of a competing predator species (Taylor 1984), conversely cooperative hunting by predators may increase choice of available prey and hunting success (Bednarz 1988, Ellis et al. 1993). All of the predators, and all of the potential prey within a system must be considered. Except in cases of very specialised predators, such as specific host/parasite systems, the implications of the behaviour and availability of a prey species for its predators can only be understood in the context of all potential prey, and their availability and response to predation.

1.2 Predator Responses to Prey Population:

The importance of predation in influencing the size of a prey population depends on the functional response of the individual predator and numerical response of the predator population as a whole. There are two main types of functional response which apply to vertebrate predators responding to prey population changes, as defined by Holling (1959a, 1959b and 1965), who described attack rates of mammals on saw-fly cocoons and attacks by parasitic wasps:

Type-2 Functional Response (Holling 1959b): Predators increase their attack rate very rapidly with initial increase in population levels, and this gradually levels off at high population levels.

Type-3 Functional Response (Holling 1959a): As prey population rises initially, the predator attack rate only increases slightly, then it accelerates very rapidly before finally levelling off at high population levels (an S-shaped curve).

The type-two response occurs as the predator takes a smaller and smaller proportion of the prey population as prey density increases.

This occurs because, as the rate of feeding goes up, the predator spends a greater proportion of its time handling prey; eventually handling time constrains any further increase in attack rate (e.g. Keith et al. 1977, Goss-Custard 1984). The type-three functional response is similar to a type-two except in its initial stages, and can occur with a predator with more than one prey type available. The sudden increase in attack rate may occur as the predator switches to specialise on the newly abundant prey type (e.g. Oaten & Murdoch 1975a, Cook & Miller 1977, Erlinge et al. 1984).

1.3 Optimal Foraging

Optimality models use the Darwinian assumption that all behaviours maximise fitness. All prey types do not have the same value to the predator. Profitability of prey will depend on, for example, relative availability (Greenwood & Elton 1979, Allen 1988), energetic value of prey (e.g. Davies 1977), conspicuousness (Baker & Parker 1979, Baker & Hounsome 1983), risk of injury during handling, nutrient quality (e.g. Bryant & Kuropat 1980), and handling time (e.g. Elner & Hughes 1978). A predator will be expected to select preferentially the prey types that are most profitable in order to maximise its fitness (MacArthur & Pianka 1966). Conventional foraging models maximise the net rate of energy gain while foraging (Stephens & Krebs 1986). Energy can be measured both as a cost and a benefit (the energy expended or gained by a particular behaviour). This leads to an expression of net energy gain for a particular behaviour. Time is critical because the time available will always determine intake rates. Schoener (1971) described two ways in which an animal could acquire more energy for less time spent foraging. Time minimisers minimise the time required to gain a fixed ration of energy. Energy maximisers maximise the amount of energy gained in a fixed time. Both alternative currencies (see Chapter 5) are equivalent to rate maximisation in many circumstances (Pyke et al. 1977). An optimality model aims to predict which particular trade-off between the costs and benefits of different behaviours will give the maximum net benefit to an individual animal. Optimality models if used wisely are a powerful tool to analyse the decisions made by predators, and many studies using optimality models have produced testable hypotheses which were borne out by field data (e.g. Goss-Custard 1977a, Zach 1979, Kacelnik 1984). However, the optimality approach has been strongly criticised (e.g. Gould & Lewontin 1979): organisms may not be free to evolve optimally (e.g. phylogenetic constraints) or when a model fails to make accurate predictions it is modified to fit the data, reducing the approach to a circular argument. But as each modification will produce testable predictions, this criticism is minor (Krebs & Kacelnik 1991).

Many optimality models have used energy intake as the currency that is maximised. Predators will take the largest prey at all times irrespective of the availability of small prey (Krebs et al. 1977). Profitability of a prey may be offset by a long handling time, and so smaller individuals of lower profitability may be selected as net energy yield per unit of handling time is greatest (e.g. Elner & Hughes 1978). Profitability of prey may be offset by a long searching time: conspicuous prey may be favoured, compared to cryptic prey (e.g. Gendron 1986).

The optimality approach makes clear predictions of where a predator should choose to feed. Marginal value theorem (Charnov 1976) makes predictions about patch residence time in terms of the diminishing returns within a patch with time, and the travel time (or spacing) between patches. Predators should maximise their overall energy gain from an area and leave a patch within the area when the rate of feeding within that patch is less than the average expected for the area. When travel time is longer between patches, then the predator should endure a lower rate of feeding in a patch before moving. For example, foraging starlings (Sturnus vulgaris), collecting prey to bring back to the nest (Kacelnik 1984).

Choice of where to feed by a predator will be very complex. Prey will not be evenly distributed across a habitat, and so there will be a very complicated interaction between the relative abundance of different prey types, in different patches, moderated by each species' degree of crypsis, vulnerability and handling time. Predators probably do not assess each of these factors separately, but instead use 'rules of thumb' (Krebs & McCleery 1984). A predator only has to monitor rate of feeding within a patch, and relate it to the rate of feeding obtained recently in other patches, in order to decide whether to move or to stay (Janetos & Cole 1981). Other examples of simple 'rules of thumb' approximating optimal solutions were shown by Waage (1979) and Waddington & Heinrich (1979).

1.4 Density Dependent Effects of Predator Numbers on Prey Numbers

Predictions from optimality models of where to feed and what to feed on may be modified according to the numbers of predators using a patch. Predators using the same area may interfere with each other, in such a way that their hunting efficiency is decreased (Griffiths & Holling 1969, Salt & Willard 1971, Salt 1974). This may be true particularly for vertebrate predators that hunt very mobile prey by surprise. Inter-attack times are analogous to time-dependent renewal of a resource within a patch (e.g. Gill & Wolf 1975, Davies & Houston 1981). Predator success rate may be very low after an attack because prey is disturbed and vigilant, but increased vigilance levels may decay in time. Several predators within one area may so frequently disturb prey that hunting or foraging success rate never has sufficient time to rise (e.g. Goss-Custard 1970a). The profitability of an area may therefore be directly proportional to the number of predators present (e.g. Goss-Custard 1970a,1976,1980, Fleischer 1983). Multiple predators in a patch may influence the profitability of a patch through kleptoparasitism (Temeles 1990), and choice of optimal prey by a predator may be modified to take into account the risk of kleptoparasitism (Ellis et al. 1993).

The number of predators, or overall level of predation exerted by the predators (which incorporates attack and success rate) on a particular species may regulate the population of the prey species (Balser et al. 1968, Virnstein 1977, Hassell 1978, Potts 1980, Hassell 1985). In conditions of high prey population density, predation is high and consequently the prey population falls; conversely in conditions of low population density, predation is low and the population rises. The net result is an observed stable population level in which any perturbations from the equilibrium are corrected (usually by a functional response) by the predator. Under certain conditions, predator-prey models predict that stability will occur in a predator-prey system (Rosenzweig & MacArthur 1963, Oaten & Murdoch 1975a,1975b, Sih 1984, Taylor 1984, Hassell 1985). The conditions that are probably most relevant to avian predators are access to alternative food that can sustain predators when preferred prey becomes scarce, predators characterised by low prey-capture efficiency and predator populations limited by factors other than food, such as territory availability. Density-dependent mortality has been shown by Erlinge et al. (1983) and Erlinge (1987) under the conditions outlined above. The important characteristic of a stable, density-dependent predator-prey system appears to be the time lag of the functional response (Erlinge et al. 1983). With generalist predators that take large numbers of a wide range of species, the functional response can be immediate and very large, and a rare prey item can become a common food of several species of predators within a short space of time. In the non-breeding season, avian predators can be very mobile and will be able to track localised abundances of prey. Over wintering predatory birds often concentrate where there is a plentiful food supply (Kenward et al. 1981). This will increase the effect of the functional response, and the corresponding degree of density-dependent mortality.

1.5 Behavioural Responses by Prey to the Risk of Predation

Not all individuals of a species are under the same risk of predation. Certain activities, such as feeding, are more risky than other activities such as vigilance. An animal must trade off conflicting activities to achieve an optimum solution, which will minimise the risk of predation and maximise some other factor, such as energy intake, or condition for future reproductive fitness. There is a wide body of evidence that suggests that animals do assess the risk of predation, and use this assessment in behavioural decisions such as feeding (Krebs 1980, Dill 1987, Valone & Lima 1987, Feener 1988) and when and how to escape from predators (Ydenberg & Dill 1986, Poysa 1987a, Savino & Stein 1989).

Animals can behaviourally moderate the risk of predation: most stages in the encounter of a predator and prey can be directly affected by prey behaviour (Lima & Dill 1990). The risk of predation is a function of the rate of encounter between the predator and prey, the probability of death in the encounter, and the time spent vulnerable to the encounter (Holling 1959a). All of these factors can be assessed by the prey and can be behaviourally moderated. The encounter rate between predator and prey will be a function, for example, of local predator density, search tactics and habitat structural complexity. Prey may use a recent sighting of a predator to indicate a high risk of attack (e.g. Sonerud 1985). The probability of death during an encounter will be composed of easily assessed factors such as the species of predator, the distance from the predator, the number of other prey animals in the vicinity, and the proximity of the prey to cover. The remaining component of the risk of predation, the time spent vulnerable to the risk of predation, will also be composed of easily assessed factors such as the time spent feeding without vigilance, or close to predator-hiding cover.

There are a variety of ways in which an animal's decision of what to do is influenced by the need to minimise the risk of predation. In the non-breeding season, the main decisions carried out by an animal that can be potentially modified by an assessment of risk will be feeding decisions. Certain times of the day are more dangerous to feed in than others: Caldwell (1986) showed that herons under intense diurnal hawk predation shifted foraging periods to the safer dusk period. Similarly, Clarke (1983) showed that foraging activity in mice was reduced in bright moonlight, as the risk of predation by owls was greater. Not all feeding areas are equally dangerous for prey: Sih (1980, 1982) showed that aquatic insects preferentially chose low risk feeding areas in the presence of predators. Similarly, Lima et al. (1985) showed that squirrels would carry prey into the safety of cover before feeding. What to eat may be modified by the risk of predation: Lima & Valone (1986) found that squirrels preferentially selected less profitable larger food items, in terms of energy gained per unit of handling time, because these could be most easily transported into cover for safe consumption.

Young animals may have different nutritional requirements from adults, and different feeding skills due to lack of experience (Partridge & Green 1985), and consequently be found in different areas to adults. Sub-dominant individuals may be excluded from the most profitable feeding areas (e.g. Goss-Custard et al. 1982,1984), or the least risky areas (e.g. Schneider 1984, Suhonen et al. 1993). The nutritional requirements of the sexes are frequently different, especially during reproduction (e.g. Clark 1980). Different individuals of a prey species under the same predatory risk may therefore differ in their vulnerability to predators, and so there will be consequent intraspecific differences in the assessment of risk of predation relative to foraging needs.

One major way in which risk of predation may be behaviourally altered by the prey is via group size. Animals gain anti-predation benefits from being in a group in three ways: vigilance, the "confusion" effect and the "dilution" effect. Many predators attack by surprise (e.g. Rudebeck 1950,1951, Schaller 1972), and so early detection of the predator by the prey ensures that the chance of making a successful hunt remains low (e.g. Bertram 1980). The probability of detection of an approaching predator increases with increasing flock size, even though an individual animal's level of vigilance within the group can decrease (Pulliam 1973). There are many studies of vigilance that show a decrease in individual vigilance with increasing flock size, and increase in probability of predator detection (see Elgar 1989 for a review, and Chapter 4). Many studies did not account for confounding variables such as formation of flocks for feeding and the effects of feeding rates on vigilance (Elgar 1989). Excellent examples of vigilance studies are Barnard (1980), Bertram (1980), Elgar & Catteral (1981), and Elgar et al. (1984). The confusion effect is thought to occur when predators attack groups of prey. With multiple potential moving targets a predator becomes unable to concentrate on any one prey individual, and so becomes less efficient at capture (Neill & Cullen 1974). The dilution effect is probably the most widespread advantage of being in a group; an animal in a group of size n has the probability of being the individual attacked during a hunt on the group of 1/n (Hamilton 1971). As group size increases the individual probability of being attacked declines rapidly. The dilution effect has been shown in the wild by Foster & Treherne (1981) and Duncan & Vigne (1979). The benefits of the dilution effect may be outweighed by the increased conspicuousness of larger groups, and corresponding higher attack rate by predators. But if groups are very large, or predator success rate declines with group size then the benefits from the dilution effect will still apply (e.g. Calvert et al. 1979).

For an animal to decide to join a group its risk of predation within the group must be less than if it decided to stay solitary. Kenward (1978) showed that goshawks (Accipiter gentilis) were less successful when they attacked larger flocks of pigeons, because they took flight earlier (e.g. through vigilance benefits). However, single pigeons are usually in poor condition (Murton et al. 1971) and so may not have been able to fly as rapidly as those pigeons in larger flocks. Disentangling the relative importance of the different benefits of flocking in reducing individual risk of predation is difficult.

Not all encounters with a predator, or all moments during an encounter with a predator, are equally dangerous. Since the decision to escape by a prey animal has costs (lost feeding time as well as energetic costs), the decision should depend on the animals assessment of risk (Ydenberg & Dill 1986). Not all predators present the same risk to the prey (Curio 1975, Walters 1990, Buitron 1983), and so different predators elicit different responses by the prey.

The risk represented by a particular species of predator will be dependent most often on the proximity the predator is from the prey (see Lima & Dill 1990 for a review), for example, a distant predator presents little risk to prey. Measurements of flight-initiation distances of prey from a predator may give a measure of the prey's assessment of individual risk.

1.6 Behavioural Responses of Predators to Anti-predation Behaviour

There are several stages of predation in which the predator can make decisions that maximize the chance of a successful prey capture. Stages of predation include: encounter, detection, identification, approach, subjugation, and consumption (Endler 1991). Much of the discussion of a predator's behavioural responses to prey concerns encounter, detection and identification of cryptic prey, typically a vertebrate hunting invertebrate prey. Predators deal with cryptic prey in two ways that are not mutually exclusive. A predator can alter the length of time spent searching in a patch (Gendron & Staddon 1983) as a longer stare may result in more and more cryptic prey being seen (Guildford & Dawkins 1987). Alternatively, a predator may learn to see particular forms of prey from experience and consequently gain an enhanced detection ability for that particular cryptic prey (e.g. Pitrewicz & Kamil 1981, cited in Krebs & Davies 1987). For large predators hunting vertebrate avian prey in the non-breeding season, the effectiveness of crypsis will be much less important because prey detection will probably not involve mechanisms as subtle as the formation of search images. Crypsis is only particularly effective when organisms are small and can be immobile for long periods. Even so, previous experience with more cryptic prey may lead to a higher detection rate in situations of very rapid sequential attacks, when the time available for prey selection is very limited.

The main behavioural response of a predator to anti-predation behaviour would appear to be hunting by surprise (Rudebeck 1950, 1951, Schaller 1967, Elliot et al. 1977). A prey animal cannot accurately assess its risk of predation without information of what type of predator is present, and where the predator is. Therefore the prey will probably not respond in sufficient time or correctly on a surprise attack, so leading to a capture for the predator. Surprise hunting will also be energetically efficient, particularly when predators are well matched by their prey in locomotory abilities. Hunting by surprise is a very widespread predator behaviour requiring no specialised adaptations, and appropriate for most anti-predation behaviour (Endler 1991).

One consequence of hunting mainly by surprise is the coevolution of responses by the prey and predator which minimise the wasting of time and energy. If a predator has a low chance of success of capture, it benefits the predator to be able to determine whether the element of surprise has been lost from the responses of the chosen prey. The predator can then give up immediately and try elsewhere. The prey benefits if it communicates clearly to the predator that surprise has been lost, because it avoids the hunt escalating into an attack, and a potentially costly chase. There are two main types of predator-prey communication systems: mobbing and more specialised pursuit-deterrent signals. Mobbing occurs when the potential prey animals assemble around a predator, and perform stereotyped conspicuous movements accompanied by loud calls (Curio 1978). The most credible explanation for this behaviour is that the predator is unequivocally informed that the element of surprise has been lost. The growing, noisy mobbing response, as more prey birds join in, rapidly makes all potential prey in the surrounding area aware of the predator's presence. The predator then 'moves on' (Curio 1978). Pettifor (1990) showed that mobbed European kestrels (Falco tinnunculus) moved further between hunting areas, and hunting efficiency was decreased by the kestrel having to leave an area prematurely. Also prey species were shown to mob predators little when the predator was not hungry, or not in hunting flight (Hammerstrom 1957). Mobbing is a costly activity, with mobbed raptors occasionally killing mobbing birds (see Sordahl 1990 for a review). Even so, there will be a benefit for every bird that mobs a predator if the strength of the response (which will be equivalent to the area made unprofitable to the predator) determines the distance the predator moves on. If the probability that a predator returns to the area is proportional to its success rate within the area (e.g. optimal foraging theory), then it benefits no potential prey species if any other prey individual is killed within the area. Alarm calls probably evolved for this reason: it benefits no prey individual to ignore a predator, if a low cost (and risk) alarm call will be a future investment in reducing the local predator density.

Pursuit-deterrent signals (Woodland et al. 1980) are specific signals directed at the predator which inform it that its probability of capturing a prey individual is low. Signals can simply inform a low risk predator that the prey species is aware of it and further approach will result in other escape responses, for example, tail-flicking by the eastern swamp hen (Porphyrio porphyrio) to humans (Woodland et al. 1980). If the predator persists, the prey birds will simply fly safely away. The signals are low-cost and benefit both the predator and the prey. If the predator is more dangerous, and does not rely on surprise for a successful capture, then there will be strong selection, over generations, for the pursuit-deterrent signal to honestly reflect the ability of the prey individual to escape capture. Otherwise the predator will simply ignore the signal because the presence of the signal will not become associated with a low probability of capture, and those individuals which signal will gain no benefit. A good example of a probable honest signal to a predator by prey is stotting in gazelles to coursing predators, but not to surprise hunting predators (Fitzgibbon & Fanshawe 1988), other examples are reviewed in Hasson (1991).

1.7 Evolutionary Consequences of Predator-Prey Interactions

Predators may select certain individuals within a population, and so cause eventual morphological or behavioural change in a prey species. For example, Hudson (1986) showed that predators selectively catch grouse with high parasite burdens; other studies have found that prey victims do not differ from the population in factors such as body size or weight (e.g. Angelstam 1984). Predators may preferentially take only weak or injured prey individuals (e.g. Rudebeck 1950,1951, Mech 1970) and so only take a 'doomed surplus'

(Errington 1946, Townshend 1984) of prey. In these circumstances predation will only be compensatory to other types of selection, and not a major selection pressure itself. If the heaviest predation occurs in the subset of the population least important for future reproduction (e.g. the very young or old), then predation will exert a relatively small influence (Rosenzweig 1978). Selection for anti-predation characters can only occur if the selected subset of the prey population differs genetically from the main population: age and environmental quality during development probably account for the vast majority of the subset of more vulnerable prey (Taylor 1984).

Prey might always be expected to be one evolutionary step ahead of predators, the so called 'life-dinner principle' (Dawkins & Krebs 1979). A predator can fail to catch several prey individuals without dying of starvation, but a prey animal must always escape to survive. Consequently there will be a greater selective pressure on the prey. However predators do not appear to coevolve tightly in step with their prey, and the adaptive gap between prey and predator in fossil ungulate-mammalian carnivore lineages increased for long periods of geological time (Bakker 1983). The 'life-dinner principle' may not apply to generalist predators with a wide range of potential prey. Generalist predators could potentially cause local extinctions of very vulnerable species, through evolving to become moderately efficient in capturing a more common non-vulnerable species.

1.8 This Study

The Tyninghame estuary is an ideal area in which to conduct a broad study of predators and prey. Estuaries are in some respects similar to islands, with relatively fixed, large populations of some bird species over the winter. Large stable populations of prey attract predators: in Britain three species of generalist avian predators, sparrowhawks (*Accipiter nisus*), peregrines (*Falco peregrinus*), and merlins (*Falco columbarius*) use estuaries as regular overwinter hunting areas, and potentially compete for the same resources. Finally estuaries are open habitats, allowing unobstructed observation of both predators and prey.

At Tyninghame, the aims of this study were:

1. To record the changes in overwinter populations and to relate these to the numbers of prey killed by predators and by other factors such as starvation (Chapter 3).
2. To compare the behaviour and morphology of the subset of the prey population that were killed with the subset that survived (Chapters 3, 4 and 8).
3. To record the behavioural interactions between a range of different predators and prey. (Chapters 4 and 8).
4. To record the importance of predation risk in determining prey behaviour. (Chapters 4, 5 and 8).
5. To record the behaviour of avian predators and to relate this to the behaviour of their prey (Chapters 6, 7 and 8).
6. To compare the ways in which three generalist avian predators solve the problems of catching avian prey (Chapters 6 and 7).

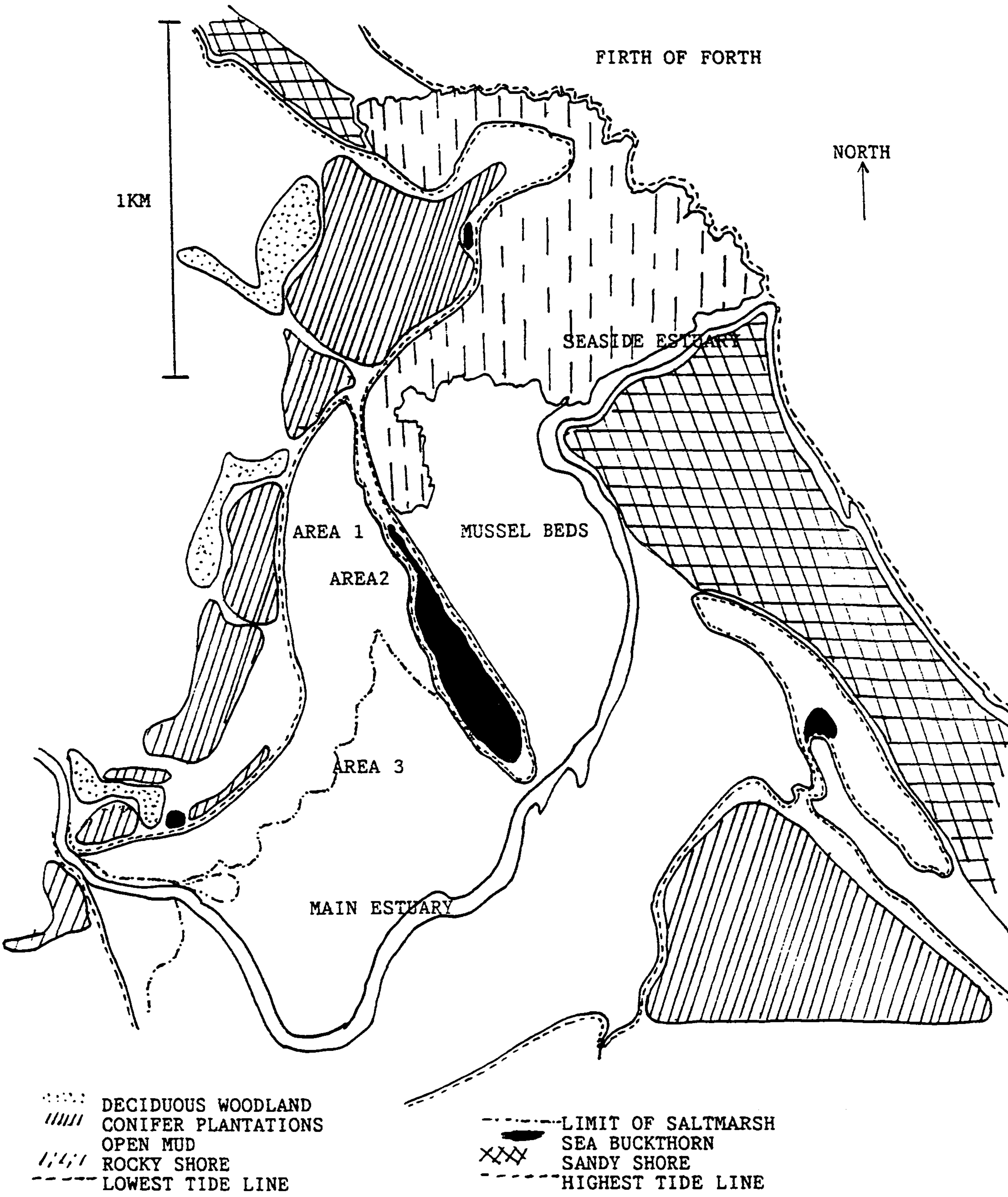
CHAPTER 2: METHODS

2.1 Study Site

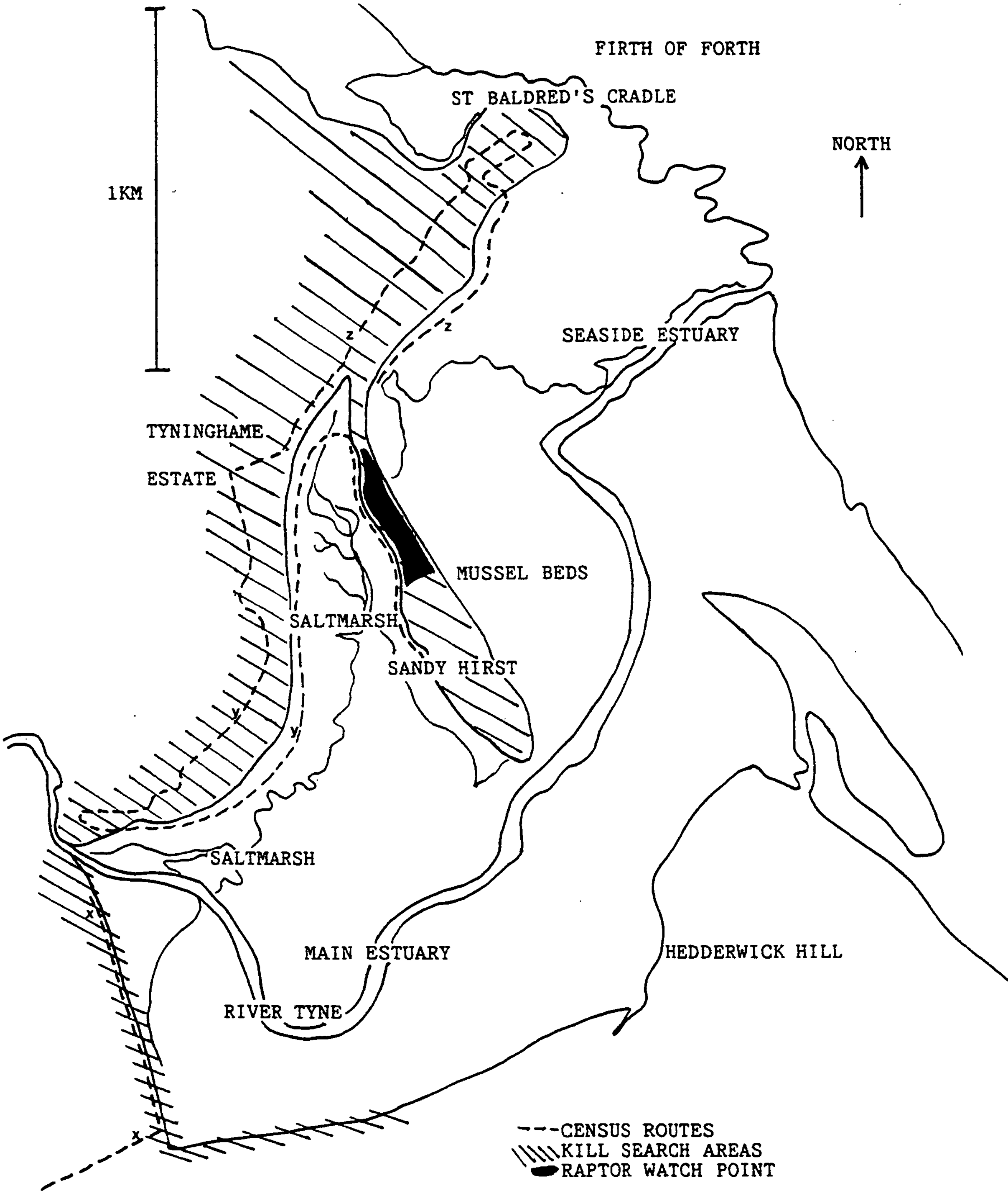
Observations were made from September to April 1989-90 (Winter 1), August to April 1990-91 (Winter 2) and August to March 1991-92 (Winter 3), during 2,557 hours at the Tyninghame estuary, East Lothian, Scotland. Most of the data were collected from three adjacent regions of saltmarsh and open mud, bordered by sea buckthorn (*Hippophae rhamnoides*) and coniferous plantations (Fig. 1). Area 1 consisted of about 30 ha of flat open saltmarsh, with an extensive network of sunken creeks running through it. Area 2 consisted of a 0.5 ha area of sparse *Salicornia* saltmarsh covered mostly by a 0.03-0.05m layer of channel wrack (*Pelvetia canaliculata*). Area 3 was an area of open mud immediately adjacent to the saltmarsh of Area 1. Area 3 was part of a large area of open mud which comprised most of the main estuary. The seaside of the estuary was a mixture of open mud with extensive areas of mussel beds around the tip of Sandy Hirst, and on both sides of the river. There was a large area of rocky shore around St. Baldreds Cradle (Fig. 2).

Around the estuary the habitat was mixed. On sandy areas such as Sandy Hirst, sea-buckthorn and sycamore woodland was the dominant vegetation. Most of the woodland around the estuary was coniferous plantation, with stands from 1 year old (still rough grassland) to fully mature Scot's pine woodland, with a low tree density, open canopy and much understorey vegetation. The majority of the plantations were about 25-30 years old. There were a few areas of

THE TYNINGHAME ESTUARY FIGURE 1:



THE TYNINGHAME ESTUARY FIGURE 2:



deciduous woodland (mainly beech Fagus sylvatica). Behind the woodland fringing the estuary was mixed farmland, with sheep and cattle grazing and potato fields. There was also extensive parkland with many mature tree stands around the Tyninghame estate. The habitats were very diverse and attracted a wide range of birds; in three winters, for example, I recorded 165 species (Appendix 10.3).

I observed raptors opportunistically using 10x binoculars or a 15-60x zoom telescope and the majority of raptor observations were made at less than 300m. Most observations were collected from a single location overlooking all of areas 1-3. Observation periods were of two types: raptor watching (RW) and non-raptor watching (NRW). During the study 772 hours were spent raptor watching, and observations were carried out from a fixed point overlooking 90% of the estuary. During a raptor watch period the whole of the estuary was continually scanned for raptors, and favoured perches checked regularly with a telescope. A single location (a 200m strip) along Sandy Hirst (marked on Fig. 2) was used for all raptor watch periods. During non-raptor watch periods, raptors were also looked for systematically but from different locations and briefly between other activities such as focal sampling of redshank and kill searching (which generally did not allow for raptor observation).

2.2 Recording of Raptors

All predators seen were recorded. When a raptor was seen it was watched continuously until it was lost from sight for over a minute (one sighting). If more than one raptor was visible at the same time then an attempt was made to watch all of the raptors, with priority being given to the raptor which was hunting. Species, age and sex were recorded for each raptor sighting, according to criteria in Ferguson-Lees et al. (1983), Porter et al. (1981) and Cramp and Simmons (1980). Sparrowhawks were sexed by size and aged by breast markings; peregrines were sexed by size and aged by back or breast plumage; merlins were sexed by size, but only adult males could be distinguished by plumage; kestrels were only identified as adult males or females/immatures and were separated by plumage. Sexing by size was only carried out in reference to other birds, such as the relative size of the merlin to the skylark that it was chasing, or relative to the size of the perch of known size that the bird then flew to. On close views (<300m) it was usually fairly obvious to me what the size of a particular raptor was, but this was always confirmed if possible by referencing it to a species of fixed size in close association with the raptor; mobbing carrion crows were particularly useful in this respect. On good views of a hunting raptor it was possible to sex and age sparrowhawks and peregrines, and sex merlins at distances of 1000+m. It was impossible to check my accuracy with respect to this. In some circumstances, for example when an adult and immature female sparrowhawk were first sexed and aged separately at a distance and then they perched next to each other very close to me, it was possible to gain confidence in use of identification characters at a distance: generally on good view ageing and sexing the raptors at Tyninghame was straightforward. Any individual plumage characteristics such as dropped flight feathers or particularly bright plumage was also recorded for each raptor sighting.

None of the raptors occurring at Tyninghame were colour marked although three male sparrowhawks were radio-tagged during winter 2 (see Appendix 10.1). An accurate count of the individual raptors using Tyninghame was therefore not possible. The number of different raptors present was estimated daily by counting the total number of differently plumaged or aged birds, the maximum number of birds seen during one sighting and the relative frequency of sightings of individually recognisable raptors. An index of the actual number of a raptor species present in each month of the study was calculated as the mean of the daily totals of the minimum number of different raptors recorded each day.

2.3 Time Budget Data

During each minute of a sighting, the occurrence of the following behaviours were recorded:

1) Hunting: Purposeful flight in an area of potential prey, in a manner that led to or could potentially lead to an attack (see 2.4). For sparrowhawks this was rapid low contour hugging or an approach flight which used cover, or direct dashes at prey. For peregrines this included any flight through or with groups of prey, except when the potential prey was mobbing. For merlins it included only periods of flight in which attacks were recorded. Merlins would use the same very low and rapid hunting flight to move between perches between long periods of inactivity as well as during definite hunting periods with many attacks. Merlin hunting was therefore split into hunting flight (which contained attacks) and hunting/moving flight which did not. For kestrels, hunting included only direct dashes at

prey or hovering flight; perch hunting (see Village 1990) was not classified as hunting. A hunt for all raptor species was defined as any period of hunting flight between periods of perching and/or high soaring. The frequency of quartering and hovering were also recorded during hunts. Quartering was hunting flight which involved slow, low, systematic searching of the ground in the manner of harrier (Circus sp.) hunting (see Kemp 1992).

2) Perching: Either on the ground or on an object. Perching did not include any time spent feeding or caching prey.

3) Preening: During any perching period.

4) Mobbed: The assemblage of birds around a raptor in which the mobbers change location, frequently peforming wing and tail movements or exaggerated flight and alarm calling (after Curio 1978). Mobbed included another raptor species flying at or attacking the raptor being observed. In all cases the species mobbing the raptor under observation was recorded.

5) Mobbing: The raptor under observation flew up to and attacked a second raptor of a different species (which was then recorded as being mobbed).

6) Interactions: When a raptor associated with a conspecific. This included, for example, attempted kleptoparasitisms between sparrowhawks as well as displays and high soaring associated with breeding behaviour. Where possible, the sexes of the interacting birds were recorded.

7) Moving: Any directed flight from one specific area to another (such as between clumps of trees or between perches), 2m or more above the ground, and not associated with high soaring or attacks.

8) Display: Specific to sparrowhawks and associated with breeding and territoriality. High flight with exaggerated deep slow wingbeats and periods of short stoops interspersed with rapid wingbeats gaining height again before another stoop.

9) High Soaring: Slow flight above 5m with few wingbeats.

10) Carry Prey: Any period the raptor was with prey including caching but excluding feeding.

11) Feeding: Plucking or eating prey.

For each sighting the time at the start of the sighting was taken as the time at which all behaviours occurred. For sightings of greater than 30 minutes, the time at the start of each 30 minute period of sighting was taken as the time at which the behaviours in the following 30 minutes occurred. For each sighting the proportion of minutes of the total length of the sighting in which each behaviour occurred was calculated, e.g. if hunting was recorded in 3 minutes out of a ten minute peregrine sighting then the proportion of minutes in which the behaviour occurred was 0.3.

2.4 Attack Data

A raptor attack was defined as a rapid directed flight (or series of stoops) at a clearly identifiable bird or group of birds (called a hunt in Rudebeck 1950, Page & Whitacre 1975, Buchanan et al. 1988, Dekker 1988). A successful attack by a raptor was one in which the prey was killed. A capture was an attack which resulted in the raptor catching hold of the prey (85.1% of captures resulted in the observed death of the prey, n=101 captures). Some captures resulted in the release of the prey, usually through attempted kleptoparasitism by carrion crows, Corvus corone. An escape was an attack which concluded without the prey being caught by the raptor or attendant crows. A kill was a capture in which I observed the death of the prey.

During an attack the following data were recorded where possible:

1. The time of the attack and the species of raptor involved.
2. The prey species attacked.
3. The position of the raptor at the start of the attack (air or perch).
4. The distance the raptor was from the prey at the start of the attack, estimated to the nearest 100m.
5. Type of attack. Attacks were classified into 5 non-exclusive categories:

(i) Surprise attacks were those in which the raptor used cover to conceal its approach during the attack or where the attacking raptor approached prey without using obvious cover but at less than 1.5m above the ground. This included, for example, a sparrowhawk flying out of some bushes closest to some redshank, or a peregrine flying in low just above the sea.

(ii) Non-surprise or open attacks were those in which the raptor was clearly visible to the prey prior to attacking (for example if the raptor made a second attack immediately within the same area, or if it soared low over the area before attacking).

(iii) Stoop attacks were those in which the raptor made a steep or vertical dive down onto a bird below it; this type of attack was frequently impossible to classify into surprise or non-surprise.

(iv) Passerine mimic attacks. The raptor used a method of flight which disguised its flight profile, by closing its wings between beats. The resultant flight was undulating and similar to that of a mistle thrush (Turdus viscivorus).

(v) Ringing attacks. The prey flew straight upwards followed by the raptor, frequently for long periods.

6. The flock size. A flock was any cluster of birds separated from others of the same species by more than 25m. For redshank attacks a more rigorous definition of a flock was used: a cluster of birds in which the maximum nearest neighbour distance was less than 25m and less than one-tenth of the distance between clusters, with inter-cluster distance always being greater than 25m. During raptor watches all redshank flock sizes visible were assessed regularly. These flocks remained stable enough to use the prior accurate assessments of flock size as estimates of flock size during an attack, if the flock size had been recorded less than 5 minutes prior to the attack. In analysis of flock size data, flock sizes were classified into broad categories (e.g. for dunlin, 100+), as accurate assessment of differences in the sizes of very large flocks, during often very rapid attacks was impossible.

7. The chase length. These were estimated by counting elapsed seconds, or timing with a digital watch for long chases such as merlin or peregrine hunts. Timing was started from the point I could identify which bird was being attacked and at which it began to first respond to the attacking raptor. The imprecise method of counting the initial few seconds of a chase allowed for maximum

concentration on the attack, and as most chases were less than 1 second in length it seemed sufficiently accurate.

8. The number of stoops (dives in which prey was grabbed at).

9. The type and duration of any call during attacks on redshank and skylarks (Alauda arvensis) were recorded where possible. Only attacks which occurred reasonably close to me (<300m) were classified, so that I could be sure that if no alarm call was heard it was not because I was too far away from the attacked bird to hear it. For redshank (Tringa totanus), calls were classified as:

(i) none

(ii) contact/moving (a slow melodius 'teu-hu'; Fig II, sonograms in Cramp & Simmons 1983, Volume 3, Tringa totanus)

(iii) mobbing/alarm (a rapid, extended version of the moving call above, 'tuhuhuh-tuhuhuhu-tihihi', Cramp & Simmons 1983 as above).

For skylark calls were classified as:

(i) none

(ii) flight calls (a rippling 'chirrup' or rattling 'prrt', occasionally strung together into short sub-song like phrases lasting a few seconds; see Fig. V, and text description 5, Cramp 1988, Volume 5, Alauda arvensis)

(iii) full song (complete continuous phrases as given by territorial singing birds in the summer; this included both male type and female type song, Fig. I, and text descriptions 1 and 2, Cramp 1988 as above).

10. The position of the prey at the start and finish of the attack was recorded. Responses of the prey on attack were classified in

terms of the position of the attacked bird at the start of the attack (e.g. ground or flight) and its position on escape or capture. The responses were classified as:

(i) Crouching (G/CR) on the ground.

(ii) Creek-dive (CD), where a wader ran or dived into the nearest creek or pool and submerged.

(iii) Flying (F) without either crouch or creek dive occurring during the response.

(iv) Bush-dive (BD) where a non-wader flew into or remained within the dense cover of a bush or tree.

11. The outcome of the attack as defined above. Attacks in which the raptor was lost for less than 10 seconds and then relocated carrying prey were classed as successful. For merlin ringing chases when the merlin was lost while still chasing a skylark because they had flown so high, an attack was classed as successful if the merlin was relocated within 1 minute carrying an intact skylark, from the same area in which they were lost. Any factors which may have affected the outcome of the hunt, such as another raptor joining the attack or mobbing of the hunting bird, were recorded.

All attack and time budget data were written down in a notebook at the end of each sighting or during periods of perching during a sighting. As most raptor hunts were very short interspersed with long periods of perching it was possible to record information directly (condensed into shorthand) in this way. With peregrine hunts, which frequently involved many attacks over several minutes, continuous dictation into a tape recorder was used where possible.

2.5 Prey of Raptors

2.5.1 Census Methods

Most waders were censused monthly by counting mid and high tide roosts from a fixed point over several days until a consistent maximum figure was obtained (a <5% difference between the two highest counts, expressed as a percentage of the highest count). The number of waders present for the month was then determined by averaging the two highest counts. Turnstone (*Arenaria interpres*) were counted at mid-tide while they formed sub-roosts by walking along the entire edge of the estuary. Snipe (*Gallinago gallinago*) were counted by walking along the saltmarsh creeks and directly flushing birds. Most effort was put into redshank censuses (described below).

Non-waders were censused by following a regular census route through the areas which were searched for raptor kills, in order to obtain an index of the relative abundance of non-wader prey. Due to the wooded nature of the habitat around the estuary it was impossible to count all of the available prey. In each of the months of the study from November 1989 inclusive onwards, 5 passerine censuses per month were carried out. Three different routes were used (see Fig. 2): route x was censused at the start of each month, and routes y and z were censused twice each over the month, usually route y in weeks 1 and 3, and route z in weeks 2 and 4. The census procedure was to walk at a constant slow speed along a fixed route and to record the numbers of all species heard and/or seen in front of me. All blackbirds (*Turdus merula*) and chaffinches (*Fringilla* coelebs) seen were sexed where possible, to determine the sex ratio of the populations for these species.

The flock sizes available for redshank (see below), dunlin (Calidris alpina) and skylark were censused. Skylark flocks were counted by walking a regular route around the saltmarsh twice weekly and flushing the skylarks, October to February inclusive, winter 3. 'Flush' censuses were augmented by twice weekly raptor watch periods of one hour in which all skylark flocks in flight were recorded. Dunlin flocks were censused from two fixed points overlooking the seaside estuary, and area 3, at low tide, and from one fixed point overlooking the saltmarsh at high tide, twice weekly, September to February inclusive, winter 3.

2.5.2 Kills

Tyninghame was searched regularly for raptor kill remains, in order to assess the degree and type of mortality that was occurring. Three days every month were spent searching a fixed area covering the entire north shore of the estuary and the woodland or cover adjacent to it for about 100-200m inland. The south shore was found to contain few kills and was searched once each winter. The saltmarsh was searched before each set of spring tides, and remains were also found opportunistically.

The efficiency of recovery of the wader remains was tested in two ways in conjunction with Philip Whitfield, during winter 1. Marked kills were placed out on the estuary by one person. The second person then searched for them at regular intervals over the following weeks.

(i) Efficiency of recovery of kills on the saltmarsh. Ten redshank and 10 dunlin feather piles, simulating merlin and peregrine kills, and 10 intact dunlin corpses were placed on the saltmarsh (simulating birds which had starved). In 4 subsequent weekly searches, there was good evidence found for 9 wader kills (45%) from the feather piles (4 sets of feathers were recovered on the strandline) and 9 (90%) corpses were recovered (5 on the strandline). Generally remains with intact wings such as corpses and crow/kleptoparasitisms were observed to float and wash up on the strandline allowing for reliable recovery. Feathers also floated but were easily dispersed and washed up over a wide area of strandline. Estimates of the exact numbers of birds killed from strandline feathers was therefore impossible. During winters 2 and 3, the frequency of saltmarsh searches was increased in an attempt to recover remains before tidal dispersion. It is likely that the experimental estimate of 45% recovery of saltmarsh kills is therefore too low, but the relative proportion of kills found in this area was certainly lower than the proportion found above the strandline.

(ii) Efficiency of recovery of kills in cover, by simulating sparrowhawk kills. Ten redshank feather piles were placed within a 5 ha area of coniferous plantation at the start of a month, while searching the area for natural kills very thoroughly each week in that month. The second 'naive' person then searched the area at the end of the month, and the month following, as part of the normal search programme. Two separate kill placements and searches were carried out. Combining the two tests 35/38 wader kills were found during the first monthly search afterwards, rising to 37/38 in the following month. At least 97% of remains within cover were found. Therefore nearly all sparrowhawk kills of waders on the estuary, and probably also those peregrine and merlin kills eaten in trees within the search area, were recovered.

In contrast to wader kills, which were comprised of many highly conspicuous white feathers, passerine kills were much smaller in size and were comprised of mainly dark or cryptic feathers. Passerine kills became much harder to find over time than wader kills. A goldcrest kill, for example, would be practically invisible after a few weeks of wet, warm weather. Fewer passerine kills than wader kills were found by the 'naive' searcher during the tests on recovery of kills in cover described above (80.0% in the first month, rising to 83.3% in the second, $n=30$). Wader kills were probably over estimated in the total diet of sparrowhawks at Tyninghame because of recovery biases. This was tested with merlin kills. Because dunlin kills were comprised of mainly white feathers and skylark kills of more cryptic brown feathers, more dunlin kills may have been found, biasing the data presented in Chapter7: Table 1. However there was no significant difference in the rate of recovery of observed merlin kills of different types: waders 8/18 kills seen were recovered, skylarks 16/30, and other passerines 5/7; $G=0.41$, 2df, $p>0.05$.

Another possible source of bias was the classification of most merlin and peregrine prey remains found under trees as falcon/owl. This bias was fairly small in merlin because in only 15.2% (7/46) of cases of merlins observed eating prey within the study area did they use tree perches and, of the 41 cases that left remains, 12.2% were classified as falcon/owl kills. Five out the 7 kills (71.4%) eaten in trees involved wader prey, and 2 involved passerine prey. For peregrines 7 out of 11 (63.6%) peregrines observed feeding fed in trees and of the 10 that left remains, 60% would have been classified as falcon/owl kills. Many of the falcon/owl kills in Chapter 7: Table 2 were peregrine kills, but it was impossible to estimate which ones. If smaller prey items such as dunlin and redshank were more likely to be eaten in trees then the kill data presented for peregrines will not be representative.

Another possible source of bias was the relationship between the size of prey and the number of locations in which remains of that kill were found. In general the larger the prey, the more locations where it was eaten, or the higher the probability of finding each kill location (see Figure 23, chapter 6). The relationship between the probability of finding the remains of a prey bird and the size of that bird may not have produced much of a bias in the results because of the search methods. The search effort was designed to find most wren and goldcrest kills, and a much less intensive search pattern would have been needed for the efficient recovery of only wader kills.

Recovery of kills was also estimated by direct observation of the frequency of raptors leaving prey remains within the whole search area: 98.8% of sparrowhawks (n=81), 36.0% of peregrines (n=25) and 44.4% of merlins (n=18), seen carrying wader prey caught within the previous minute, left remains in the search area. The remains were searched for immediately after the raptor had finished feeding, to confirm the location of visible remains within the normal monthly search area. Overall, considering the export of kills out of the search area by raptors and the search efficiency, the number of prey killed by raptors was under- recorded.

Prey remains were classified into the following causes of death on the basis of location and conditions of the remains (after Welty 1963; Baker 1967; Ratcliffe 1980; Davidson and Clark 1985; Newton _et al._ 1984; Whitfield 1985a; Newton 1986; Village 1990):

1) Sparrowhawk: Feathers in cover (under low canopy woodland or bushes, in tall grass or bracken); all neatly plucked. Usually on the ground or from a low (<1m) perch. Bones rarely present, if present only front part of the keel and wing bones uneaten and wing bones entirely or almost entirely clean of feathers. Presence of distinctive sparrowhawk faeces (a long thin white streak), although this was present only in 9% (n=489) of remains classified as sparrowhawk, winter 3.

2) Peregrine: Remains not in cover. Head and legs frequently bitten off but body, apart from breast and belly, usually whole; wings rarely completely bitten off. Little plucking, mainly on the breast, rarely on the wings. Presence of large very sharp notches in the sternum but bones otherwise present and uneaten. Presence of large puncture wounds or gashes on the body.

3) Merlin: Remains not in cover. All feathers neatly plucked, only small fragments of bitten off bone present (bones usually eaten). Entire wings and head rarely and bill frequently bitten off and uneaten. Occasional presence of small (up to 4cm), dark and very dense pellets containing distinct and undigested feathers.

Occasional presence of characteristic faeces (oval, creamy yellow in colour with small, dense, black cylinders in the centre). Occasionally whole body intact or just missing head, or partly neatly plucked and cached next to or under post, log or grassy tussock on saltmarsh.

4) Crow Kleptoparasitism: Remains not in cover. Whole body intact or intact keel with wings attached, legs still attached to pelvis. Wings raggedly plucked, rarely past humerus. Large blunt notches in the sternum occasionally present.

5) Falcon/Owl: Feathers below a tree and plucked at a height of greater than 1.5m; also remains plucked on old nest platforms. Prey plucked entirely, no bones found.

6) Owl: Under a low perch, tree or on the ground, in cover. Small quantity of flight feathers, at least one bitten cleanly across the shaft or in association with large (>4cm) pellets with indistinct feathers or mammal remains inside.

7) Fox (Vulpes vulpes): Feathers chewed or bitten off at the base rather than plucked; bones bitten.

8) Starvation/Disease: Whole body intact or marginally plucked on the breast (through crow scavenging). Uneaten parts of pectoral muscles very thin.

As a check of the above classification, all observations of identified raptors eating prey were followed up by a description and classification of the remains. For sparrowhawk 71% (n=87) of remains after a sparrowhawk was seen carrying prey in the area were classified as category 1, 29% were classified as category 4, all after the sparrowhawk was seen being kleptoparasitised by carrion crows. For Peregrine 40% (n=10) of remains were classified afterwards as category 2, 60% as category 5. For Merlin 88% (n=41) of remains were classified afterwards as category 3 and 7% as category 5. In 5% of cases of merlin kills remains were left as category 3 in one area and category 5 in another area as the merlin moved with the prey between feeding bouts.

All remains found were recorded along with location, weeks since death (see Newton and Marquiss 1982) and approximate numbers and type of feathers; they were then buried or collected to prevent recounting remains in subsequent searches. Raptors were found to eat single prey in several locations, for example 245 redshank in winter 3 were found in 377 different locations (mean number of locations per kill, x=1.5+/-0.05). Therefore a new kill was only recorded if there was some body part in common between locations (usually outer primaries) or the age of the kill was different by more than a week. All redshank kills were collected for later biometric measurement. Where possible the age and sex (particularly for blackbird and chaffinch kills) of the prey was recorded.

2.6 Redshank Data

2.6.1 Biometrics

Biometrics were taken from the redshank kills collected. On intact birds this included weight, bill length, tarsus and toe, tarsus, maximum wing chord and length of outer primary. The final measurement was the only non-standard one and involved straightening the removed feather against a stopped wing rule in order to record the maximum length. On non-intact birds as many biometrics as possible were recorded, although often only the length of one outer primary could be recorded. Outer primaries were easily identified, as they were the only flight feathers to have entirely pale shafts on both sides of the feather.

Redshank kills were aged by the shape of the tip of the outer primary. Juvenile outer primary tips were very worn and pointed (at an angle of c45°) whereas adult primary tips were much less worn and had a paddle shaped tip (at an angle of c80°); see Figure 3. I tested my ability to use these characters reliably by taking outer primaries from intact whole kills aged by the presence or absence of juvenile tertials (Prater et al. 1977). The outer primaries were then aged 'blind' and the results compared. Less than 1% were aged incorrectly by this method ($n=90$ juvenile and 50 adult, arranged randomly).

Biometrics of dead birds were compared to those taken from live redshank caught in two cannon-nets ($n=12$ October 1990, and $n=35$ March 1991; see Appendix 10.2 for details of methods). Outer primary length could not be taken from live birds and so a conversion factor was calculated using a regression analysis to relate maximum wing chord measurement to outer primary length. When fresh intact corpses were recovered, right wing length was measured and then the right outer primary was removed and measured. The conversion equations calculated to obtain right wing length (RWI) from right outer primary length (ROP) were: juveniles, $RWI=1.14(ROP)+26.0$ calculated from 44 birds ($T=18.3$, $p<0.0001$); adults, $RWI=1.18(ROP)+21.7$ calculated from 9 birds ($T=8.3$, $p<0.0001$).

FIGURE 3:

Outer Primary Tip Shape of Adult and Juvenile Redshank

JUVENILE

ADULT

Feathers from redshank killed by raptors and selected randomly from c800 outer primaries collected.

Redshank captured during the during the cannon-nets were measured by Philip Whitfield and Jeremy Wilson, while all dead birds were measured by myself. Individual variation in measurement of maximum wing chord was checked by the three of us measuring the wings of fresh redshank corpses. The mean of two right wing measurements for 22 redshank was calculated for each person and then the mean difference in measurements between people was calculated. The mean difference was then added to the wing lengths of the shorter measurer when comparing measurements taken by the two different people.

2.6.2 Numbers of Redshank Present

Redshank were usually counted every two weeks on maximum height spring tides, when all the redshank within the estuary were spread out linearly on a small area of saltmarsh. All could be counted easily from one point in about 5 min; problems of visibility in the habitat and recounting birds were avoided. The redshank were counted until a consistent maximum was obtained (+/- 20 birds) and then the two highest counts for that day were averaged. During winter 2, 47 redshank were cannon-netted and colour-ringed so that individual recognition was possible. At least 36 of these returned to the estuary for winter 3, and so the percentage of redshank colour-ringed was recorded on each redshank census for that winter. Individual colour-ring combinations were recorded opportunistically throughout the study to determine which colour-ringed birds were still present over the whole estuary.

2.6.3 Ageing

The percentage of the redshank population which were juveniles was recorded at the start and finish of each winter by the presence or absence of juvenile tertials (Prater et al. 1977). Between 100 and 200 redshank were observed daily over three days, at less than 30m with a telescope; all ratios for the period were then averaged. Population ageing was carried out at high tide when adults and juveniles were not segregated by location (see Chapter 5). Changes in location specific adult/juvenile ratios were recorded by scan samples, at low tide (+/-1 hour) from July to March inclusive winters 2 and 3. All redshank were scanned and aged using a telecope from the two fixed locations overlooking the seaside estuary and the saltmarsh. A matched pair format was used, coincident with collecting feeding/risk data. Age ratios were opportunistically recorded during the collection of all feeding data in all winters.

My ability to age redshank correctly was tested by ageing birds which were wading or feeding in tall vegetation, where it was impossible to see the birds legs or colour rings. If a bird was found to be colour-ringed after ageing then its combination was recorded and its known age (from several observers in the hand) was compared to my field ageing. I was mostly correct in field ageing (98% correct n=23 adults, n=37 juvenile, including 17/18 correct after January 1st, and 21/22 correct at distances of observation at greater than 50m).

2.6.4 Territorial Interactions

At all times during the study, and especially during feeding data collection in winter 3, any territorial interactions between redshank were recorded. A territorial interaction was defined as any exclusion (by chasing away) of one bird from a feeding area by another bird. The winner of an interaction was defined as the bird which chased the other away and remained feeding in the area under dispute. The loser was defined as the bird which was forced out of the area. Where possible both birds were aged.

2.6.5 Flock Size Availability

I censused the frequency of flock sizes occurring in areas 1 and 2 at low tide and just before the saltmarsh flooded 89 times from October to February inclusive in winter 2. A flock of redshank was defined as a cluster of birds in which the maximum nearest neighbour distance was less than 25m and less than one-tenth of the distance between clusters, with inter-cluster distance always being greater than 25m. In practical terms this meant that data were collected only from obvious flocks, which were typically tight clusters of birds spaced at less than 3m apart separated by several hundred metres from other tight clusters. All flocks present on the saltmarsh were recorded by scanning with a telescope from a fixed point. The scan censuses were augmented by regularly walking a constant route through the saltmarsh from which all of the creeks could be checked for inconspicuous single birds.

2.6.6 Spacing and Distance to Cover

Changes in spacing between redshank, and distance to cover through a winter were recorded from September to March inclusive during winter 3. Spacing and nearest neighbour distance were recorded in 41 scan samples from the saltmarsh and 37 scan samples from the seaside estuary. The scans were taken in matched pair format where possible (hence the uneven sample sizes), scanning one area immediately followed by the second, with the order being reversed for the next scan. Scans were made from a fixed location on Sandy Hirst overlooking both areas at low tide (+/-1 hour). For each redshank the nearest neighbour distance was recorded to the nearest half meter; distances of greater than 25m were only recorded as being greater than 25m. For each redshank the distance to cover was estimated to the nearest meter if less than 10m to cover and to the nearest 5m if greater than 10m. Cover was taken to be any topographical feature which could hide an approaching sparrowhawk such as a saltmarsh creek, as well as bushes and trees.

2.6.7 Vigilance and Feeding Data: Winters 1 and 2

I collected data on vigilance and its relation to flock size and other variables such as feeding rate in the areas 1-3 by focal sampling with a telescope at a distance of between 30 and 80m. Within areas 1 and 2, a feeding bird's vision was obscured by vegetation and, in order for a redshank to scan for predators, it had to lift its head up. Vigilance was taken to be any time period a redshank had its head above the level of its body. It was measured in three ways; the length of time (THU) and the number of times

(NHU) a bird raised its head above its body in a fixed time period (2-3 min) and the inter-scan interval (ISI, mean ISI calculated from THU and NHU). Fixed time periods were measured with a digital audio-alarm timer, THU cumulatively with a stop-watch and NHU with a hand counter. ISI were measured directly only in area 2 from September to early November of winter 2, and were recorded continuously by dictating the start and stop of head-up periods into a tape recorder for 2-min. A 1-min period of observation for each bird sampled was used to estimate the degree of visual obstruction (visibility) in each area. The number of seconds all of the length of the redshank's legs was visible was measured cumulatively on a stop-watch, the assumption being that if the bottom of the legs was visible the redshank would be able to scan to some degree even while feeding. The feeding data I recorded were the number of picks or probes and the number of swallows observed in a 2 or 3-min period. Feeding success rate was then calculated as the proportion of picks or probes that resulted in a swallow.

A 10-min period was left between my arrival (or any disturbance) before the recording of any data, to ensure that only basal undisturbed activity levels were recorded. Typically, vigilance levels would decay rapidly to a constant for a particular flock size within 2-3 min after a raptor attack or human disturbance. During the ten minute waiting period I recorded flock size, average nearest neighbour distance, distance to cover, age of bird, date and time.

In each flock sampled, a complete set of observations was taken from a different bird in the flock each time. It was possible to use minor plumage differences to keep track of birds already sampled over a short period. When, in the case of very small flocks, all the birds were sampled once, the flock was left and another found. However the same birds were resampled on different days and in different flocks to unknown degrees. If the flock being sampled was disturbed all uncompleted observations were discarded.

I collected feeding and vigilance data from all areas in February and March winter 1, from area 2 from mid October to mid February winter 2. All feeding and vigilance focal samples in winter 1 were of 3 minutes, and in winter 2, of 2 minutes. In winter 2, feeding or vigilance data, from area 2, was frequently collected in a matched pair format. Pairs of focal samples were taken from adult and juvenile birds, close to cover and c10-20m further from cover birds, edge and centre of flock birds, birds with near nearest neighbour distances (0.5m) and birds with further nearest neighbour distances (>1.5m), and birds just after a disturbance and ten minutes later.

In area 2, the redshank fed by routing (flicking over and feeding underneath) the layer of channel wrack there. The distance of observation was limited in these cases to 30-50m to ensure that all swallows were recorded in a constant manner. Every week invertebrates were sampled within area 2. Two sets of $0.25m^2$ quadrats were set out, one in a transect pattern and repeated each week along the same line, and a second from the patches within area 2 that the redshank had been feeding in that week. The invertebrates were sampled by lifting up the covering layer of channel wrack (as feeding redshank did) and counting all the animals within the quadrat. The channel wrack was then replaced so very little disturbance was caused. Invertebrates found were classified into five types: Orchestia or similar amphipod species, isopods (mainly Sphaeroma), fly larvae, molluscs (mainly Littorina), and others (e.g. beetles and spiders). Size of prey was recorded in three categories, less than or equal to 5mm, 6-10mm and greater than 10mm.

2.6.8 Feeding Data: Winter 3

Data comparing adult and juvenile feeding rates in a two week period at the start of September were collected from the seaside estuary. Data were collected in a matched pair format, using 2 minute focal samples recording the number of picks, number of swallows, the feeding location and method, and age for each bird of the pair. Where possible, adults and juveniles feeding less than a meter apart were used, and all cases involved pairs of birds less than 20m apart.

During October to February inclusive, feeding data were collected from redshank feeding on the mussel beds of the seaside estuary, and from redshank feeding on the saltmarsh grass of Area 1. Data were collected to compare the energy intake in the two areas at low tide and at different distances to cover on the saltmarsh. Ten to 15 focal samples of two minutes in length (measured with a digital, audio-alarm timer) were collected from feeding redshank in both areas within 2 hours of low tide. A telescope was used for all focal samples: redshank were sampled at distances of between 15 and 120m away. Groups of samples were taken in a matched pair format, alternating the area sampled first, on different sampling days. Focal samples were taken from different redshank (identified by minor plumage differences and locations) each time in each area. The same birds were sampled again on different sampling days to an unknown degree. Feeding data collected was number of picks and number of swallows, using hand counters. The size and type of prey being taken, where possible, was recorded. Size of prey was measured relative to the bill length of the redshank (assumed to be c2.5cm): for most prey, length was estimated, but for crabs and molluscs, maximum carapace and shell width respectively was estimated. All worm lengths were estimated unstretched. Type of prey taken could usually only be identified into broad categories such as mobile, small prey, amphipods or molluscs.

Other data recorded per focal sample were the age of the bird, the average nearest neighbour distance during the focal sample, the distance the redshank was from cover (tree and bushes at the edge of the estuary), the distance the redshank was from me and the number and outcome of any territorial interactions. After the feeding focal samples from an area had been collected, five additional one minute focal samples were taken. During the one minute samples the number of paces a redshank made while feeding was counted. During all data collection in the area, the number of minutes in which redshank could not feed was recorded. Redshank were prevented from feeding due to disturbance by raptors, or anti-predator behaviour due to raptor attacks. After all focal sampling had been completed, I walked into the area where the redshank had been feeding and obtained 5 estimates of wind speed, at 15cm above the ground, using a hand-held digital anemometer. The five readings of wind speed were then averaged.

In area 1 the redshank fed by picking at the surface or just under the surface of the short saltmarsh grass. Invertebrates were sampled in area 1 in winter 3 (October to March inclusive) by a stratified sampling technique. Quadrats ($0.04m^2$) were thrown at random within a fixed band of distance to cover. Quadrats were carried out in a matched pair format. The second quadrat was thrown randomly within a band 10-15m further (or closer, the order being reversed each time) from cover. The number of invertebrates within the quadrat was then counted (in size categories of 1-5, 6-10, and 10+mm) on the surface and up to 2cm below the surface by prising apart the bases and roots of the grass plants with a blunt probe. Each quadrat took up to 15 minutes to complete in most areas. As sample quadrats were carried out in small numbers throughout winter 3, a large number of quadrats were carried out on a single day to confirm the distribution of invertebrates with respect to distance to cover. On the 24th of February, winter 3, 60, $0.01m^2$ quadrats were thrown randomly in area 1, 30 at distances of greater than 50m to cover and 30 at distances of less than 30m to cover. Ten quadrats were taken in each area alternately to control for order effects.

The method of sampling employed was non-invasive and left all invertebrates in situ. Most of the invertebrates in the grass were Orchestia which were found in small pits or very shallow tunnels under the grass and could be readily seen once the overlying vegetation had been pushed aside. The efficiency of this method was not checked by more vigorous sampling due to the fragile nature of saltmarsh vegetation and the status of Tyninghame as a SSSI. The method appeared to be sufficient, as many invertebrates were found in most quadrats, but the results will be biased to an unknown degree towards those invertebrates which live closer to the surface. As redshank rarely probed deeply in area 1, this bias was unlikely to have been significant in the analysis of redshank prey availability between areas.

On the mussel beds redshank fed by shallow probing between the mussels or in the mud around or in the pools. Redshank also waded in the pools and caught very mobile prey with rapid heron-like lunges. Invertebrate prey available in the mussel bed area were only sampled qualitatively in order to facilitate identification of prey being seen taken during focal samples. Between October and January inclusive, 19, 675cm^2 surface mud cores were taken on four separate days. A length of tubing was inserted into the mud around a mussel pool, and then dug out with the mud contents intact. The mud was then sieved through 0.01cm^2 mesh in the laboratory. All invertebrates found were identified to family, and species where possible (using Fish & Fish 1989), and classified into size categories (1-5, 6-10, 10+mm, and then to the nearest centimeter). On two days in January, 100 sieve samples were taken by rapidly sweeping a small hand sieve (0.01cm^2 mesh) through the shallow water of the pools. The sieve was held just below the surface and swept for approximately 5m. Each sieve sample was taken from a different area of the large pools and from several small pools. All invertebrates collected in this way were identified and recorded according to size as described above.

Data on the weights and energy content of the different prey being taken were obtained from other studies (see Chapter 5). No relevant data could be found on the dry weight of fish, so dry weight measurements of the fish collected from the mussel pools were taken. The wet length of 5 Gobius fish (as seen eaten by redshank feeding in the mussel pools) was measured. The fish were then dried to a constant weight in a low temperature oven (50°C) over a four month period.

2.6.9 False Alarm Flight and Alarm Call Data

During feeding and vigilance data collection in area 2, in winters 1 and 2, the behaviour of the redshank flocks as a whole was recorded. A continuous time record was kept, to the nearest minute, of flock responses such as alarms and changes in flock size. Alarms were one or more rapid escape flights and were classified into two categories. Either due to a raptor (one in which a raptor was visible) or as a false alarm flight (one in which a raptor was not visible). False alarm flights were further classified into two categories: non-raptor, for example a flight away from an approaching low flying raptor-like curlew (Numenius arquata), or no-cause, when an alarm flight occurred with no apparent cause. Obviously the latter classification is subjective but the data were collected only from area 2, a small area which was watched completely from a 2m high point immediately adjacent to it. From this point it was easy to see any raptor or other relevant species within the area which may have caused the response.

In total 215.4 hours of redshank flock watches were collected in winters 1 and 2. From this 138.1 hours of observations could be used to assess the rates of false alarm flights with different flock sizes, fulfilling the criteria of a constant flock size (within a class of 10 birds, e.g. 11-20), over at least 15 minutes. During long watches when the flocks frequently left area 2 briefly, the record was ignored until the same flock size class returned to the area, when rate estimations were resumed.

During redshank flock watches the details of redshank alarm calls were recorded. Redshank made several types of call but alarm calls were identified as very strident, loud 'teu-huhu' calls (corresponding to the call type 'contact-alarm', Fig. 1B Cramp and Simmons, 1983, p. 536). This was frequently shortened to a very rapid shriek like call when under close raptor attack. The much slower, unhurried and low pitch form of this I called a contact/moving call. When a redshank flock made an alarm flight the occurrence of any redshank call (alarm or contact) and whether it occurred before or after flight was recorded, along with the circumstances, such as a human disturbance, raptor attack or no apparent cause.

During any period of redshank focal sampling where redshank were being watched closely during the approach of a raptor within 100m, and in circumstances which permitted the hearing of any calls, the occurrence of calls and the circumstances coincident with them were recorded. These included the raptor species and the closest distance it approached the flock, whether the approach was an attack, and whether the alarm call was heard before or after the flock flew. This type of data was only collected during winter 1. Alarm call data was also recorded during human approaches (see 2.6.10 below).

2.6.10 Approach Distances

Attack and response distances in cases of redshank reaction to a sparrowhawk were recorded opportunistically during winter 1. Three variables were recorded: the flock size, the distance at which the sparrowhawk first became visible to the flock, and the distance between the flock and the sparrowhawk as the flock took flight. Only cases in which the distances were obvious were recorded, for example when a sparrowhawk flew out of the closest piece of cover to the flock. This was to remove subjective assessments of whether I could see the sparrowhawk before the flock could. To remove any errors in judging distances effectively in situations which happened very quickly, all responses were classified into two: whether a flock flew instantly on the first appearance of a sparrowhawk or whether there was a delay in taking flight as the raptor approached.

During winter 3, redshank flocks were approached to determine their response to human disturbance (simulating a ground predator). Approaches were carried out from August to March inclusive. When walking between observation locations, or during saltmarsh kill searches or censuses, any redshank or flock of redshank was approached. I would walk at a constant slow speed towards the flock and record the distance I was from the centre of the flock when more than 50% of the flock had flown away. For each approach I recorded the ages of the redshank where possible (and then only for small flocks), the location of the flock (saltmarsh grass, saltmarsh creek, rocky shore, mud or beach and mussel beds), the flock size and the alarm call (no call, contact call or alarm call). If a redshank or group of redshank was surprised opportunistically, for example by approaching a deep creek unseen, by first appearing to them only a few meters away, then the approach was classified as a surprise. An open approach was one in which I was first visible to the flock at >50m, and a surprise at <10m. No more than 20 approaches (and usually only c5) were carried out each day and within different areas within each day to minimise repetitive sampling, but the same redshank were sampled frequently through the winter.

2.7 Additional Data

Temperature data from a weather station (run by the Scottish Meteorological Office) at Dunbar, 3km away, were used to estimate the mean daily air temperature. The measure used was the mean of the dry bulb temperature at 9am and the maximum temperature recorded for that day to obtain an index of the mean diurnal temperature (to correspond with my daily period of observation). Tide times and tide heights were taken from Admiralty tables for Leith Docks, 35km away.

2.8 Statistical Analysis

Statistics were analysed using the SPSS statistical programs (Nie et al. 1975); hierarchical loglinear models according to Norusis 1990, and references given there, with background information of the method in Fienberg (1970). Background information on statistical tests and the method of G tests was obtained from Sokal and Rolf (1981). All probabilities quoted are two-tailed. Where matched pairs data were collected, pairs were taken within one minute of each other and the order of collection was reversed each time, unless otherwise stated. Yates' correction was used in chi-squared tests where appropriate. Williams' correction was used in G tests. A Sequential Bonferroni procedure (Rice 1989) was used when several tests were used on an unpooled data set to test the same null hypothesis, or when several tests were used to determine if there was any significant variation. The Sequential Bonferroni procedure was used to determine the table-wide level of significance for the rejection of H_0 (at the 5% level). Where a sequential Bonferroni test was applied the critical value (alpha) for rejection of H_0, for that value of p for the test statistic, is quoted after the actual value of p.

CHAPTER 3: RAPTOR PREDATION ON WINTERING WADER POPULATIONS AT THE TYNINGHAME ESTUARY, EAST LOTHIAN

3.1 Introduction

Raptor predation has been shown to be an important source of mortality in wintering waders (Page & Whitacre 1975; Whitfield 1985a, Whitfield et al. 1988). Studies of hunting raptors have shown that potentially many waders could be taken by raptors in the non-breeding season (Bertochi et al. 1984; Buchanan et al. 1988; Dekker 1988). Much of wintering wader behaviour is dominated by responses to predators. Flocking in particular is very widespread, and functions in waders as an anti-predator strategy (Myers 1980; Buchanan et al. 1988; Whitfield 1988; Cresswell in press a, chapter 4) but it often does not increase feeding rate and in some cases even reduces it (Goss-Custard 1970a,b; Blick 1980; Fleischer 1983; Cresswell in press a, chapter 4). The major source of mortality for wintering waders has been traditionally identified as insufficient availability of food, usually through a conjunction of particular tide heights and cold weather (Heppleston 1971; Goss-Custard et al. 1977; Hale 1980). The view that raptors are not a major cause of wader mortality probably results from a lack of relevant studies (Townshend 1984) and the low numbers of raptors at many sites through persecution and the effects of pesticide usage (e.g. Newton & Haas 1984).

The high rates of mortality due to raptors reported for waders over the winter, for example, 20% of redshank (Whitfield 1985a) and 21% of dunlin (Page & Whitacre 1975) suggest that raptor predation may affect the population dynamics of waders. Sparrowhawks show a response to the availability and vulnerability of prey, killing more of a species as it becomes more available (Newton & Marquiss 1982). Both peregrines and merlins, as well as sparrowhawks, are generalist predators taking a wide range of wader and non-wader prey (Cramp & Simmons 1980) and so have the potential to specialise on particularly vulnerable or available prey, at any time. Also wintering raptors such as peregrines are very mobile (e.g. Baker 1967) and so more raptors can move into an area in response to increased numbers of available prey. Raptors can therefore potentially regulate wintering wader populations through density-dependent mortality. As more redshank, for example, become available (due to a successful breeding season), or more vulnerable (through cold weather causing loss of condition), more redshank would be killed by raptors. Mortality will be most pronounced in years where there is strong competition for limited resources (through a high population, or shortage of feeding sites). Conversely in mild winters, after a poor redshank breeding season the proportion of the population killed due to raptors would be much less, as few redshank would be available to raptors.

Previous work on the study site at Tyninghame suggested that wintering redshank suffered a high mortality rate. Enough dead redshank from the population could potentially be found to determine whether body size or other factors were under selection. Body size is important as it will determine daily energy requirements and ability to withstand prolonged periods of cold weather (Peters 1983). Salomensen (1954) and Hale (1971) found that populations of smaller redshank tended to winter further south than populations composed of large individuals, suggesting that selection may be operating on the wintering grounds according to Bergmann's rule. Summers & Underhill (1991) showed an advantage for larger body size which allowed earlier breeding, and Hale (1973) established a correlation between the mean body size of redshank and temperature on their respective breeding grounds. Both studies suggested that some selection for body size in redshank occurred on the breeding grounds. However Davidson & Evans (1982) showed that smaller individual redshank were more likely to die in cold weather on the wintering ground. As a final energy reserve in severe weather waders will metabolise their pectoral muscles (Davidson 1981a,b) which reduces their ability to fly. In severe weather, therefore, smaller birds might be expected to be less able to escape from raptors.

Age-dependent mortality in waders has been shown in several studies (e.g. Boyd 1962, Goss-Custard 1980, Clark 1982a and 1982b), and some studies have been able to attribute this to selection of first-winter birds by raptors (Kus et al. 1984, Whitfield 1985a). First winter birds may be more vulnerable to predation from raptors through lack of body condition due to exclusion from profitable feeding areas by adults (e.g. Goss-Custard et al. 1984, Whitfield 1985b), or because of poor foraging efficiency compared to adults (e.g. Groves 1978, Burger 1980, Whitfield 1985b), and due to exclusion from safe feeding areas (e.g. Shanewise & Herman 1979, Whitfield 1985a, Chapter 5). First-winter birds may be taken more frequently than adults because of lack of experience of predators, and inappropriate escape responses (Whitfield 1985a, Cresswell in press b, Chapter 4).

This chapter aims to show the continuing high rate of mortality of some wader species, particularly redshank, at Tyninghame. It also aims to determine the extent of age-dependent mortality due to raptors, and whether mortality varied with body size in redshank. Many years data are needed to determine whether raptors have any regulatory effect on wintering wader populations, and the three winters data presented in this chapter can only provide an indication of whether density-dependent wader mortality was occurring at Tyninghame.

3.2 Results

3.2.1 Predators

Tyninghame had a high density of raptors in all winters, typically 5-10 regular sparrowhawks, 3 peregrines, 1-2 merlins and 1-2 kestrels resident or visiting regularly (Table 1). Without individually marked birds it was impossible to determine the exact numbers of raptors using the estuary, but in any one day up to 14 different raptors (estimated by distinguishing individual raptors by plumage differences, age, sex and species) could hunt waders on the estuary. Merlins almost always perched openly and on habitual perches. Similarities of plumage from day to day and the frequent exclusion of any second merlins which were seen to enter the estuary area led me to conclude that only one merlin was responsible for most of the merlin prey remains found. At the most, in any of the winters, two individual merlins were attacking waders each day.

Table 1: The occurrence of avian predators, and wader attack and kill rates at Tyninghame 1989-92, per hour spent at Tyninghame (T) and per hour of intensive observation (RW).

	SP	PE	ME	KE	LO	SO	TO
1989-90: T=671, RW=204 hrs							
Total Sightings	333	83	72	94	3	0	4
Sightings/RW	0.97	0.28	0.26	0.21	0	0	0
Minutes of Sightings/RW	5.62	3.19	2.07	0.96	0	0	0
Attacks/RW	0.28	0.20	0.025	0.005	0	0	0
Kills/RW	0.020	0.015	0	0	0	0	0
1990-91: T=922, RW=198 hrs							
Total Sightings	705	117	289	57	2	2	5
Sightings/RW	1.91	0.30	0.64	0.061	0	0	0
Minutes of Sighting/RW	8.04	6.52	12.65	0.33	0	0	0
Attacks/RW	0.55	0.40	0.19	0	0	0	0
Kills/RW	0.061	0.020	0.005	0	0	0	0
1991-92: T=964, RW=370 hrs							
Total Sightings	765	123	292	103	2	6	9
Sightings/RW	1.40	0.22	0.50	0.15	0	0.01	0
Minutes of Sighting/RW	6.12	2.99	16.92	0.51	0	0.06	0
Attacks/RW	0.88	0.25	0.27	0.005	0	0	0
Kills/RW	0.092	0.016	0.024	0	0	0	0

SP Sparrowhawk PE Peregrine ME Merlin KE Kestrel

LO Long-eared Owl SO Short-eared Owl TO Tawny Owl

Peregrines also perched openly and on habitual perches; if a peregrine was present on the estuary it almost always could be seen. Peregrines at the most spent only a few hours a day on the estuary, and in late winter most visits were rapid hunts lasting only a few minutes. At most two peregrines hunted on the estuary at the same time, and even this was rare. Sparrowhawks were secretive and launched attacks on waders mainly from cover, almost always returning to it afterwards. Male sparrowhawks killed few waders (98.7%, n=78, of observed wader kills by sparrowhawks were by females). In winters 1 and 2 there were probably 2 adult and 1 juvenile female sparrowhawks hunting waders; in winter 3 there were probably 2 adult and 2 juvenile females.

In the three winters 1271 wader attacks were seen on at least 12 species; of 1253 wader attacks of known outcome (Table 2) 121 were successful. Of all wader attacks seen sparrowhawk attacks were seen most frequently (53.1%) followed by peregrine (29.3%) and merlin (17.2%) (Table 2). Kestrels only occasionally attacked birds. Owl species included tawny owl Strix aluco, long-eared Asio otus and short-eared owls A. flammeus, and were recorded mainly by disturbing roosting birds during kill searches. Only short-eared owls were seen hunting, but were not seen to take waders. Mammalian predators recorded were stoat Mustela erminea (n=52 sightings), weasel M. nivalis (n=9) and fox (n=10); no wader hunts by mammals were seen. Carrion crows were occasionally seen to initiate attacks on waders, unconnected with kleptoparasitism events; 24 attacks on redshank were seen, and on 2 occasions a carrion crow was seen catching and killing a redshank without apparently any raptor initially being

TABLE 2: Wader species attacked (1) and seen killed (2) by raptors at Tyninghame, data pooled from the three winter periods. Only attacks of known outcome are included.

	SP1	SP2	PE1	PE2	ME1	ME2	KE1	KE2
Oystercatcher:	1	0	14	0	0	0	0	0
Grey Plover:	7	0	13	1	0	0	0	0
Lapwing:	1	0	12	0	0	0	0	0
Knot:	0	0	1	0	1	0	0	0
Dunlin:	92	11	76	10	134	17	1	0
Snipe:	1	1	1	0	1	0	0	0
Jack Snipe:	0	0	0	0	1	1	0	0
Bar-tailed Godwit:	0	0	4	0	0	0	0	0
Whimbrel:	0	0	1	0	0	0	0	0
Curlew:	22	0	46	0	2	0	2	0
Redshank:	538	65	157	12	48	0	1	0
Turnstone:	2	1	7	0	0	0	0	0
Wader species:	11	0	36	2	18	0	1	0
TOTAL:	675	78	368	25	205	18	5	0

SP Sparrowhawk   PE Peregrine   ME Merlin   KE Kestrel involved (see Tinbergen 1953 for a similar example); for dunlin 5 attacks were seen with 1 kill.

3.2.2 Waders as Prey

The maximum monthly counts for the different wader species along with the number of waders found dead or seen killed in each month are summarised in Table 3. Between October and March inclusive the resident wintering wader species, oystercatcher *Haematopus ostralegus*, ringed plover *Charadrius hiaticula*, grey plover *Pluvialis squatarola*, snipe, bar-tailed godwit *Limosa lapponica*, curlew, greenshank *Tringa nebularia* and turnstone had broadly similar numbers from month to month; knot *Calidris canutus* and purple sandpiper *Calidris maritima* numbers peaked in late winter; dunlin numbers peaked in mid-winter and redshank numbers peaked in October declining steadily until April. Golden plover *Pluvialis apricaria* and lapwing *Vanellus vanellus* visited the estuary irregularly, the latter species often in large roosting flocks which varied daily in size by an order of magnitude. The remaining species recorded were passage migrants in very small numbers, usually in September and October: avocet (*Recurvirostra avocetta*), sanderling (*Calidris alba*), little stint (*Calidris minuta*), curlew sandpiper (*Calidris ferruginea*), ruff (*Philomachus pugnax*), jack snipe (*Lymnocryptes minimus*), whimbrel (*Numenius phaeopus*), spotted redshank (*Tringa erythropus*), green sandpiper (*Tringa ochropus*) and common sandpiper (*Tringa hypoleucos*).

The majority of waders killed were redshank (50.6%) and dunlin (38.8%); the numbers of kills found peaked in periods of cold

TABLE 3: Maximum monthly counts (C) and number of deaths (D) of wader species at Tyninghame in each winter September-April inclusive: 1989-90 (1), 1990-91 (2), 1991-92 (3). Where no D values are given for a species, no remains were found.

			MONTH							
			SE	OC	NO	DE	JA	FE	MA	AP
Oystercatcher	C	1	366	505	532	500	550	525	-	-
	D		0	0	0	0	0	0	0	0
	C	2	345	535	530	500	430	278	184	91
	D		1	0	0	0	1	0	2	0
	C	3	544	320	456	-	-	400	220	-
	D		0	0	0	0	0	0	0	-
Avocet	C	1	0	0	0	0	0	0	0	0
	C	2	0	1	1	0	0	0	0	0
	C	3	0	0	0	0	0	0	0	-
Ringed Plover	C	1	30	15	17	31	20	17	2	6
	D		1	1	0	0	0	0	0	0
	C	2	116	50	55	50	6	6	20	12
	D		2	0	1	0	0	0	0	0
	C	3	10	48	25	-	16	30	30	-
	D		1	0	0	0	0	0	0	-
Grey Plover	C	1	61	73	69	38	58	84	10	37
	D		3	1	1	1	0	0	0	0
	C	2	80	99	95	120	107	157	90	44
	D		2	0	0	1	0	1	0	0
	C	3	111	129	121	-	123	148	122	-
	D		2	4	1	0	2	1	0	-
Golden Plover	C	1	0	15	35	0	21	16	0	0
	C	2	3	10	20	20	10	0	0	0
	C	3	2	14	0	0	0	0	0	-
Lapwing	C	1	22	550	460	350	130	46	150	-
	D		2	0	0	0	0	0	0	0
	C	2	75	200	200	30	20	20	10	4
	D		0	0	1	0	0	0	1	0
	C	3	200	350	65	170	90	200	50	-
	D		0	0	0	0	0	0	0	-

Knot	C	1	0	5	70	125	208	71	40	2
	D		1	0	2	2	2	0	0	1
	C	2	20	16	40	30	35	180	30	6
	D		0	0	0	0	0	6	3	0
	C	3	5	5	20	150	70	130	6	-
	D		2	0	0	2	0	1	0	-
Sanderling	C	1	0	1	0	0	0	0	0	0
	C	2	15	5	2	1	0	0	0	0
	C	3	25	0	0	0	0	2	1	-
Little Stint	C	1	0	0	0	0	0	0	0	0
	C	2	0	0	0	0	0	0	0	0
	C	3	1	0	0	0	0	0	0	-
Curlew Sandpiper	C	1	0	1	0	0	0	0	0	0
	C	2	14	2	0	0	0	0	0	0
	C	3	3	0	0	0	0	0	0	-
Purple Sandpiper	C	1	0	0	0	0	10	10	0	0
	D		0	0	0	0	0	0	0	0
	C	2	0	2	2	10	11	16	0	0
	D		0	0	0	0	0	1	0	0
	C	3	0	0	0	1	6	8	1	-
	D		0	0	0	0	0	1	0	-
Dunlin	C	1	125	200	585	750	775	550	85	138
	D		1	6	12	10	4	3	1	1
	C	2	676	992	1200	1234	1300	886	272	246
	D		19	19	19	19	23	50	10	1
	C	3	150	372	1076	1000	900	652	200	-
	D		12	35	53	76	53	18	2	-
Ruff	C	1	0	0	0	0	0	0	0	0
	D		0	0	0	0	0	0	0	0
	C	2	3	2	0	0	0	0	0	0
	D		0	0	0	0	0	0	0	0
	C	3	3	1	0	0	0	0	0	-
	D		2	1	0	0	0	0	0	-

Jack Snipe	C	1	0	0	0	0	0	0	0	0
	D		0	0	0	0	0	0	0	0
	C	2	0	1	0	0	1	0	0	0
	D		0	0	0	0	0	0	0	0
	C	3	0	1	0	0	1	0	0	0
	D		0	0	0	1	0	0	0	-
Snipe	C	1	7	14	6	2	2	1	2	0
	D		0	2	0	2	0	0	0	0
	C	2	6	3	5	3	0	1	0	0
	D		0	1	1	0	0	0	0	0
	C	3	5	7	5	9	2	0	0	-
	D		0	2	0	1	0	0	0	-
Bar-tailed Godwit	C	1	40	39	53	100	59	68	61	23
	D		0	0	0	0	0	0	0	0
	C	2	40	69	105	102	105	132	66	61
	D		0	0	0	0	0	0	0	0
	C	3	50	80	75	85	127	105	118	-
	D		0	1	0	0	0	0	0	-
Whimbrel	C	1	5	0	0	0	0	0	0	1
	D		0	0	0	0	0	0	0	0
	C	2	15	1	0	0	0	1	1	3
	D		0	0	0	0	0	0	0	0
	C	3	11	1	1	1	1	1	1	-
	D		1	0	0	0	0	0	0	-
Curlew	C	1	230	204	195	203	241	200	221	117
	D		0	0	0	0	1	1	0	0
	C	2	200	220	286	175	200	250	220	99
	D		1	0	0	0	0	0	0	0
	C	3	265	189	310	-	275	250	312	-
	D		0	0	0	0	0	0	0	-
Spotted Redshank	C	1	0	1	0	0	0	0	0	0
	C	2	1	1	0	0	0	0	0	0
	C	3	1	1	0	0	0	0	0	-
Redshank	C	1	360	349	360	-	303	266	292	260
	D		17	13	19	29	18	6	10	1
	C	2	379	366	344	-	331	186	180	175
	D		13	10	16	27	60	61	3	1
	C	3	443	440	438	325	270	217	180	-
	D		9	16	50	74	59	37	10	-

Greenshank	C	1	15	7	8	7	7	7	6	0
	D		1	1	0	0	0	0	0	0
	C	2	10	9	7	7	6	6	6	0
	D		0	0	0	0	0	0	0	0
	C	3	5	5	3	3	3	3	3	-
	D		0	0	0	0	0	0	0	-
Green Sandpiper	C	1	0	0	0	0	0	1	0	0
	C	2	0	0	0	0	0	0	0	0
	C	3	0	1	0	0	0	0	0	-
Common Sandpiper	C	1	0	0	0	0	0	0	0	0
	C	2	1	0	0	0	0	0	0	0
	C	3	1	0	0	0	0	0	0	-
Turnstone	C	1	6	29	37	30	36	32	-	15
	D		3	0	3	1	3	2	0	0
	C	2	27	48	64	63	62	77	47	57
	D		2	0	0	1	1	4	0	1
	C	3	10	36	35	30	54	50	61	-
	D		0	0	1	1	4	2	0	-

weather and mid-winter. Over the three winters, remains from 1140 waders of 19 species were found, another 20 waders were seen being killed but were not recovered. Sparrowhawks were the main cause of death in waders (53.4%). Overall, raptors were the main agent of wader mortality (86.1%) and starvation accounted for only 1.1% of deaths (Table 4.). Carrion crows were a major factor contributing to the high mortality of waders, with 12.0% of kills classified as carrion crow/kleptoparasitism. Sparrowhawks were most prone to kleptoparasitism; in 29.6% (n=81) of kills seen crows gained possession of the wader. Crows, most often in pairs, would dislodge sparrowhawks standing on newly caught prey or grab the prey as it was being carried in flight. The prey was often still alive and on 3 occasions escaped temporarily and was chased and caught in flight after a few seconds by a crow. Only 2 (8.0%, n=25) peregrine kills were kleptoparasitised; in one case a struggling dunlin was dropped by a peregrine and eaten by a great black-backed gull Larus marinus, and in another, two carrion crows forced a feeding peregrine away from a redshank. Overall, 24.5% of observed wader kills were kleptoparasitised.

3.2.3 Estimates of Mortality

The minimum overwinter mortality rate of a wader species caused by raptors was estimated by calculating the proportion of the maximum single count of live birds that was represented by the number of raptor kills (from remains or seen directly) during the winter period September to March inclusive (Table 5). This method underestimated the effect of raptor predation in some species (e.g.

TABLE 4: Cause of Death in waders regularly occurring at Tyninghame, August - April inclusive 1989-92.

	SP	CK	PE	ME	FO	OW	ST	FX	TOT
Oystercatcher	0	0	0	0	0	0	1	3	4
Ringed Plover	3	0	1	0	1	1	0	0	6
Grey Plover	6	0	10	0	2	0	0	2	20
Golden Plover	0	0	0	0	0	0	0	0	0
Lapwing	5	0	0	0	0	0	0	3	8
Knot	7	2	2	1	6	4	1	0	23
Sanderling	0	0	0	0	0	0	0	0	0
Purple Sandpiper	2	0	0	0	0	0	0	0	2
Dunlin	194	20	14	126	81	13	2	0	450
Ruff	3	0	0	0	0	0	0	0	3
Jack Snipe	0	0	0	1	0	0	0	0	1
Snipe	7	0	0	0	2	0	0	0	9
Woodcock	6	0	1	0	0	0	0	1	8
Bar-tailed Godwit	0	0	1	0	0	0	0	0	1
Whimbrel	0	0	1	0	0	0	0	0	1
Curlew	0	0	1	0	0	0	2	0	3
Redshank	356	117	34	11	47	15	7	0	587
Greenshank	3	0	0	0	0	0	0	0	3
Turnstone	27	0	0	0	3	1	0	0	31
TOTAL:	619	139	65	139	142	34	13	9	1160

SP Sparrowhawk PE Peregrine CK Carrion Crow/Kleptoparasitism
ME Merlin FO Falcon/Owl OW Owl ST Starvation FX Fox

Table 5: Mortality rates of waders at Tyninghame due to raptor predation during the winter, September-March inclusive.

	Average Monthly Mortality Rate	Minimum Overwinter Mortality Rate		
	1989-92	89-90	90-91	91-92
Ringed Plover	1.0%	6.1%	2.6%	2.0%
Grey Plover	1.0%	7.9%	2.5%	5.1%
Lapwing	0.1%	0%	1.0%	0%
Knot	1.6%	3.3%	4.4%	3.3%
Purple Sandpiper	2.6%	0%	6.3%	12.5%
Dunlin	3.0%	4.6%	11.4%	21.2%
Ruff	33.3%	0%	0%	60.0%
Jack Snipe	25.0%	0%	0%	50.0%
Snipe	11.3%	28.6%	33.3%	25.0%
Bar-tailed Godwit	0.1%	0%	0%	0.8%
Whimbrel	2.5%	0%	0%	8.3%
Curlew	0.02%	0%	0.3%	0%
Redshank	8.3%	31.1%	48.5%	57.3%
Greenshank	1.5%	13.3%	0%	0%
Turnstone	3.4%	28.6%	9.5%	11.6%

redshank) because numbers declined through the winter due to raptor predation but overestimated the effect of raptor predation in species which had a substantial mortality before their numbers peaked, through immigration (e.g. dunlin). To compensate for this, the number of dead birds recovered for a species before the maximum count was added to the maximum live count. Many wader kills were either exported (no raptor was seen to carry prey from outside the estuary into the search area) or simply not found and so the estimates were calculated to be reliable minimum figures for mortality due to raptors, and not necessarily the actual rates. Despite this, the minimum estimate for overwinter losses to raptors of many species which commonly occured at Tyninghame such as dunlin, snipe, redshank, and turnstone were over 10% and up to 57%. Another approach was to calculate the average monthly mortality rate. This was calculated by dividing the total number found killed or seen killed by raptors over the total count of live birds. Both totals were calculated using the numbers in each month over the 21 monthly periods September to March inclusive (Table 5). The effects of peaks in population each winter were then much reduced (counts changed only gradually from month to month in most cases) and the assumption of a fixed population was more likely to be true; the numbers of raptor kills was still being underestimated due to raptors exporting kill remains out of the study area. Again many species showed significant monthly losses. Starvation accounted for a relatively very small amount of the mortality compared to raptor predation in all species apart from the larger waders such as curlew and oystercatcher. In any month, the largest mortality due to starvation was in February 1991 where 5 redshank starved out of a minimum count for that month of c200 (2.5%).

3.2.4 Redshank Population

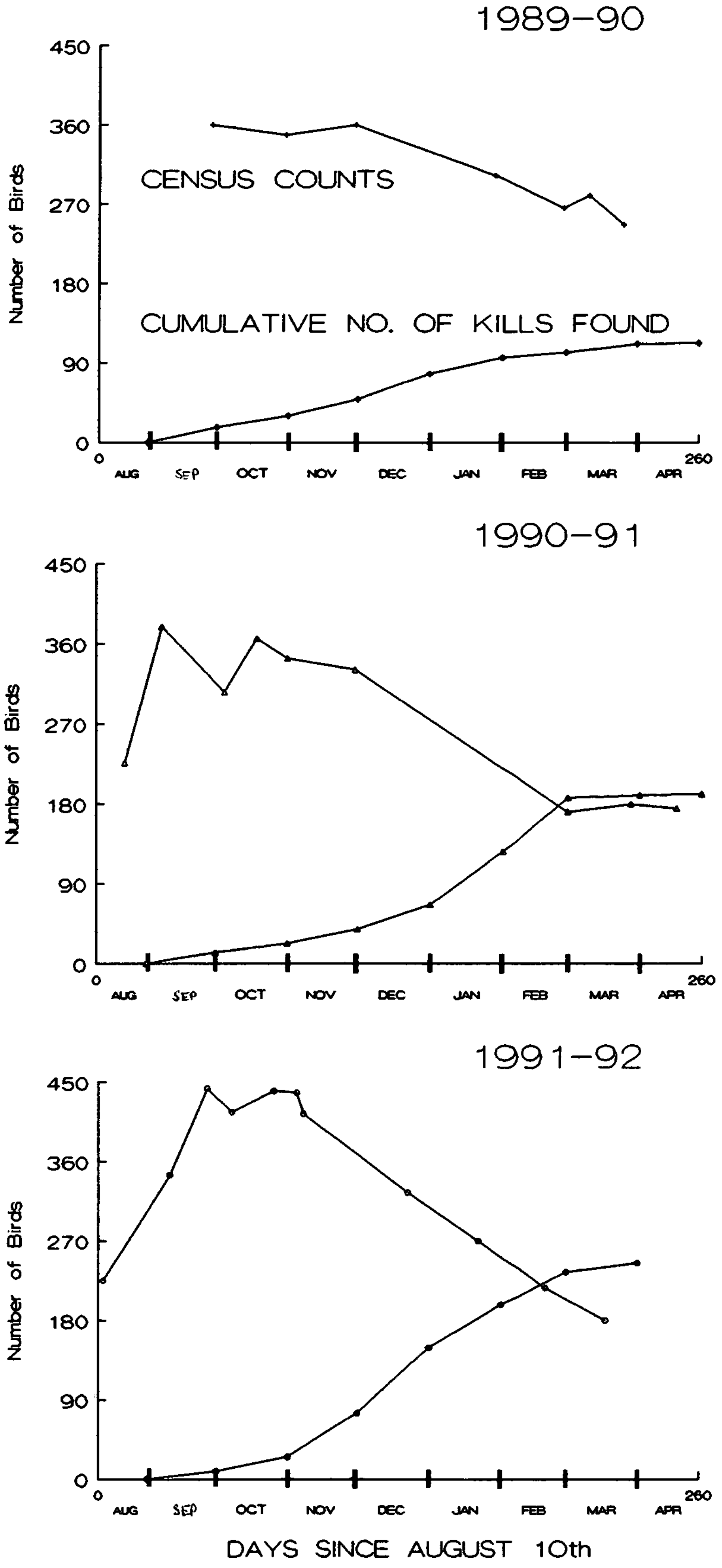
There was good evidence that the very high overwinter mortality rate recorded for redshank was accurate and relevant. The population of redshank at Tyninghame appeared to be closed, with little emigration or immigration between October and March inclusive. Redshank numbers peaked in late September and then declined consistently until the end of March; the relative changes from month to month within a winter were broadly similar between winters. The decline in numbers from October to March was probably due to mortality rather than emigration, because the number of dead redshank found matched the decrease in numbers of live redshank counted (Figure 1).

The difference between maximum counts of live birds in October and at the end of March agrees very closely with the number of redshank found dead on the estuary (Table 6). The numbers of redshank found dead were corrected for the proportion of redshank kills seen that were exported out of the search area by peregrines and so not recovered (8/12 peregrine kills were not recovered). Nearly all sparrowhawk kills were recovered (n=80/81 kills), and no estimates of the percentage of kills recovered from merlins or owls could be made, so the number of redshank killed was only adjusted for peregrine exports. The observed decrease in live counts and the total number of redshank estimated killed (including the peregrine export estimate) agree closely: 11%, 2% and 1% for each of the

Rates of Decrease in the Population of Redshank

FIGURE 1

and Rates of Increase in the Number of Dead Redshank Found in each Winter



winters, the difference expressed as a percentage of the observed decrease in live counts. The peregrine export correction is based on a small sample size of observed redshank kills, which may account for the subsequent over-estimate of kills versus observed decrease in numbers of live birds in 2 out of 3 winters (Table 6).

Many more juvenile redshank than adults were found killed at Tyninghame in each of the winters. If the population at Tyninghame was closed then the percentage of juveniles in the population would be expected to fall in accordance with the number of juvenile redshank found dead. In each of the three winters the number of juveniles in the population (estimated from sampling the proportion of juveniles present during counts) decreased by a similar amount to that expected from the number of juvenile and adult redshank found dead during the same period (Table 7). The difference between observed (from live counts) and expected (from kills) was 2%, 21%, and 8% (expressed as a percentage of the observed decrease in the number of live juvenile redshank for each winter).

During winter 3 the number of individually colour-ringed birds remained fairly constant. On a redshank count, the proportion of colour-ringed birds in a sample of birds was multiplied by the total redshank count to give an estimated total number of colour ringed birds on the estuary. This was compared with the observed number of individual colour-ring combinations recorded during the month period before the count. On 5 counts between the end of September and mid March the average difference between the number of colour-ringed birds expected from the count samples and those observed as present on the estuary during the previous month was 1.6+/-0.4 birds

Table 6: Observed counts of redshank at the start and finish of the winter with predicted numbers of redshank at the finish of the winter based on the number of redshank found dead.

	89-90	90-91	91-92
Maximum Count October	360	366	443
Count End March	247	180	180
Decrease in Count October-March Inclusive	113	186	263
Number Found Dead October-March Inclusive	93	177	246
Estimate of Peregrine Exports	30	12	9
Total Estimated Redshank Mortality	123	189	255
Predicted Numbers at End March	237	177	188
Difference Predicted-Observed	-10	-3	+8

Table 7: Observed proportions of juvenile redshank within the wintering population and predicted proportions based on the numbers of dead juveniles found each winter.

	1989-90	1990-91	1991-92
Observed % Juveniles Start of October	40%	39%	47%
Number of Juveniles Start of October	144	141	209
Observed % Juveniles Mid March	25%	13.5%	8%
Number of Juveniles Mid March	62	24	14
Observed decrease in numbers of juveniles	82	117	195
Total No. Juveniles found dead October-Mid March inclusive	80	142	216

(estimate from sample 29.8+/-1.1 compared to number of birds with colour-rings present 31.6+/-1.2). The similarity in the two sets of numbers shows that, at least for a monthly period, the number of colour-ringed redshank remained constant and that the redshank counts included all of the population (assuming a random spatial distribution of colour-ringed redshank over the whole estuary). During winter 3 all colour-ringed birds on the estuary were adults. More juveniles were killed than adults over the winter, so the proportion of colour-ringed/unringed birds would be expected to increase if the population was closed. At the end of September the proportion of colour-ringed birds was 6.8%, this rose to 15.8% by mid-March.

3.2.5 Selection of Redshank by Raptors

Right wing length, as an accurate index of body size (Davidson 1983), was compared between live birds from the start and finish of winter 2 in order to determine whether selection had occurred. Redshank were split by age for analysis, because there was a significant difference between adult (174.2mm+/-0.76) and juvenile (169.9mm+/-0.67) right wing length ($t=-3.62$, $n=47$, $p<0.0001$). The first cannon-net catch was carried out on 7th October, after at least 15 redshank (juveniles) out of a maximum count of 379 were found dead from the start of September. The second cannon-net catch was on 3rd March; 137 juveniles and 35 adults were recovered dead between the two catches. There was no significant difference in wing length between the two catches: juvenile, mean for October 169.3+/-1.2 n=7, mean for March 170.6+/-0.78, $t=-0.88$, $n=9$; adult, mean for

October 173.6+/-2.5 n=5, mean for March 174.3+/-0.80, t=-0.36, n=26; pooled variance estimate t-test. For both age classes the variance in October was higher than in March, although this was not significant (Juveniles F=1.83, comparing n=7 juveniles in October, with n=9 in March; Adults F=1.89, comparing n=5 adults in October, with n=26 in March). There was no significant difference between right wing lengths of redshank which were killed by raptors before the second catch and the survivors as measured at the second catch: juveniles, mean for raptor kills 169.8+/-0.40, t=0.55, n=116; adults, mean for raptor kills 173.2+/-0.93, t=0.93, n=49; pooled variance estimate t-test.

There were no significant differences in the wing lengths of redshank killed by raptors between any of the monthly periods (September to March inclusive) of the three winters: juveniles F=1.57, n=298; adults F=1.03, n=46; One-way ANOVA over 21 monthly periods. There were no significant differences in wing lengths of redshank killed by the different raptor species; sparrowhawk, peregrine, merlin, owl, falcon/owl, crow/kleptoparasitism: juveniles, F=1.39, n=298; adults, F=0.60, n=46; One-way ANOVA.

On 7 occasions it was possible to recover and weigh an intact redshank which had been caught by a sparrowhawk and then kleptoparasitised by crows. There was no significant difference between the mean weight of the killed birds (138.7 g +/-5.8, n=7) and the mean weight of the juvenile redshanks caught in both cannon-nets (143.9 g +/-2.5, n=16); all kill weights were from juveniles (t=-0.72, pooled variance estimate t-test). There was no significant difference between the mean size (as expressed by weight over right wing length) of the killed (0.82 +/-0.03) and caught (0.84 +/-0.02) redshank (t=-0.98, pooled variance estimate t-test).

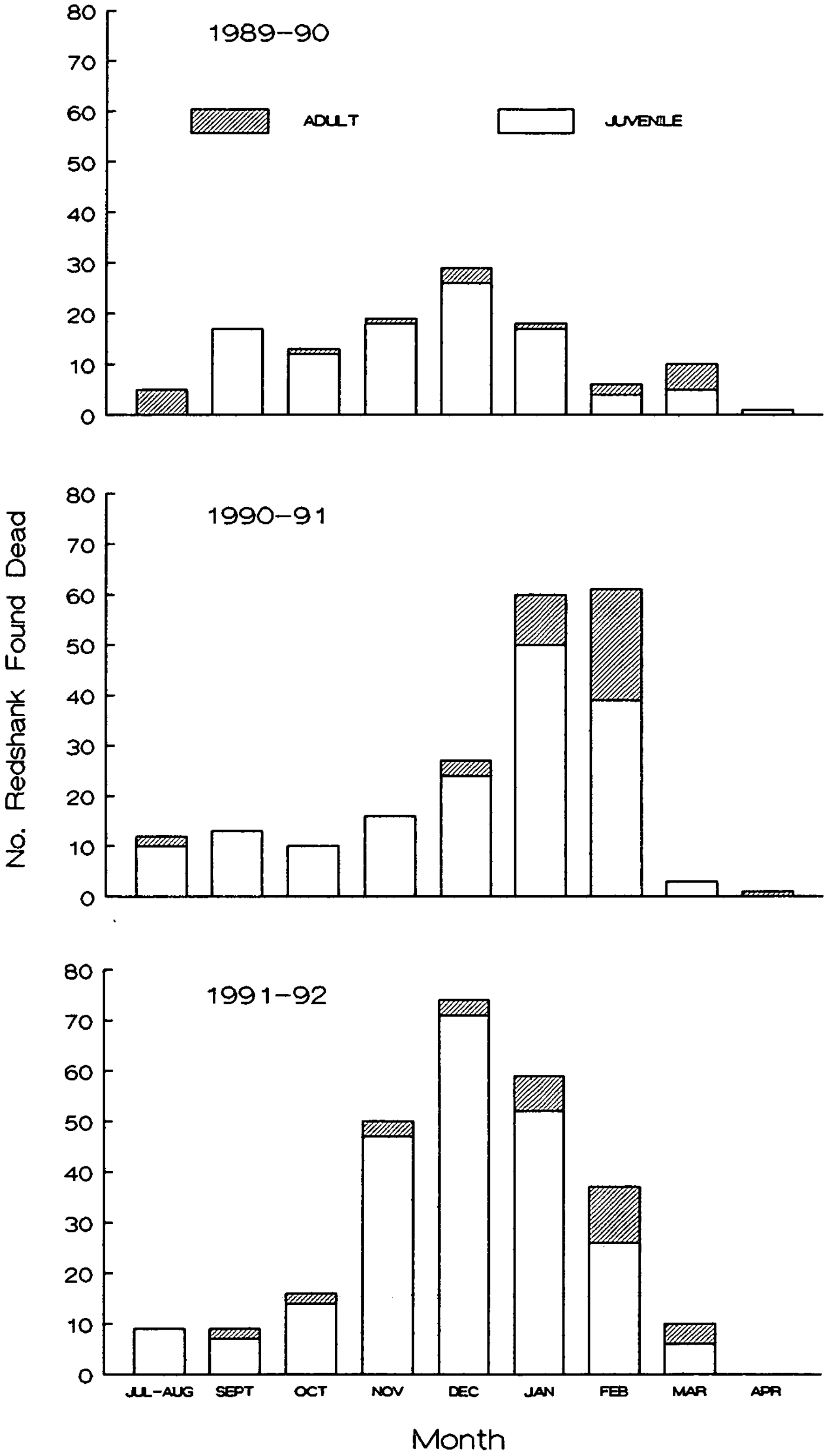
Significantly more juvenile than adult redshank were killed by raptors than would be expected from their relative occurrence in the population (using the maximum estimate of proportions of juveniles in each winter). In winter 1, 99/13 juveniles/adults were killed from September to March inclusive compared to a juvenile/adult ratio of 48/72 recorded in September (G=62.5, $p<0.001$). In winter 2, 150 juveniles and 36 adults were killed, compared to a juvenile/adult ratio of 104/145 (G=69.3, $p<0.001$). In winter 3, 186 juveniles and 26 adults were killed, compared to a juvenile/adult ratio of 176/205 (G=108.8, $p<0.001$). Sparrowhawks took significantly more juvenile redshank than peregrines (sparrowhawk juvenile/adult 375/57 and peregrine juvenile/adult 11/6; G=4.7, $p<0.05$). The proportion of adult redshank found dead increased through each of the winters, September to March inclusive (Figure 2). A significantly larger proportion of raptor kills were of adult redshank later in the winter: winter 1, $x^2=20.8$, n=112, $p<0.005$; winter 2, $x^2=23.9$, n=184, $p<0.001$; winter 3, $x^2=23.9$, n=253, $p<0.001$; Kruskall-Wallis One-way ANOVA).

3.2.6 Dunlin Population

Dunlin were killed frequently by merlins, peregrines and sparrowhawks. Unlike redshank, most dunlin kills were probably not recovered. Of sightings of a raptor with a newly caught dunlin, merlins left remains within the study area in 41.2% of cases (n=7/17 kills seen which were recovered within the study area), peregrines

The Number of Redshank Found Dead in Each Winter

Classified by Age



50.0% (n=5/10), and sparrowhawks 90.9% (n=10/11). Estimates of mortality based purely on kills found within the study area were therefore substantial underestimates. Using these percentages of kills recovered, estimates of overwinter mortality were made for each winter, September to March inclusive (all falcon/owl kills were assumed to have been recovered). The number of dunlin probably killed in each of the winters 1-3 was 37, 196 and 403 respectively, which resulted in a minimum mortality estimate (using the maximum count for that winter) of 4.7%, 14.0%, and 34.3%. The major differences in mortality rate between each winter can probably be accounted for by the frequency of merlin hunting on the estuary, which varied in each winter (Chapter 7.2.1).

3.3 Discussion

3.3.1 Is Tyninghame unusual in terms of raptor predation on waders?

Over each winter of the study a substantial proportion of the waders at Tyninghame was killed by raptors. Mortality due to starvation or mammalian predators was comparatively small except in the case of larger species such as oystercatcher and curlew. Raptors have been the main agent of mortality at Tyninghame and the adjacent area of Scoughall for at least 10 years (Whitfield 1985a; Whitfield unpublished data). Page & Whitacre (1975) reported similarly high rates of mortality due to raptors at Bolinas lagoon, California: a single merlin accounted for 6.7% of the local population of dunlin-sized waders during a winter, in comparison a single merlin at Tyninghame probably accounted for 5.2% in winter 2, and 19.4% in winter 3, of the local population of dunlin-sized waders (only dunlin at Tyninghame). Hale (1980) stated that 'predation rates in Europe are much lower' (compared to Page & Whitacre's study site) and that 'predation is not a very common cause of mortality and starvation in winter is generally regarded as the greatest cause of mortality'. This view has arisen becaused previous studies were based on the larger wader species, and because relevant studies have not been made in areas which still have good numbers of wintering raptors. At the three sites in Britain so far investigated specifically for raptor kills of waders, raptor predation has been found to be the major cause of wintering wader mortality (Whitfield et al. 1988).

During the three winters of the study some very large mortality rates for waders were recorded, particularly for redshank, dunlin, turnstone, snipe, and ruff. In the context of previous work on the subject the results were not unusual. It can be argued that studies on the impact of raptor predation on waders are biased towards sites where it is high because that is where predation attracts attention. Rates of mortality reported due to raptor predation may then only be of limited local interest. In order to extrapolate from the results of this study it is necessary to determine whether any of the factors that determine the degree of raptor predation on waders were unusual at Tyninghame.

Predation rates of waders should simply be a consequence of raptor density, raptor attack rate and attack success rate. Densities of raptors (expressed as sightings per hour) do not appear to be atypical at Tyninghame compared to coastal sites around Britain (Lack 1986). Good empirical data of attack rates on waders by raptors at other coastal sites are lacking, and so it is difficult to put the observed attack rates at Tyninghame into context. Attack rate can be assumed to be a function of success rate and number of raptors present in the area (in a specialist predator). Success rates of raptors can be eliminated as an unusual factor operating at Tyninghame. Observed wader attack success rates at Tyninghame of 11.6% for sparrowhawk, 6.8% for peregrine and 8.8% for merlin are very similar to other reported success rates (Rudebeck 1950, 1951: sparrowhawk 10.8%, peregrine 7.3%, merlin 4.5%; Page & Whitacre 1975: merlin 12.5%; Kus 1985: merlin 6.7%; Buchanan et al. 1988: merlin 22.5%; Dekker 1988: peregrine 9.2%, merlin 11.6%; Lindstrom 1989: sparrowhawk 8%, merlin 11%).

All of the raptor species taking waders at Tyninghame are generalist predators and so the degree of specialisation on waders must be taken into account. If, for example, one female sparrowhawk was to specialise entirely on redshank it would need to kill 1 redshank every 2 days. This estimate of average food intake is based on average daily food consumption of active captive birds (in Newton 1986) with a 10% addition to the weight to account for those parts of the prey which are not eaten in the wild (Ratcliffe 1980). The average weight of a redshank was calculated from the cannon-net samples as 146.2 g+/-1.5. Therefore during a winter (September-March inclusive) a single female sparrowhawk could kill up to 106 redshank, and with the presence of a single pair of carrion crows kleptoparasitising at observed rates this would result in a total of 154 redshank.

One aspect of the predation at Tyninghame which may be unusual is the high rate of kleptoparasitism by carrion crows. Kleptoparasitism occurred in over 25.0% of observed peregrine and sparrowhawk kills, and 21.3% of all redshank kills found (excluding owl and merlin kills, and starved birds). Sparrowhawks were most prone to kleptoparasitism, peregrines rarely and merlins not at all, despite frequent attempts by crows. There is some anecdotal data of kleptoparasitism of raptors by corvids (e.g. Sage 1963; Tinning & Tinning 1970; Newton 1986), and Newton (1986) speculated that sparrowhawk feeding habits (particularly carrying prey immediately into cover) are direct adaptations to the risk of kleptoparasitism. Crow kleptoparasitism certainly occurs at other sites on the Firth of Forth (C. Davison pers. comm.). Observed raptor kills, even in intensive studies, are rare (e.g. 52 captures during 5 years of autumn migrations, Rudebeck 1950, 1951; 97 captures in 22 years in spring and autumn periods, Dekker 1988). Correspondingly, the frequency of observed kleptoparasitism will be very low. In the context of no available comparative data it is impossible to conclude whether Tyninghame is unusual in its rates of kleptoparasitism.

The densities of carrion crows at Tyninghame are not atypical compared to most coastal sites in Britain apart from southern and eastern England (Lack 1986). Density, however, is probably not as important as the degree of specialisation, as for sparrowhawks. Despite large numbers of carrion crows present on the estuary, up to 150 at times, only between 1-3 pairs (associated with three areas of the saltmarsh where they habitually fed and perched) appeared to be regular, successful kleptoparasites. It took a pair of crows about 10-20 minutes to eat a redshank completely, and many of the kleptoparasitised prey were cached. Caching allows crows to be potential kleptoparasites at all times, only limited by prey handling time. Caching by crows occurs widely (e.g. Simmons 1968, Simmons 1970). Carrion crows were a significant cause of wader mortality at Tyninghame. Crow kleptoparasitism increased the redshank winter mortality rates (September-March inclusive) by 12.1% in winter 1, 33.8%, in winter 2, and 29.4% in winter 3 (calculated as the number of crow/kleptoparasitism kills found over the total number of dead redshank eaten by raptors, and assuming that the raptors exactly compensated for prey lost to crows).

The local topography, such as woods around the estuary or the small size of the Tyninghame estuary, may have had an effect on the amount of wader mortality occurring. Peregrines, merlins and sparrowhawks hunt mainly by surprise (Rudebeck 1950, 1951; Page & Whitacre 1975; Ratcliffe 1980; Newton 1986; Buchanan et al. 1988; Dekker 1988; Chapters 6 and 7). The presence of woods or buckthorn bushes, rocky shore and saltmarsh creeks close to the waders' feeding areas make waders at Tyninghame especially vulnerable. The distance to cover of prey is very important in the hunting success of sparrowhawks (Whitfield 1985a; Newton 1986; Chapter 5); but I observed several successful sparrowhawk attacks several hundred meters from cover. Sparrowhawks use a variety of hunting methods (Owen 1932; Rudebeck 1950; Naunton 1973; Newton 1986; Chapter 6) and, even on large coastal mud-flats, surprise attacks can be launched after long periods of perching hunched on the ground or by a stoop from a high soaring bird. Merlins and peregrines use very low contour-hugging approach flights or stoops to attack waders, and are not reliant on obvious cover such as bushes or trees. Success rates of raptor hunts in very large open estuaries such as The Wash are needed in order to determine whether topography has anything other than a very local effect.

The presence of cover close to the waders' feeding area may have resulted in more kills by sparrowhawks being recovered. The apparently high mortality rate at Tyninghame may then be a consequence of high recovery rate. Sparrowhawks carry their prey into the closest piece of cover (96.6% of observations of carrying newly caught prey, n=87), presumably to reduce their chance of being kleptoparasitised. If cover was further away from the estuary, a much larger area would need to be searched to recover the same number of kills. Peregrines carry prey a long distance, frequently to favoured tall trees well away from the estuary. To recover peregrine kills, a huge area must be searched and individual peregrines must be watched more or less continuously (Baker 1967).

3.3.2 Selection of redshank by raptors

Despite the very high mortality of redshank each winter, there was apparently no selection for body size, nor any change in the size of redshank killed in each month. Redshank are particularly susceptible to mortality even in very short periods of cold weather (Beecroft & Clark 1986; Davidson & Clark 1985; Clark 1982; Davidson 1982a,b; Davidson & Evans 1982). In winters 2 and 3 there were three periods of sustained freezing weather coincident with low tide heights, so that the saltmarsh and some of the mud adjacent to the saltmarsh remained frozen for several days. The most severe extended freezing period occurred in January and February winter 2. In these months 46.8% of the redshank present on the estuary on the first of January were killed by raptors; this coincided with the only recorded deaths of redshank by starvation. In the cannon-net catch at the start of March, 20.5% of the surviving population was caught. The lack of selection recorded was probably a definite result and not simply a consequence of sample size or lack of mortality. This result agrees with Hale's (1980) assertion that selection for body size and other morphological characters in redshank occurs mainly on the breeding grounds. Although more redshank were killed by raptors in periods of cold weather (and also in Whitfield et al. 1988) small body size (leading to earlier starvation and weaker birds) was probably not a major factor.

Juvenile redshank were preferentially taken by raptors. This result agrees with Whitfield 1985a and Kus et al. 1984. Starvation may be a factor contributing to increased juvenile mortality, possibly through less efficient foraging by juvenile birds (Ashmole 1963, Partridge & Green 1985). Foraging by juvenile redshank however, did not appear to be markedly less efficient than adults (Chapters 4 and 5), and rates of energy intake by juveniles, at low tide, were higher than adults (Chapter 5). The high mortality for juveniles was probably because juvenile waders were excluded by adults from low-risk feeding areas (Shanewise & Herman 1979; Whitfield 1985b; Chapter 5).

3.3.3 The Effects of Raptor Predation on Redshank Populations

A very significant proportion of the redshank population, overwintering at Tyninghame, was taken by raptors. In one winter, approximately 55%, and in two winters, approximately 90% of the juveniles, were taken by raptors. Numbers of redshank wintering at Tyninghame have not declined (Whitfield 1985a, this study, and P. Gordon pers. comm.), despite high levels of raptor-caused mortality over at least the last ten years. Excluding the possibility that Tyninghame is a 'sink' for surplus redshank from other areas each winter, it seems likely that density-dependent predation has been occurring (Whitfield et al. 1988). In years with high breeding success there will be large numbers of juvenile redshank in the population each winter. Wintering habitat is limited and some of the population (the juveniles, see Chapter 5) will be excluded from favoured areas. Juvenile redshank must then overwinter in sub-optimal habitat where they will be more likely to be preyed on by raptors. Sparrowhawk success rate is dependent on factors such as position of prey with respect to cover (Chapters 4 and 5) so juveniles which feed on the fringes of the estuary are more likely to be killed. Population size will be regulated by density-dependent mortality particularly during periods of cold weather (Whitfield et al. 1988). If there are large numbers of redshank feeding in sub-optimal habitats, competition for limited resources will lead to loss of condition and/or starvation, which will reduce their ability to escape from raptors.

The degree of raptor predation on redshank may not exactly follow the population of redshank. As peregrines and sparrowhawks are generalist predators (Ratcliffe 1980, Newton 1986, Chapters 6 and 7), it would be possible for a sparrowhawk, for example, to locally remove a species entirely, and then shift to alternative prey. Newton (1986) hypothesised that bullfinches (Pyrrhula pyrrhula) may be absent from some areas as they are preferentially selected by sparrowhawks, possibly due to their conspicousness and ease of capture. Similarly, escaped budgerigars (Melopsittacus undulatus) would probably be prevented from forming feral populations, as sparrowhawks would preferentially select this very conspicious species, despite its low abundance.

A species habits may make it preferred prey to a sparrowhawk, even when it occurs in very low numbers, particularly if the sparrowhawk has learnt where to find the species previously (e.g. Dawkins 1971). Those waders which fed in small numbers close to cover, such as snipe and redshank for example, would be encountered by a hunting sparrowhawk more often, and so be more 'available' to be attacked, compared to wader species such as knot which, although available in very large numbers, fed over 1km from cover. Sparrowhawks were most successful at catching redshank in terms of attacks per gram of prey gained (see Chapter 6): redshank were probably the largest prey at Tyninghame that sparrowhawks could catch relatively easily. Redshank were therefore probably preferentially selected compared to other waders (see Table 2, Chapter 6).

Overall, it seems that the redshank population could sustain a high over-winter mortality rate, as those redshank which were killed were excess to the availability of optimal wintering habitat. Most wader mortality occurs during the non-breeding season, in first winter birds (Boyd 1962, Baker 1971). This accords with the idea of density dependance: those juveniles which could not find a suitable vacant over-wintering site were killed through competition for limited resources and/or raptors in sub-optimal habitats. Raptors may in some areas be directly controlling wader populations, as they prevent waders from spreading into sub-optimal areas, although availability of suitable breeding habitat may also be limiting the population size. Redshank are a species which is particularly susceptible to starvation in cold weather periods (Davidson & Evans 1982, Beecroft & Clark 1986) and so competition for food/optimal feeding areas must be intense. Redshank are also a widespread, successful breeding species throughout Britain and Europe, and nest in a broad range of widely available habitats (Sharrock 1976, Cramp & Simmons 1983), although strong patterns of natal philopatry (Thompson & Hale 1989) may suggest that breeding territory is limited. It is possible therefore that redshank are limited in their numbers on their wintering grounds and will show density dependent mortality caused by competition for limited numbers of profitable, low risk feeding areas.

Raptor predation has a major impact on the population of wintering waders at least on a local level. The available evidence shows that raptors are the major cause of mortality in small (less than c180 g) wintering waders and future studies of wintering wader behaviour or ecology must take into account the effects of raptor predation.

CHAPTER 4: ANTI-PREDATION STRATEGIES IN REDSHANK

4.1 Introduction

Wintering waders typically inhabit large open areas without cover to retreat into when they are~~d~~ attacked by a predator. Consequently many wader species such as redshank respond to the presence of a predator by flocking (e.g. Caraco et al. 1980a; Myers 1980; Buchanan et al. 1988, Whitfield 1988). Flocking is thought to have three main anti-predator benefits: "dilution", "confusion" and vigilance. The "dilution" effect occurs because the probability of an individual bird being a victim in one attack on a larger flock is less than in a smaller flock (e.g. Hamilton 1971, Foster & Treherne 1981). The reduced risk of being a victim in a large flock may be offset if larger flocks are preferentially attacked (e.g. if large aggregations are more conspicuous). The "confusion" effect (e.g. Neill & Cullen 1974) is based on the idea that it is easier for a predator to follow any one individual on its own, than an individual surrounded by other possible targets. Testing for both "dilution" and "confusion" benefits requires data on flock size distribution, and predator attack and success rates on different flock sizes. The third major benefit for flocking is increased overall vigilance levels in larger flocks, for a given level of individual vigilance (Pulliam 1973). To analyse vigilance effects it is essential to remove the effects of confounding variables (see Elgar 1989 for a review): for example, high food availability may lead to both large flocks forming and high feeding rates which will then cause low individual vigilance levels.

Despite many studies of anti-predator behaviour (in particular vigilance) that might reduce risk of predation, only a few field studies have actually demonstrated that flocking itself reduces the individual risk of predation (Page & Whitacre 1975; Kenward 1978; Kus 1985). At Tyninghame, redshank mortality rates were high (see Whitfield 1985a and chapter 3) for example over 55% of the wintering population was killed by raptors in 1991-1992. Redshank were therefore studied to determine the individual's risk of predation by raptors within different sized flocks and the factors that were determining this risk.

The distance a predator was from a group of animals when they began to escape (flight-initiation distance) appears to be a measure of the degree of risk perceived by an individual prey animal within the group (assuming detection of the predator is not a factor). Prey will be expected to flee at great distances from a very dangerous predator, but will ignore moderately dangerous predators except when approached very closely. Other factors may moderate flight-initiation distance, and identification of these factors should give an idea of how the prey are assessing their own risk. For example several studies have shown the influence of distance to a predator or cover, and number of individuals in a group on flight-initiation distances . For example, Dill & Houtman (1989) showed that flight-initiation distance of grey squirrels (Sciurius carolinensis), on attack by a remote-controlled predator, increased as distance to safety increased. Dill (1990) showed that African cichlid fish (Melanochromis chipokae) feeding further from cover started fleeing back to cover earlier than those fish initially closer to cover.

Flight-initiation distance in larger groups of juvenile water-striders (*Gerris remigis*) was shorter on approach of a cannabilistic adult (Dill & Ydenberg 1987). In contrast Grieg-Smith (1981) found that barred ground doves (*Geopelia striata*) detected an approaching human long before flight, and that larger flocks tended to fly at greater distances from the 'predator'. At Tyninghame, flight-initiation distance as a measure of perceived prey risk could be recorded in conjunction with factors such as flock size and temperature, by observing raptor attacks and by experimental approaches by a person functioning as a ground predator.

That animals can distinguish between different species of predators is obvious, but there are few empirical field studies that have demonstrated that predator discrimination benefits the prey's survival. Different predators present different risks to a prey species, and prey species respond differently to the presence of different predators. For example, Boyce (1985) found that three large wader species in northern California only exhibited anti-predator evasion behaviour in the presence of large falcon species such as peregrines and prairie falcons (*Falco mexicanus*) but ignored small and non-dangerous merlins. Walters (1990) showed that lapwings (*Vanellus* spp.) discriminate between various types of predators in the field and Buitron (1983) showed that black-billed magpies' (*Pica pica*) responses varied according to the risk different predator species presented to the adults, eggs, or young. Snakes, for example, would only be mobbed or attacked when eggs or newly hatched young were present. Seyfarth et al. (1980) showed that vervet monkeys (*Cercopithecus aethiops*) clearly identified different predators (giving different alarm calls) and reacted to them in a way that appeared to reduce the risk of predation. Ring-tailed lemurs (*Lemur catta*) were also shown to give different alarm calls to different predators when the distance to the predator species (response-urgency) was controlled for (Periera & Macedonia 1991). Ridpath (1972) showed that the Tasmanian native hen (*Tribonyx mortierii*) gave different "pursuit-deterrent" signals (Woodland *et al.* 1980) to different predator species, tail-flicking to ground approaching predators but exclusively wing-flicking to wedge-tailed eagles (*Aquila audax*). Similarly Thomson's gazelles (*Gazella thomsoni*) were more likely to stott in response to coursing predators such as wild dogs (*Lycaon pictus*) than to stalking predators such as cheetahs (*Acinonyx jubatus*; Fitzgibbon & Fanshawe 1988). Curio *et al.* (1983) showed that mobbing great tits (*Parus major*) would approach apparently less dangerous tawny owls closer than sparrowhawks. Tawny owls were classified as being less dangerous because great tits were a smaller component of their diet compared to that of sparrowhawks - this was a poor definition of relative risk.

Observed captures of prey by predators are rare, so most of these studies lack data on whether the changes in response were adaptive. In the present study, frequent observations of attacks and kills by different raptor species were made. The consequences of different escape responses by redshank in terms of capture or escape could be recorded frequently enough to determine whether the alteration of the redshank's response to different predator species was adaptive.

Alarm calls are warning sounds given by a prey in the presence of a predator. There are several hypotheses for their specific function. Alarm calls may serve to warn genetically related neighbours (e.g. Hoogland 1983) according to the hypothesis of kin selection (Hamilton 1964). Alarm calls may prevent a successful attack on an unrelated neighbour which otherwise would lead to the predator returning to the area in the future (as the area would then be recognised as profitable by the predator). Alarm calls may also function as pursuit-deterrent signals, informing a predator that the element of surprise has been lost and consequently its likelihood of capturing the prey has been greatly reduced; both predator and prey avoid a chase (e.g. Hasson 1991). The last two types of alarm calls may be combined as a predator is mobbed (Curio 1978). Redshank give a variety of distinct alarm calls (Cramp & Simmons 1983) but the explicit function of these with respect to predators has not been tested and most observations of redshank alarm calls are in the context of a redshank reacting to the presence of the observer as the potential predator. At Tyninghame it was possible to record the circumstances which led to alarm calls in the presence of avian predators compared to the circumstances of alarm calls to a standardized approach by a human 'predator', in order to test the specific function of alarm calls in redshank.

4.2 Results

4.2.1 'Dilution'

The results from all redshank censuses of flocks occurring on the saltmarsh were combined (Table 1). Single birds and small flocks

TABLE 1: Distribution of redshank flock size classes and raptor attacks upon them on the Saltmarsh Area 1.

Flock Size Class	1	2-5	6-10	11-20	21-30	31-40	41-50	51-60	61-100
No. of Flocks	399	72	69	66	28	17	11	8	7
Flocks Per Census Mean	4.48	1.80	0.78	0.74	0.32	0.19	0.12	0.09	0.08
Standard Error	0.12	0.15	0.08	0.09	0.05	0.05	0.04	0.03	0.03
% Birds in Each Class	7.6	10.7	10.5	19.5	13.6	11.5	9.6	8.5	8.4

n=89 censuses

No. Sparrowhawk Attacks	41	33	40	62	71	62	35	33	40
No. Sparrowhawk Captures	13	5	9	15	5	4	4	4	1
% Captures	31.7	15.2	22.5	24.1	7.0	6.5	11.4	12.1	2.5

n=417 attacks n=60 captures

No. Peregrine Attacks	35	14	5	13	6	5	1	1	3
No. Peregrine Captures	5	1	0	0	0	0	0	0	0
% Captures	14.3	7.1	0	0	0	0	0	0	0

n=83 attacks n=6 captures

were recorded most frequently; most redshank occurred in mid size flocks, e.g. 11-30. The frequency of occurrence of flock sizes was compared to the distribution of raptor attacks on the different flock size classes (Table 1). Larger flocks were attacked preferentially, especially by sparrowhawks (sparrowhawk $x^2=350.8$, $p<0.001$; peregrine $x^2=18.8$, $p<0.05$). The probability of a redshank being captured on attack declined with increasing flock size. Across all attacks individual risk of attack decreases with increasing flock size demonstrating that the 'dilution' effect applies to redshank (Figure 1).

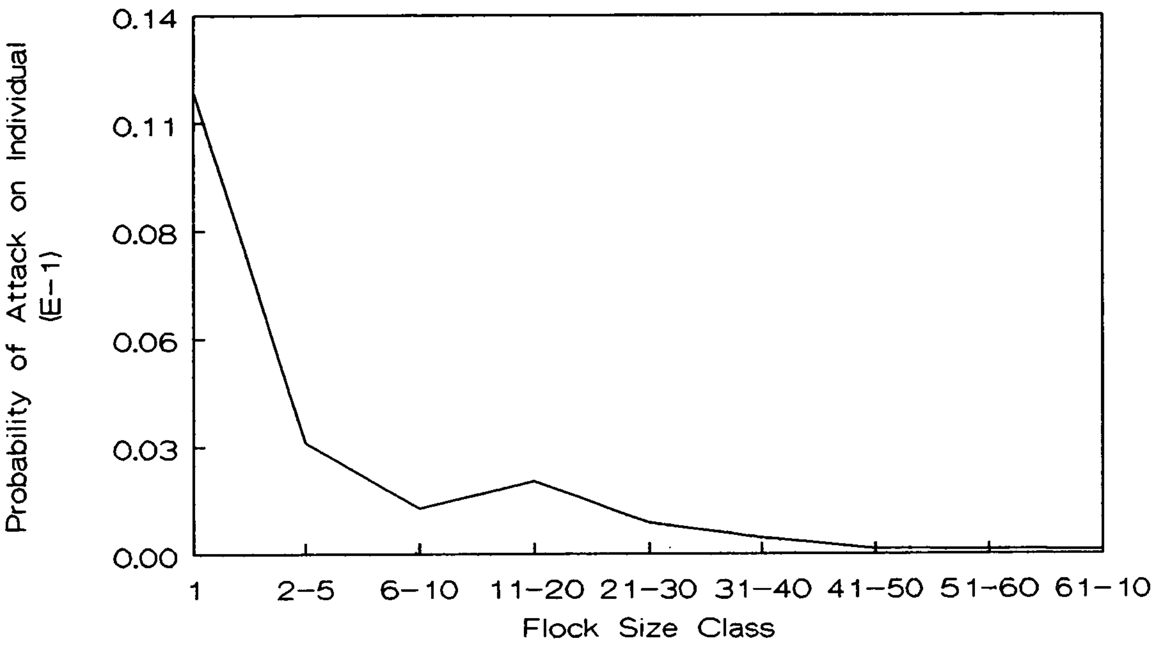
4.2.2 'Confusion'

To remove the confounding variable of increased vigilance in larger flocks leading to an earlier escape response, only non-surprise attacks were used to analyse the 'confusion' effect. Sparrowhawks hunt predominantly by surprise (85%, n=517 redshank attacks); only 5.0% of attacks were second attacks before the sparrowhawk returned to cover. Even in attacks which did not originate from cover, the sparrowhawk's hunting method of keeping close to the ground and redshank's habit of feeding in creeks often made it difficult to assess whether the attacked bird was aware of the sparrowhawk before the attack. For this reason only second sparrowhawk attacks within the same area (less than 50m) and attacks with open approaches at least 1.5m above the ground were included. With peregrines I could confidently classify more attacks as non-surprise (56% n=145). Peregrines made an average of 2.0 attacks per hunt (n=277 hunts all species), and a common hunting tactic was to circle about 10m above

FIGURE 1

THE DILUTION EFFECT

The probability an individual will be attacked within different flock sizes



the estuary to stoop periodically on a bird below (32%, n=145 redshank attacks).

Data on open attacks by peregrine and sparrowhawk were pooled due to the small sample sizes of open captures. There was a significant difference between the capture rate of single birds compared to the capture rate for flocks (G=3.9, n=5/53 captures/open attacks for single birds and 1/69 for flock sizes of greater than one, $p<0.05$). Open attacks where prey is picked on the spot would likely be more vulnerable to the confusion effect than surprise attacks (where prey is preselected). The relative frequency of open attacks (pooled for peregrine and sparrowhawk) on single birds and flocks was compared to the surprise attack frequency to test whether raptors could be compensating for the 'confusion' effect by avoiding flocks. Open rather than surprise attacking sparrowhawks and peregrines were highly significantly more likely to attack a single bird than one in a flock ($x^2=46.0$, n=76/415 surprise attacks single/flock compared with 53/69 non-surprise attacks, $p<0.001$).

4.2.3 Vigilance

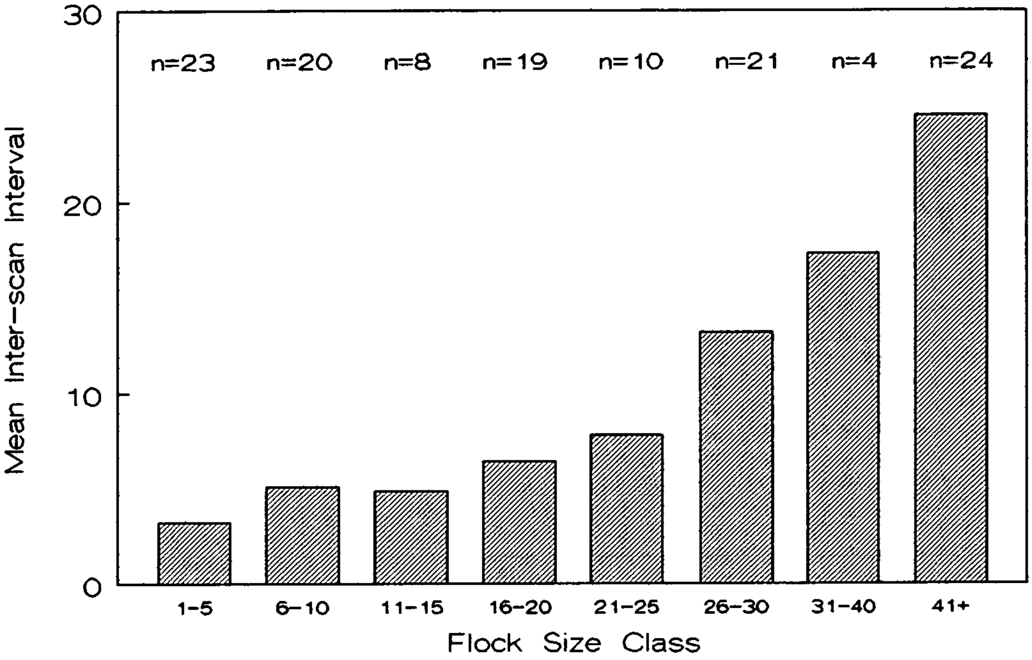
Inter-scan interval increases highly significantly with flock size (Fig. 2; $x^2=399.2$, n=1546 intervals from 129 birds in 22 flocks, Kruskall-Wallis one-way ANOVA, $p<0.0001$).

Stepwise multiple linear regression analyses were carried out on the data collected from areas 1 and 2 separately, to determine which factors correlated with feeding and vigilance rates. Vigilance measures were transformed by Log10 to obtain approximately normal distributions. In the analysis for area 2, invertebrate abundance

FIGURE 2

THE EFFECT OF FLOCK SIZE ON INTER-SCAN INTERVAL

Area 2, Sept-Nov 1990



data were used from the transect quadrats as they were more controlled and comparable from week to week, showing the temporal variability of prey. Analyses using the second set of quadrat data gave similar results. The numbers of all types of invertebrates were combined each week to give an index of total prey availability in the analyses.

In the multiple regression analyses for area 1 (Table 2), flock size was the only variable to correlate significantly with any of the vigilance measures. Feeding rates remained fairly constant over all flock sizes. Feeding success rate was not correlated with any vigilance measures (e.g. T=-0.005; Log10 mean ISI as dependent variable, p=0.99).

In the multiple regression analyses for area 2 (Table 3), the number of swallows was significantly positively correlated only with total number of prey available and not with flock size. Feeding success rate actually declined significantly in larger flocks, as the number of picks increased without any corresponding increase in swallow rate. This would be expected if in larger flocks there was more time to pick due to reduced vigilance, but not if flocks had gathered because of greater prey availability. Flock size was significantly negatively correlated with total prey availability (T=-5.7, n=546, Kendall rank correlation, p<0.001); large flocks formed when there was less prey present within the area.

To eliminate the effect of prey availability on flock size, vigilance samples were analysed from an 11-day period when levels of total prey available in area 2 were approximately constant. On the 15 November 1990 the average number of prey per transect quadrat was

TABLE 2: Multiple regression analysis of redshank vigilance and feeding rates with flock details. Data from saltmarsh Area 1, February-March, winter 1.

n=37 complete cases

Dependent Variables:	Log10 Mean ISI (Inter-scan Interval)		Log10 THU (Time head up)		Log10 NHU (No. head ups)	
	T	Sig.T	T	Sig.T	T	Sig.T
Variable in equation:						
Flock Size	3.3	0.0022	-3.2	0.0027	-3.5	0.0012
Variables not in equation:						
Nearest Neighbour Distance	-0.21	0.84	0.34	0.73	1.6	0.51
Meters to Cover	-0.70	0.49	1.6	0.11	1.2	0.23
Visibility	-0.52	0.60	0.15	0.88	0.76	0.46
Number of Swallows	0.06	0.95	0.63	0.53	-0.12	0.91
Number of Picks	-0.30	0.76	0.34	0.97	0.10	0.92
Mean Daily Air Temperature	-0.77	0.44	-0.17	0.87	0.83	0.41
Time	0.25	0.81	-0.52	0.61	0.48	0.64

Table 3: Multiple regression analyses of redshank feeding rates with flock details. Data from saltmarsh area 2,

October-February, winter 2. n=545 complete cases

1. Dependent variable = Feeding Success Rate (Proportion of picks that resulted in swallows)

	T	Sig. T
Variables in equation:		
Total Prey Number	8.6	0.0000
Flock Size	-3.2	0.0014
Date	-2.0	0.041
Variables not in the equation:		
Time	0.15	0.88
Mean Air Temperature	-0.01	0.99

2. Dependent variable = Number of Picks

	T	Sig. T
Variables in equation:		
Date	6.6	0.0000
Flock Size	2.0	0.04
Variables not in the equation:		
Time	-1.5	0.13
Total Prey Number	-0.016	0.99
Mean Air Temperature	1.7	0.08

3. Dependent variable = Number of Swallows

	T	Sig. T
Variables in equation:		
Total Prey Number	10.3	0.0000
Variables not in the equation:		
Date	-0.43	0.66
Time	-0.22	0.83
Flock Size	-1.2	0.22
Mean Air Temperature	0.90	0.37

10.8, compared to 10.9 for the 26 November; for the quadrats taken in areas where the redshank had been feeding the means were 21.9 compared to 23.0. Within this period 36 2-min samples containing 330 inter-scan intervals were collected from flock sizes varying from three to 100 (grouped into flock size classes as in Fig. 2). Inter-scan interval increased highly significantly as flock size increased (x^2=172.5, Kruskall-Wallis one-way ANOVA, $p<0.0001$). During this period mean daily temperature only varied from 6.0°C to 11°C, with over 80% of the data collected from 6-7°C.

Other possible confounding variables that might have given rise to the observed flock size effect on vigilance were considered separately (following points made in Elgar 1989).

4.2.3.1 Are redshank scanning for predators?

If redshank head-up movements are to scan for predators it is reasonable to expect that head-up rates will increase in the presence of a raptor. If a flock was disturbed or attacked by a raptor, resulting in the redshank flying a short distance within area 2, vigilance rates were recorded for an individual redshank on landing for 3 min and then 10 min later from the start of the first recording period if there were no further disturbances or any change in flock size. In each of nine matched pairs collected vigilance rates (NHU) were lower 10 min after disturbance than immediately after (T=0, Wilcoxon matched pairs test, n=9 pairs, $p<0.01$). Sample sizes are so small as most redshank flock disturbances resulted in a flock size change.

For single birds it is possible that most scanning is looking for other redshank to join (possibly to find good feeding areas as with solitary great blue herons, Ardea herodia, see Krebs 1974). This effect is unlikely to have accounted for the flock size effect on vigilance because, in the analysis for area 1, no flock sizes of fewer than five could be included (despite their almost continual vigilance) as none remained in one area for more than 10 min to satisfy my 'vigilance decay' criterion.

4.2.3.2 Competition within the group

A decrease in vigilance in larger groups may be due to increased competition between individuals. No aggressive interactions were ever seen between redshank in areas 1 and 2 but feeding interference was occurring in larger flocks in area 2 (because feeding success rate declined significantly with increasing flock size, independent of prey availability). The effect of feeding interference was tested further by taking matched pairs from the feeding data collected in area 2, comparing birds of nearest neighbour distance of 1-3 and greater than 5 body lengths. There was no significant difference in success rate between birds feeding close together and more spread out ($z=-0.12$, Wilcoxon matched pairs, $n=108$ pairs, $p=0.91$), suggesting that the redshank within a flock distributed themselves so that feeding interference was uniform.

4.2.3.3 The 'edge' effect

Birds at the edge of a flock are assumed to be more at risk and so are more vigilant. Large circular flocks have a relatively smaller circumference and so relatively fewer edge to centre birds leading to a reduced overall vigilance level (e.g. Jenning and Evans 1980). Redshank at Tyninghame usually fed in lozenge shaped flocks so that most birds could be considered as on the edge. When circular flocks with distinct edge and centre birds were observed in area 2, there were no significant vigilance differences between edge and centre birds (THU T=56, n=17 pairs; NHU T=32, n=11 pairs; mean ISI, T=21, n=11 pairs, Wilcoxon matched pairs). However sample sizes were small and the differences in position between the edge and centre birds was often only 10-15m.

4.2.3.4 Individual variation in foraging behaviour

Murton et al. (1971) showed that pigeons of poor foraging ability tended to occur on their own or in small flocks. Redshank in smaller flocks had a similar or higher feeding rate than those in larger flocks.

4.2.3.5 Age

No interactions according to age were recorded; data from area 1 came entirely from juvenile birds and almost entirely from juvenile birds in area 2. From November winter 2 onward, in area 2, feeding rates were compared between adults and juveniles taking matched pairs where flock size and nearest neighbour distance (+/- 1 body length) was constant. There was no significant difference between feeding success rates in adults and juveniles throughout the winter ($z=-0.46$, $n=73$ pairs, Wilcoxon matched pairs, $p=0.97$) or in November only ($z=-0.23$, $n=29$ pairs, $p=0.82$). Age specific differences found in redshank (Whitfield 1985b and see Chapter 5.2.5), and other wader species (e.g. Metcalfe & Furness 1984; Whitfield 1985b) were associated with adult early season experience or spring pre-migratory feeding; my period of feeding and vigilance data collection appears to have missed these effects. Data in Chapter 5 shows adults were more efficient at feeding than juveniles in some habitats early on in the winter (September).

4.2.3.6 Distance from cover

Raptors attacked redshank from all directions in area 2 (Figure 3); although the majority of attacks came from 'cover' (sea-buckthorn adjacent to the saltmarsh), there was no significant difference between the frequency of attacks coming from the 'open' (flat saltmarsh for over 200m) or from 'cover' (x^2=2.8, 1df, n=127 attacks, p=0.10) or the rate of capture from the two different directions (g=0.32, 1df, 3/51 from 'open' compared to 6/67 from 'cover', p=0.6).

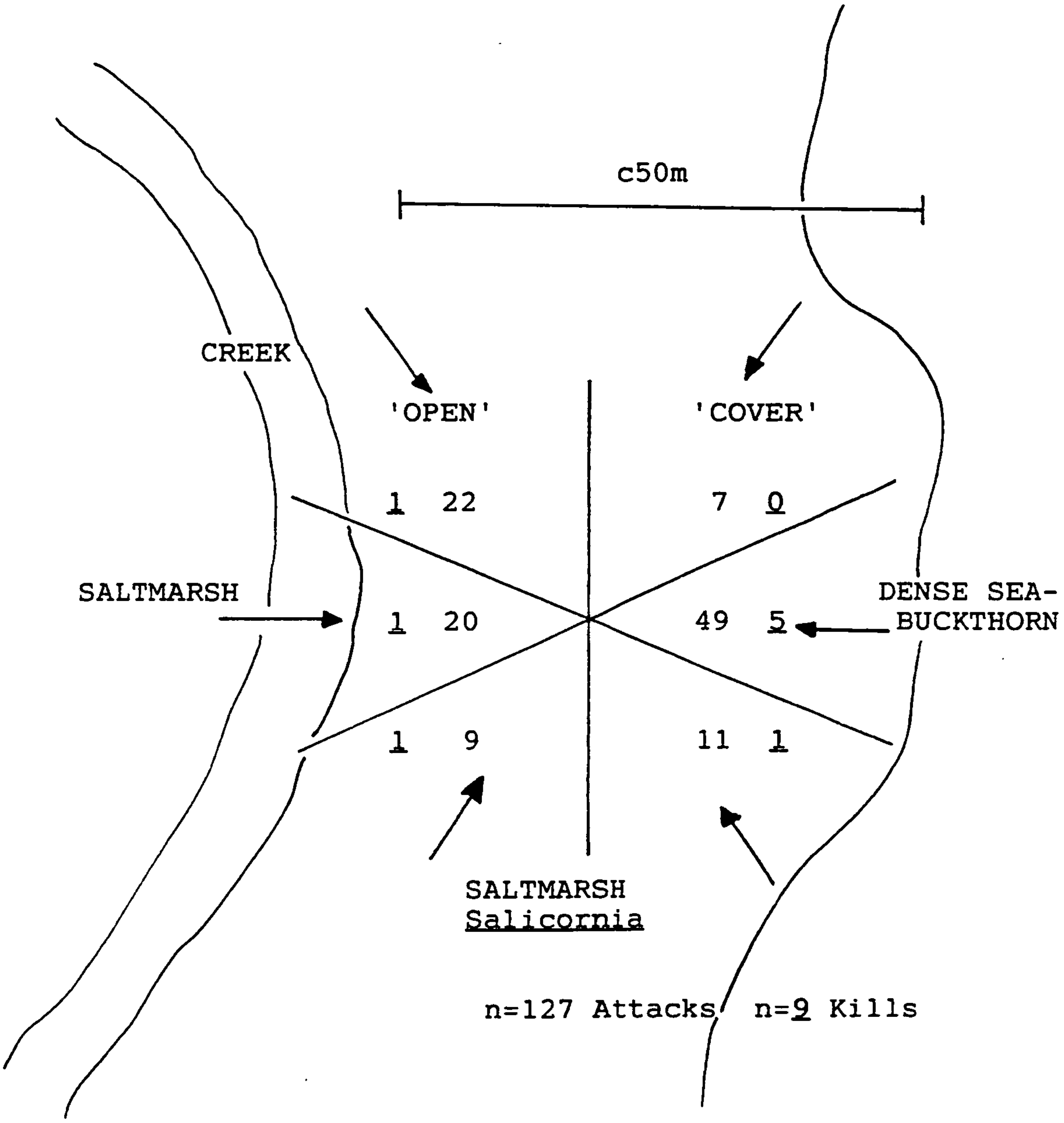
4.2.3.7 Temperature

Temperature was probably excluded as a variable affecting vigilance only because vigilance data were collected in area 1 over a narrow range of relatively high temperatures. Vigilance data (Number of head ups: NHU) from flock sizes of 19-25 in area 2 collected in September winter 2 (x=12.7+/-0.39 ^{o}C) was compared with data from two of the coldest days in February winter 2 (x=1.7+/-0.05 ^{o}C). There was a highly significantly reduced NHU at the lower temperature (z=-5.4, n=41 Mann-Whitney U test, p<0.0001). The data from February were taken at the end of a sustained very cold period, at the peak of recorded deaths by starvation.

4.2.3.8 Visibility

Metcalfe (1984) showed that the degree of visual obstruction within the habitat affected vigilance rates in two wader species. The degree of visual obstruction in area 2 was constant due to the very uniform layer of Salicornia and channel wrack. In area 1,

FIGURE 3:


c50m
CREEK
'OPEN'
'COVER'
1 22
7 0
SALTMARSH
1 20
49 5
DENSE SEA-
BUCKTHORN
1 9
11 1
SALTMARSH
Salicornia
n=127 Attacks n=9 Kills

although variable, the vegetation seemed to be always high enough to prevent clear scanning while feeding. Visibility was almost certainly the factor which determined the very low head up rate of redshank feeding on the open mud of area 3. Visibility was the most significant variable correlating (negatively) with vigilance rates in a multiple regression analysis combining data from all areas (for example mean ISI $T=-0.47$, $p<0.0001$, $n=72$ complete cases). However, comparisons across habitats are less valid due to differences in prey and feeding methods.

Considering all of these variables, it is reasonable to conclude that the reduced individual vigilance observed in larger flocks is a direct consequence of flock size, although other factors, in particular prey availability, also affect it.

4.2.4 Vigilance Benefits

If individual vigilance rates are put into probability models such as Pulliam's (1973) the overall probability that at least one individual will be looking up at any one time is greater in larger flocks, despite a decrease in individual vigilance rates. Pulliam's model is appropriate for redshank because its main assumptions appear to apply. Sparrowhawks are surprise hunters, emerging from cover to make a rapid approach at a flock. Redshank head up periods were typically very rapid, when feeding undisturbed, typically less than one second ($x=0.80s+/-0.03$ from $n=77$ 3min samples). The values may be artificially high due to the difficulty of starting and stopping a stop-watch quickly enough. The mean length of a head up period became significantly smaller with increased flock size, e.g.

flock size class 6-10 mean length THU=0.91 seconds, 61+ mean length THU=0.59 seconds, ($x^2=15.9$, Kruskall-Wallis one-way ANOVA from n=77 3min periods, $p<0.002$). Elgar & Catterel (1981) discuss the implications of this violation of the assumption that head ups are of negligible length; there will be a slight increase in probability of detection at larger flock sizes (when the probability of detection is already high). The frequency distributions for all inter-scan intervals recorded (in Fig. 2) were highly significantly different from a Poisson distribution, for each flock size class (seven out of eight classes $p<0.001$, the other $p<0.01$, Kolmogorov-Smirnov goodness of fit test). I have therefore used the actual inter-scan distributions for each flock size, to obtain the probability that a bird will have its head down for a defined length of time, rather than the Poisson probability function used by Pulliam. I have no good data on whether head ups were independent between flock members, but casual observation suggested that they were.

As flock size and distance to cover increased so did the probability that at least one bird would have its head up and so detect an approaching sparrowhawk (Fig. 4). Above flock sizes of about 30, the probability of detection fell when flocks were very close to cover. To analyse for vigilance effects on raptor capture rate, only surprise attacks by sparrowhawks were considered. An attack was highly significantly more likely to result in a capture on a small rather than a large flock ($x^2=20.3$, n=426 attacks, n=64 captures, Kruskall-Wallis one-way ANOVA, $p<0.0001$: Table 4). This result applies if distance to cover is controlled for (see Chapter

FIGURE 4

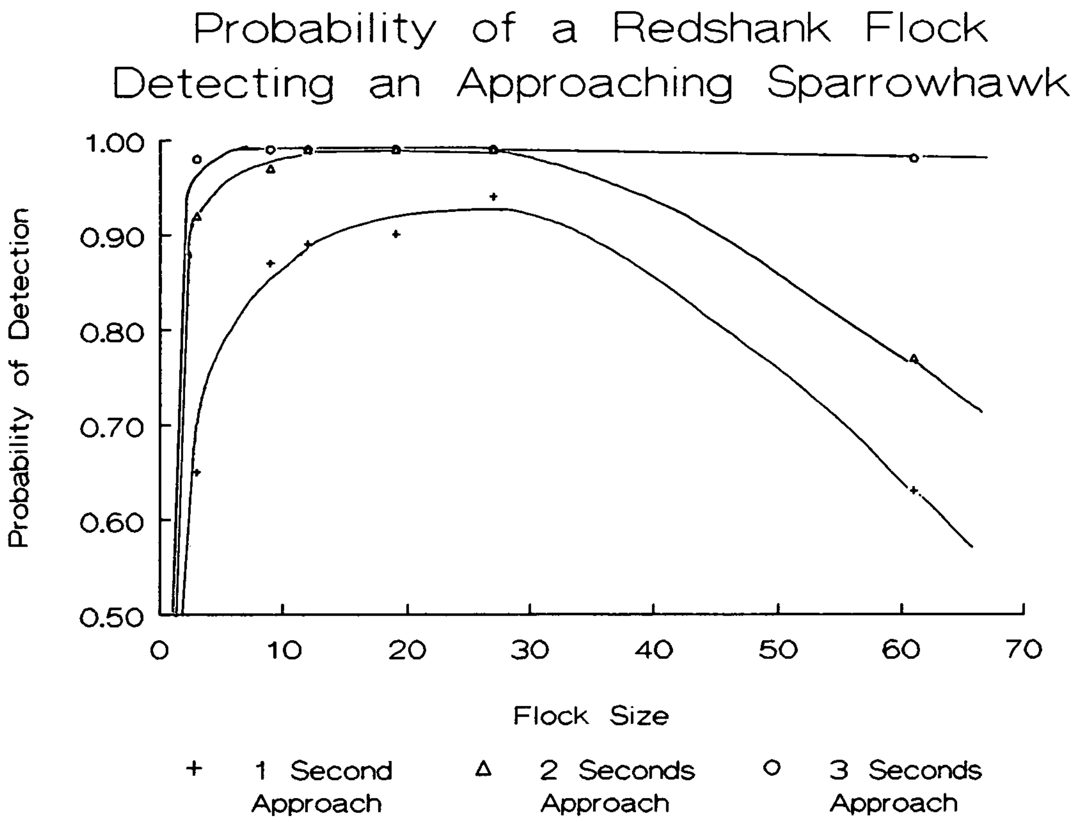

Probability of a Redshank Flock
Detecting an Approaching Sparrowhawk
Probability of Detection
1.00
0.90
0.80
0.70
0.60
0.50
0
10
20
30
40
50
60
70
Flock Size
+ 1 Second Approach
Δ 2 Seconds Approach
O 3 Seconds Approach

TABLE 4: Raptor attacks upon Different Flock Size Class Over the Whole Estuary

Flock Size Class	1	2-5	6-10	11-20	21-30	31-40	41-50	51-60	61+
No. Sparrowhawk Surprise Attacks	44	37	42	62	71	62	35	33	40
No. Sparrowhawk Surprise Captures	13	9	9	15	5	4	4	4	1
% Successful Surprise Attacks	29.5	24.3	21.4	24.1	7.0	6.5	11.4	12.1	2.5
n=426 attacks n=64 captures									
No. Sparrowhawk Open Attacks	11	7	2	3	5	4	5	1	5
No. Sparrowhawk Open Captures	1	0	0	0	0	0	0	0	0
n=43 attacks n=1 captures									
No. Peregrine Surprise Attacks	32	9	3	8	5	5	1	0	3
No. Peregrine Surprise Captures	1	1	0	0	0	0	1	0	0
% Successful Attacks	6.3	11.1	0	0	0	0	0	0	0
n=66 attacks n=3 captures									
No. Peregrine Open Attacks	42	15	5	9	4	1	2	1	0
No. Peregrine Open Captures	4	1	0	0	0	0	0	0	0
% Successful Attacks	9.5	6.7	0	0	0	0	0	0	0
n=79 attacks n=5 captures									
TOTAL SPARROWHAWK ATTACK SUCCESS RATE	25.4	20.5	20.5	23.1	6.6	6.1	10.0	11.8	2.2
n=469 attacks n=65 captures									
TOTAL PEREGRINE SUCCESS RATE	6.7	8.3	0	0	0	0	-	0	0
n=145 attacks n=8 captures									

5, Figure 3B; e.g. for attacks on flocks at less than 10m to cover, $x^2=19.1$, n=35 attacks, n=15 captures, Kruskall-Wallis one-way ANOVA, $p<0.0001$; the largest flocks rather than mid-size flocks had the lowest probability of capture contrary to the predictions of the probability of detection very close to cover). An attack was significantly more likely to succeed if the flock was closer to cover ($x^2=20.8$, n=287 attacks, n=50 captures, Kruskall-Wallis one-way ANOVA, $p<0.0001$: Chapter 5, Fig. 3A). The success rates of attacks occurring within a flock size class at less than 15m to cover were matched with success rates of attacks within the same flock size class at distances from cover of greater than 15m (15m was chosen to spread the number of captures most equally for comparison). In all pairs success rate was greater closer to cover (T=0, $p<0.01$ Wilcoxon matched pairs test, n=9 flock size classes).

Although the 'confusion' effect cannot be eliminated as a confounding variable, it is likely that the increased probability of capture when smaller flocks were attacked was a direct consequence of the vigilance benefits in larger flocks as broadly predicted by Pulliam's model. In at least 19 (29%) of captures the redshank was caught on the ground, and a further 8 (13%) captures involved birds that were chased away from the flock (Whitfield 1985a observed a similar pattern). In at least 42% of cases late detection of an approaching sparrowhawk was the cause of capture, although the victim in these cases may have been chosen by the sparrowhawk in order to minimise the 'confusion' effect.

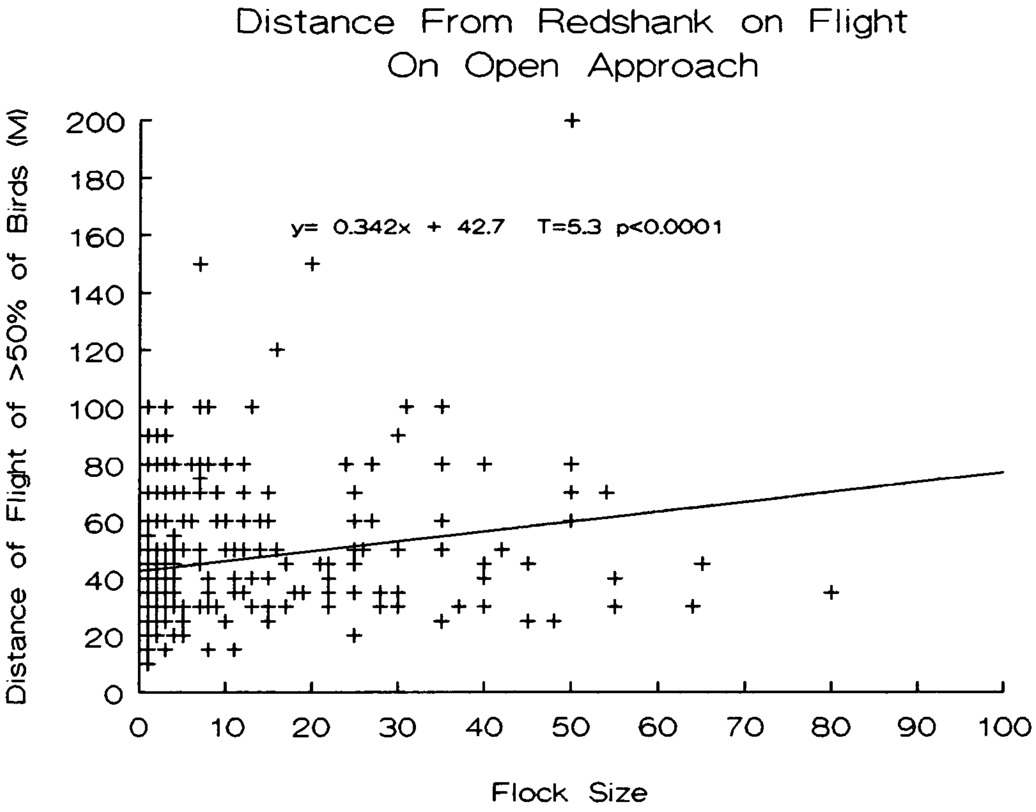
4.2.5 Approach Distance

I tested whether redshank in larger flocks reacted sooner than those in smaller flocks in 103 cases of reaction to an approaching sparrowhawk. A discriminant function analysis was carried out, with three variables - flock size, distance of first appearance, and distance of flight from the sparrowhawk. A flock was more likely to fly instantly if a sparrowhawk appeared closer to it ($F=13.0$, $p<0.001$, $n=103$), and if it was small ($F=5.5$, $p<0.025$, $n=103$). The frequencies of instant and non-instant flights were compared using only cases where the sparrowhawk appeared initially at less than 35m, in order to determine if the probability of detection was responsible for smaller flocks being more likely to respond instantly on appearance of a sparrowhawk. Flocks of around 30 were more likely to detect an approaching sparrowhawk when approach distances were small (Fig. 4). The frequencies of non-instant and instant responses were not significantly different when the data were split into two flock size classes of 21-39, and 1-20 pooled with 40+ ($x^2=0.04$, 1df, $n=43$ responses at less than 35m initial appearance of the sparrowhawk, $p=0.84$). The results suggest that the smaller flocks were not more likely to fly because of earlier detection; rather it seems that larger flocks were delaying flight after detection.

The importance of flock size on response distance to predators was tested by approaching flocks of redshank as an experimental ground predator. During winter 3, 488 approaches were made towards different sized redshank flocks. A multiple regression analysis was carried out to determine which continuous variables were correlated with the distance of my approach from the flock at which more than half the redshank flew. Distance of approach was approximately normally distributed and was the dependent variable. Flock size, time of day, days since the first of August and the mean daily temperature over the last three days were put into a regression equation and deleted stepwise. The mean temperature over the last three days was used as this was assumed to be a reasonable time period over which the redshank will have estimated its risk of starvation prior to the approach. There were significant correlations between approach distance and temperature whatever time period was chosen to average temperature over. The significance of the correlation increased as the time period of average temperature was increased: Spearman's Rank correlation, approach distance with mean daily temperature T=7.7; the previous day's temperature T=8.5; the last three days' mean temperature T=9.8; the last 7 days' mean temperature T=10.2; and the last 14 days mean temperature T=10.6. Only open approach data were used (n=413 cases) as distance of flight was a function of defining a surprise approach (an escape flight could only be classified as a surprise if approach distances were very short).

Using cases from all locations the most significant factor correlating with distance of approach was temperature (closer approaches at lower temperature; T=10.5, $p<0.0001$, Fig. 6), with flock size also a significant factor in the equation (closer approaches to larger flocks; T=5.3, $p<0.0001$). The regression equation with flock size, although highly significant, has a very slight gradient. In real terms there was only a very slight increase

FIGURE 5


Distance From Redshank on Flight
On Open Approach
y= 0.342x + 42.7 T=5.3 p<0.0001
Distance of Flight of >50% of Birds (M)
0
20
40
60
80
100
120
140
160
180
200
Flock Size
0
10
20
30
40
50
60
70
80
90
100

in the probability of a larger flock allowing a person to approach more closely. Days since the first of August did not significantly correlate with approach distance (T=0.35, p=0.72) showing that the decrease in the distance at which the redshank would fly from a person was not due to simply to habituation. Time of day was also not correlated with approach distance (T=1.3, p=0.21). Flocks sizes were not randomly distributed according to location, with few flocks of more than about 5 birds found in rocky shore, saltmarsh creek or mussel bed habitats. The significant correlation of flock size and approach distance may then have been an effect of sampling unequally between locations. A further backwards deletion regression analysis was carried out controlling for location, by using only open approaches on the saltmarsh grass. There was still a significant positive correlation between approach distance and temperature ($y=3.6x + 26$, $T=8.6$, $p<0.001$) but there was no significant correlation with flock size (T=0.40, p=0.69). This result was confirmed using a hierarchical loglinear analysis of all of the human approach data with location as an included variable (for details see alarm call section 4.2.9 below): there was no significant effect when flock size and approach distance were removed from the saturated model (partial $x^2=47.4$, 44DF, p=0.26).

4.2.6 Redshank Responses on Attack

In total I observed 696 raptor attacks and 73 captures of redshanks in which the redshank's response was seen clearly. The null hypothesis that the relative response frequencies on attack was independent of raptor species was rejected (Tables 5 and 6).

TABLE 5: Proportion of escape responses by redshank on attack which led to capture or escape.

Response Type	Ground/Crouch	Creek Dive	Fly
SPARROWHAWK Attacks			
Captures	19	10	32
Escapes	2	41	396
Total Responses	21	51	428
% Responses that resulted in captures	90.5	19.6	7.5
PEREGRINE Attacks			
Captures	1	1	8
Escapes	40	51	48
Total Responses	41	52	56
% Responses that resulted in captures	2.4	1.9	14.3
MERLIN Attacks			
Captures	2	0	0
Escapes	7	6	32
Total Responses	9	6	32
% Responses that resulted in captures	22.2	0	0

Table 6: Escape responses by redshank on different types of attack by sparrowhawk, peregrine or merlin.

Response	Ground/ Crouch	Creek Dive	Fly
SPARROWHAWK:			
Surprise	1	28	364
Non-Surprise	0	6	37
Stoop	1	5	10
PEREGRINE:			
Surprise	20	18	25
Non-Surprise	3	15	10
Stoop	17	18	12
MERLIN:			
Surprise	7	6	29
Non-Surprise	0	0	0
Stoop	0	0	1

Sparrowhawk compared to peregrine, G test g=129.7, p<0.0001, alpha=0.016; sparrowhawk compared to merlin, G test g=13.0, p<0.01, alpha=0.05; and peregrine compared to merlin, G test g=14.7, p<0.001, alpha=0.025; all tests 2df, sequential Bonferroni K=3). Redshank responded by taking flight on 86% of sparrowhawk attacks, compared to 38% on peregrine attacks and 68% on merlin attacks. On attack by a peregrine a redshank would more frequently creek dive, (35%), or crouch on the ground, (28%), than on sparrowhawk attack (10% and 4% respectively) or on merlin attack (13% and 19% respectively).

Both peregrine and sparrowhawk used a variety of attack strategies. To test the relative importance of attack type compared to species of raptor, escape responses were split by type of attack (Table 6; sample sizes of attacks are smaller than in Table 5 as not all attacks could be classified discretely) and a saturated hierarchical log-linear model was used with backwards deletion of factors. Response depended significantly on raptor species (change in likelihood-ratio x^2=145.5, 4df, p<0.0001) and attack type (change in likelihood-ratio x^2=19.0, 4df, p<0.001).

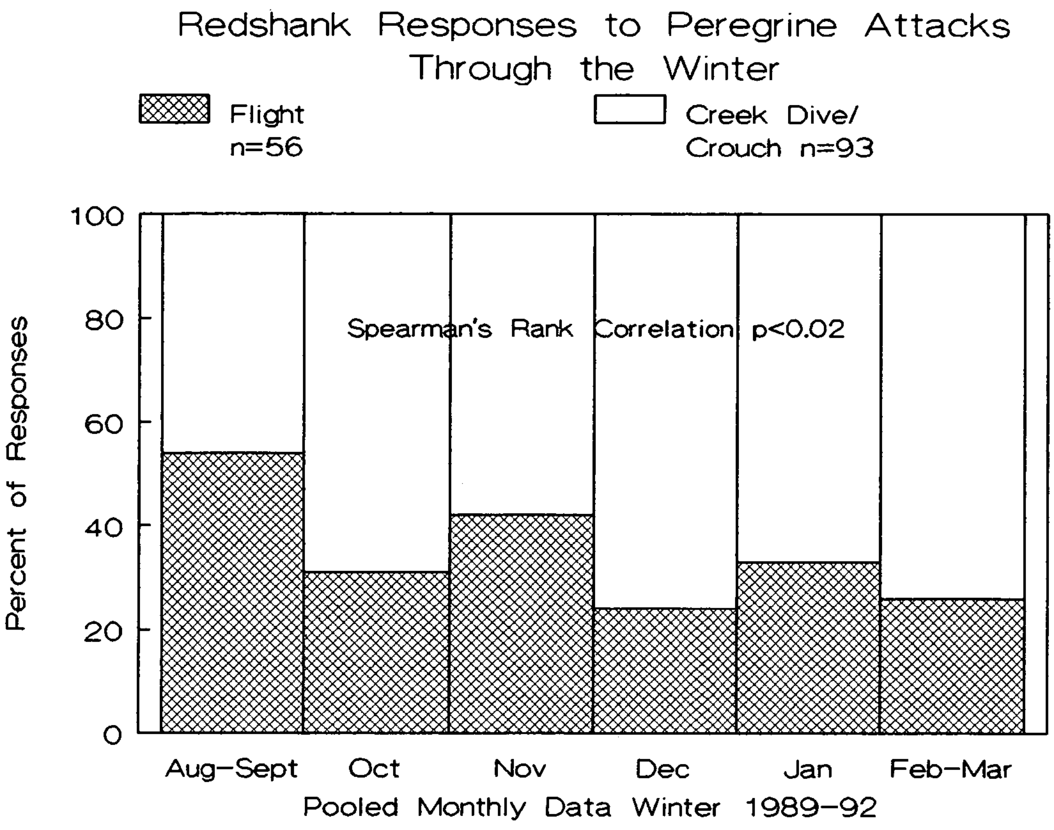
I estimated the relative risk of each escape response on attack by calculating the percentage that resulted in capture (Table 5). The null hypotheses that the probability of capture on attack was independent of response, for attacks by a single raptor species were rejected in all cases of reasonable sample size. On attack by sparrowhawks, the capture rate was: fly 7%, creek dive 20% and ground/crouch 90% (fly vs creek dive G=6.4, p=0.02, alpha=0.05; fly vs ground/crouch G=72.0, p<0.001, alpha=0.016; creek dive vs ground/crouch G=32.5, p<0.001, alpha=0.025; all tests 1df, sequential Bonferroni K=3). For attacks by peregrines and merlins sample sizes of observed captures were small and so response data were pooled into the major difference of response: either staying on the ground (combining creek-diving and ground/crouch) or flying. On attack by peregrines the capture rate was: ground 2% and fly 14% (G=7.7, 1df, p<0.01). On attack by merlins the capture rate was: ground 15% and fly 0% (Fisher's Exact Test, 1df, p=0.10).

The null hypothesis that capture rate was independent of raptor species for the same response by the redshank was tested. A sparrowhawk was more likely than a peregrine to catch a redshank on the ground (G=53.6, p<0.001, alpha=0.017) or when creek-diving (G=9.2, p<0.01, alpha=0.025); there was no significant difference in their relative rate of capture for a flying redshank (G=2.5, p=0.11, alpha=0.05); all tests 1df, sequential Bonferroni K=3.

4.2.7 Changes in Responses to Peregrine Attack through the Winter

The relative frequencies of redshank responses (either flight or ground crouch and creek diving) on attack by peregrine were compared by month (Figure 6). Responses were pooled from the three winters. From August to February there was a significant decrease in the frequency of flying or staying in flight on attack. A redshank which flew on peregrine attack was much more likely (14.3% capture rate) to be captured than one which responded by ground crouching or creek diving (2.2%). Therefore the frequency of inappropriate responses declined through the winter.

FIGURE 6


Redshank Responses to Peregrine Attacks
Through the Winter
Flight
n=56
Creek Dive/
Crouch n=93
Percent of Responses
0
20
40
60
80
100
Spearman's Rank Correlation p<0.02
Aug-Sept
Oct
Nov
Dec
Jan
Feb-Mar
Pooled Monthly Data Winter 1989-92

4.2.8 False Alarm Flights

In 215.4 hours of watching redshank flocks in area 2 there were 170 raptor alarms (90 of these being attacks), 115 alarms to birds other than raptors (non-raptor alarms), and 572 no-cause alarms. Over 75% of the 913 alarm flights (some alarms consisted of more than one flight) were false alarm flights. Data from the 138.1 hours of flock watches used to analyse the effect of flock size on the rate of false alarm flights (Table 7), and was analysed using Kendall's rank correlation. In winter 2 the rate of false alarm flights was found to significantly decrease with time of year ($t=-0.33$, $n=77$ flock watch periods, $p<0.001$ for days since September) and significantly increase with temperature ($t=0.31$, $n=77$ flock watch periods, $p<0.001$), but not in winter 1 ($t=0.15$, $n=28$ flock watch periods, $p=0.26$ and $t=0.24$, $n=28$ flock watch periods, $p=0.08$ respectively).

4.2.9 Alarm Calls

Overall the frequency of alarm calls (not including contact calls) was low. An alarm call was recorded in only 36.0% ($n=913$) of alarm flights during 215.4 hours of redshank flock watches. Redshank were significantly more likely to give an alarm call in the pre cence of a raptor. An alarm call was heard in 53.0% of raptor alarms ($n=170$) compared to 31.1% ($n=572$) for no-cause alarms during redshank flock watches ($G=26.2$, 1df, $p<0.001$). Opportunistic data on redshank response to raptors at less than 100m away showed that an alarm call was significantly more likely to be heard if the raptor was attacking the flock: in 47.6% of attacks ($n=82$) an alarm call was heard compared to 19.5% of sightings of a raptor close to a

Table 7: Mean period between false alarm flights with flock size

Flock Size	10-20	21-30	31-40	41-50	51-60	61-70	71+
1989-90:							
Mean	12.9	9.0	19.1	16.2	31.7	17.2	17.0
SE	-	2.0	2.2	4.8	14.0	4.4	8.0
n	1	5	5	4	5	6	2
n=28 samples, total 2,615 minutes							
1990-91:							
Mean	25.6	30.4	30.6	30.8	39.0	40.7	25.8
SE	3.9	4.3	6.5	7.8	12.3	10.4	3.8
n	22	23	14	9	7	4	9
n=88 samples, total 5,671 minutes							
Total 1989-91;							
Mean	25.0	26.6	27.5	26.3	35.9	26.6	24.2
SE	3.8	3.8	4.9	5.8	8.9	6.0	3.5
n	23	28	19	13	12	10	11
n=114 samples, total 8,286 minutes							

flock but not attacking (n=82); G=14.7, 1df, p<0.001. This was probably a function of proximity as attacking raptors came closer to the flock. Redshank were significantly more likely to give an alarm call when approached closely by a sparrowhawk: an alarm call was heard in 75% of approaches of less than 10m (n=20) compared to 45% (n=40) of greater than 10m (G=4.9, 1df, p<0.05). Sample sizes were small here due to the difficulty of being totally sure about the approach distances coincident with being in a close enough position myself to be sure of hearing any call made. Alarm calls were almost invariably after the redshank took flight away from the raptor: only 1 out of 54 alarm calls (recorded under good enough conditions to be sure of this) was heard before the flock took flight.

Redshank were found to give a call on approach by a human far more frequently than on approach by a raptor. In 78.5% of approaches (n=488), by a single human at a redshank or group of redshank, a call was made by the redshank flying away compared to only only 47.6% of direct raptor approaches (n=82 raptor attacks): G=30.9, 1df, p<0.001). Redshank were more likely to give an alarm call when attacked by a sparrowhawk (55%, n=60) than a peregrine (20%, n=10): G=4.2, 1df, p<0.05.

A hierarchical loglinear analysis was carried out on 488 approaches I made towards redshank in order to determine which variables were coincident with alarm calls. Six variables were included: flock size (7 levels, 1-10 11-20, 21-30, 31-40, 41-50, 51-60, 61+), distance of flight from me of >50% of the redshank (4 levels, <20m, 21-40, 41-60, 61+m), age (2 levels, adult and juvenile), location (5 levels, categories in methods), approach type

(2 levels, surprise and open) and alarm call type (3 levels, none, contact and alarm). Groups of variables were then removed to determine which variables were significant components of the saturated model. The highest significant level of interaction was at the 2-way level (x^2=1046, 3338 df, test that 2-way and higher order effects are zero, p=0.99). There were three significant 2-way interactions: location and call type (partial x^2=33.7, 8df, p<0.0001); location and age (partial x^2=85.2, 4df, p<0.0001); and call type and age (partial x^2=9.0, 2df, p<0.02). The main determinant of whether a redshank gave an alarm call was location: 55.5% of rocky shore approaches (n=137) resulted in an alarm call being heard, 34.8% of mud/beach approaches (n=46), 38.0% of saltmarsh creek approaches (n=79), 5.3% of saltmarsh grass approaches (n=150), and 67.1% of mussel bed approaches (n=76). The frequency of contact calls heard on approach was more similar across the habitats but more frequent on the saltmarsh, and less frequent on the mussel beds: 35.8% rocky shore, 47.8% mud/beach, 40.1% saltmarsh creek, 55.3% saltmarsh grass, and 21.1% mussel beds. Adults were more likely to give an alarm call on approach compared to juveniles (59.8% to 38.4% respectively), but juveniles were more likely to give a contact call (43.7% compared to an adult frequency of 26.4%). The frequency of no calls being made on approach was approximately equal between adult and juveniles (13.8% compared to 17.9%; n=87 adult approaches and n=151 juvenile approaches). A redshank was most likely to make an alarm call on approach if it was an adult on the rocky shore or mussel beds. The significant

interaction between age and location was due to the segregation of adult and juvenile redshank according to habitat (see Chapter 5).

4.3 Discussion

Vigilance benefits in large flocks of redshank (over 38% of redshank on average were in flock sizes of greater than 30) were very small because the probability of detection was already very high, except when a flock was close to cover. The nature of the saltmarsh habitat and the hunting behaviour of the sparrowhawks probably meant that many flocks were effectively much less than 30m to some sort of cover (such as creeks). Therefore even large flocks were still subject to changes in the probability of detecting a predator with increasing flock size as shown by Pulliam's model. The inter-scan intervals were distributed so that the probability of detecting a predator actually decreased with large flocks close to cover, although the capture rate was apparently not affected by this. Within these larger flocks the "confusion" effect must be the main factor in reducing rate of capture. Vigilance benefits alone cannot explain large flock size in many waders: Myers (1984) pointed out that vigilance in waders reaches an asymptote at intermediate flock sizes. Many wader species feed in very open situations where the probability of detecting a predator even in small flocks is very high; the 'dilution' and 'confusion' effects would seem to be the main reason for flocking.

According to Pulliam's model the probability of a redshank flock detecting a predator would be expected to peak at mid-flock sizes. My measures of probability of detection did not show this expected peak: mid-size flocks reacted no sooner to a close attacking sparrowhawk and the rate of false alarm flights was approximately constant over all measured flock sizes (>10). Without simultaneously focal sampling all redshank within a flock it is difficult to measure directly the probability of detection but false alarm flight rate is probably a good indirect measure. The probability of making a false alarm flight will reflect the probability of detection if there is a constant level of stimuli which might be mistaken for raptors (such as low flying curlews) and the probability of a redshank flying as a result is uniform over different flock sizes. The first assumption that the level of stimuli was constant was controlled for by only taking data from the same small area over a long time period: visibilty, distance to cover and proximity to other birds was a constant. The second assumption of an equiprobable response across different flock sizes probably did not apply. Redshank within larger flocks were less likely to fly instantly on appearance of a sparrowhawk and so would be less likely to respond to very brief stimuli, which would cause a small flock to respond instantly. Despite this it seems reasonable to infer that a change in the rate of false alarm flights with flock size was a good measure of change in the probability of detection in redshank, with the expectation that rate of false alarm flights would decrease with increasing flock size independently of probability of detection.

Probability of detection as measured by rate of false alarm flights was higher than expected for the mean levels of individual vigilance in large flocks (>30) and despite the effect of larger flocks being less willing to fly instantly: the rate of false alarm flights did not decline in larger flocks. A decrease in the probability of detection in larger flocks may be compensated for by the fact that larger flocks may have an 'increased propensity to startle' due to interference competition reducing profitability at a marginal feeding site (Stinson 1988). Interference competition was occurring in the redshank flocks from which the false alarm rates were taken, but the flocks returned to the same area afterwards. Alternatively Grieg-Smith (1981) suggested that responsiveness by flock members might be greater in the presence of one or more particularly 'nervous' individuals, and the probability that a flock would contain at least one 'nervous' bird would increase with flock size. Predictions of probability of detection based on mean vigilance rates would be much lower than the actual probability of detection (and consequent rate of false alarm flights) which would be dependent on the very vigilant individuals.

Redshank may be able to assess some intra-individual vigilance variation. For example large flocks tended to have more redshank at any one time which were joining or leaving the flock. These birds, on arrival, tended to be highly vigilant for the first few minutes compared to birds that had been in the flock for several minutes (and from which basal vigilance levels were recorded). The pattern of vigilance decay over several minutes was very similar to that for birds in a flock after a raptor attack or disturbance flight. An individual within the flock could monitor the rate of change in flock size to determine if there were new, more vigilant individuals joining the flock. Established flock members, which were aware of local risks specific to each flock at any time, could afford safely to parasitise newly arrived flock members' vigilance. New arrivals probably always have to be initially very vigilant as they would not be aware of the local risks such as the presence of a raptor perched inconspicously nearby. A new flock member would also have to scan more in order to determine the scanning rate of its neighbours.

With redshank, rate of false alarm flights remained constant despite the risk of predation decreasing uniformly with increasing flock size. This suggests that redshank can only partly assess the probability of detection by the flock they are feeding in. Flock size can be easily assessed and a default, 'safe' level of individual vigilance can probably be determined. In most flocks however, the probability of detection was probably actually dependent on the presence of more vigilant, 'nervous' individuals. The presence of these individuals would be difficult to assess and would not be guaranteed in any flock, but was probably dependent on flock size. Flock size was probably being used by an individual redshank as a guide to the probability of a flock containing 'nervous' individuals as well as the probability of being killed by a raptor, as the observed relationship between inter-scan intervals to flock size was so strong. Where particularly vigilant individuals can be identified easily, such as gulls within mixed flocks of waders, then responsiveness by the waders to alarms will reflect the gull numbers and not the wader numbers (Thompson & Barnard 1983). Models that use mean vigilance rates to predict the probability of detection may not be relevant in many situations as the probability of detection of a predator will depend on the most vigilant individual, not the group mean.

Redshank were probably aware of their own risk of predation at all times. In situations of high risk, such as the close initial appearance of a raptor, redshank in any size flock tended to fly as soon as possible. As attack distances became longer, redshank were significantly less likely to fly immediately on first appearance of a raptor and larger flocks especially so. As the individual risk of capture declined in larger flocks, an individual redshank could probably afford to remain on the ground longer as a raptor approached. By approaching redshank flocks slowly and openly as a 'ground predator' it was assumed that probability of detection was not a factor in response distances. Under these circumstances, flock size was not found to correlate with flight-initiation distance. Ground predators present little risk to wintering birds in an open habitat. For example, La Gory (1986, 1987) showed that white-tailed deer (Odocoileus virginianus) would flee at greater distances from a human in forest habitats compared to open habitats where the risk of a sudden surprise approach is minimal. As risk was probably perceived to be so low on my approaches, other factors such as temperature may have been masking any slight effect of flock size on flight initiation distance.

The exact relationship between flight-initiation distance and flock size is not simple and will vary even intraspecifically depending on the circumstances of attack. Ydenberg & Dill (1986) evaluated fleeing from a predator in terms of economic costs and benefits: in certain situations the risk of a successful attack is so low that the cost that an animal would incur in stopping feeding to flee is greater than the risk of capture. They argued that in assessing the costs and benefits of fleeing for different group sizes of prey, a variety of factors will have to be considered. As well as the benefits already discussed, risk will also vary according to how close a bird is to starvation and even the condition of neighbouring birds. Feeding rates as a consequence of vigilance levels, food availability and feeding interference or facilitation must also be considered. Redshank were altering their levels of anti-predator behaviour in accordance with temperature. Vigilance rates, flight-initiation distances and rate of false alarm flight all decreased with decreasing temperature. The risk of starvation in cold weather is very high for redshank (Clark 1982a,b, Davidson & Evans 1982) and the increase in the threshold of stimuli necessary to elicit an escape response at low temperatures probably reflects this. Reduced temperatures have been shown to correlate with increased feeding priority in several species (e.g. Caraco 1979, Barnard 1980a, Barnard & Stevens 1981). Thompson & Barnard (1983) showed that responsiveness to a standardised alarm (an approaching human) in mixed flocks of lapwings, golden plovers and black-headed gulls (Larus ridibundus) decreased with temperature and daylength.

Larger flocks were preferentially attacked by sparrowhawks implying that they were more conspicuous. Optimal foraging theory (e.g. Krebs & Davies 1987) predicts that sparrowhawks would attack flocks in relation to their availability and profitability. Small flocks were the most common and the most profitable but were attacked the least. If flocks were distributed randomly then a sparrowhawk would encounter different flock sizes in accordance with their relative availability, but sparrowhawks were attacking according to the percent of birds in each flock size class (Table 1). Conspicousness of a flock will generally be a function of size and also equivalent to the overall percent of birds within each flock size class. Andersson & Wicklund (1978) showed that groups of fieldfare (Turdus pilaris) nests attracted more predators than single nests, but the benefits of group defence reduced losses per individual nest in groups to below that of single nests. In redshank the increased conspicousness of larger flocks was offset by the reduced probability of an individual redshank being killed if it stayed in a large flock.

In waders there is little evidence of foraging benefits for flocks compared to single birds (Goss-Custard 1970a; Blick 1980; Fleischer 1983). In area 1, patches of high prey availability may have allowed larger flocks to form until the increased feeding interference caused as more birds used the area balanced the profitability of the patch. Feeding rates over all flock sizes may have remained fairly constant, as redshank maintained a minimum intake level according to the "ideal free" distribution (Fretwell & Lucas 1970) while maximising flock size. In area 2, patches of very low prey availability could probably only be exploited by large flocks as the time required for vigilance by smaller flocks would have prohibitively reduced the time available for feeding, intake rate per unit time being too low. Larger flocks only gained feeding benefits as a consequence of reduced risk leading to reduced vigilance and increased feeding time.

Redshank apparently respond to each others rapid movement at the start of a false alarm flight; alarm calls were almost never heard before flight. Cramp & Simmons (1983) describe redshank behaviour as 'on the first appearance of danger, (they) give loud Contact-alarm calls which alert all birds in the vicinity'. This was not found to be generally the case. Redshank were clearly reacting to flock members movements: a rapid flight away from the flock by one bird almost always elicited a similar response from conspecifics, but alarm calls from redshank on the ground nearby were frequently ignored completely and rarely resulted in a flight response. Many bird species react to conspecific escape movements. Davis (1975) showed that experimentally induced escape flights in one pigeon would elicit flight in conspecifics unless they were preceded by a set of flight-intention signals. Reaction to alarm calls in redshank could not be quantified as it was found to be impossible to judge objectively the intensity and urgency of any call or the distance of the caller from the flock being observed.

Two hypotheses could account for the observed pattern of alarm calls, flock recruitment (e.g. Charnov & Krebs 1975) or pursuit-deterrent (e.g. Woodland et al. 1980), but they are not mutally exclusive. Alarm calls given by an individual within a flock after flight did not appear to result in recruiting neighbouring birds on the ground to the flock. If a raptor attacked, all of the birds in the area flew immediately, but it was possible that hidden redshank, in creeks for example, may have used the call as a cue to take flight. There was unlikely to be a cost associated with alarm calling in flight as sparrowhawks rarely attacked more than one bird per hunt, and the attacked individuals always appeared to be the late- or non-flyers rather than callers. The benefit to the caller of warning hidden individuals would be from preventing a successful hunt and consequent more likely return of the sparrowhawk to the area. The number of birds in the air would also be increased, adding to the 'confusion' effect. Redshank were only significantly more likely to give an alarm call on attack when approached very closely. Those birds with the most to gain by encouraging other birds to join the flying flock called. As redshank on the ground were probably more vulnerable than any flying bird, a call even by a chased bird might still result in recruiting other redshank to join it.

The hypothesis that redshank were calling as pursuit-deterrent signals fits the data less well. Redshank alarm calls were of the 'mobbing' type (Marler 1955), loud and easily locatable, and well within the most sensitive range of sparrowhawk's hearing (Klump et al. 1986). As sparrowhawks hunt by surprise, it would benefit both caller and sparrowhawk as both would avoid a chase which would be very unlikely to result in a capture (see chapters 6 and 8). However, even in long distance attacks when the sparrowhawk was spotted early, the response was still to fly and then only rarely to call; flight itself would act effectively as a pursuit deterrent signal. Redshank were less likely to alarm call on attack by a peregrine than by a sparrowhawk. As the best response on peregrine attack was to stay on the ground, recruitment to flight would not be advantageous, but peregrines hunt frequently by surprise so that, if calls were acting as pursuit-deterrent signals, they might be expected more frequently. Alarm calls were most often recorded on approach by a human ground 'predator'. Species which have the lowest chance of success on a non-surprise attack would be the most likely to be affected by a pursuit-deterrent signal. Again, alarm calls on approach by a human were after flight, and many waders including redshank in the study give visual signals such as wing raising or head bobbing (Cramp & Simmons 1983). A flying redshank in any size flock would be safe from a ground predator so further recruitment to the flock would not be advantageous except to guarantee that the predator would be unsuccessful within the area and so reduce the probability that it would return in the future.

Owens and Goss-Custard's (1976) version of the flock-recruitment hypothesis predicts that alarm calls would be given most often by those waders most widely spaced and in visually obstructed habitats: auditory signals would be more necessary in these situations in order to coordinate a flock response. On approach a redshank was most likely to make an alarm call if it was on the rocky shore or mussel beds where birds were most widely spaced. Where redshank were closest together and in fairly open habitats, such as saltmarsh grass, alarm calls were rarely heard. Overall redshank probably call in order to recruit conspecifics to the flying flock to increase the 'dilution' and 'confusion' effects; these calls may also act secondarily as pursuit-deterrent signals.

If a redshank made the appropriate response to the raptor species that was attacking, then the probability of capture was very low. Rudebeck (1950,1951) described the low attack success rate of sparrowhawks (10.8%), peregrines (7.3%) and merlins (4.5%). Successful attacks were often associated with inappropriate behaviour by the prey, such as a starling, Sturnus vulgaris, leaving a flock and landing on attack. He also described how the different species of raptor have differing modes of hunting and ability to capture prey in different positions relative to the ground. Other studies have found similar low rates of capture for attacking raptors (Dekker 1988; Page & Whitacre 1975) with Buchannan et al. (1988) reporting the highest rate (22.5%). These studies also described the importance of surprise as the main strategy of attack; this agrees with my data (at least 87% of sparrowhawk, 45% of peregrine and 97% of merlin attacks being surprise - with the percentages probably being actually higher due to not classifying stoops as surprise).

Surprise attacks allow a predator to approach the prey close enough to avoid a long, costly chase and minimise the 'head start' a fleeing prey animal might have. Vigilance rates and consequent probability of detection will then be the most important anti-predator behaviour, particularly where a predator such as a sparrowhawk is most successful at catching prey on the ground. Where, as at Tyninghame, a redshank is at risk from peregrines, which are least successful at catching redshank on the ground, then surprise may be being used as a strategy to evoke an incorrect response. Considering all of the attacks and captures by the three raptor species involved at Tyninghame, if a redshank is attacked by an unknown raptor, it is most likely to escape if it flies. A similar situation was probably occurring with false alarm flights which would represent an attack by an unknown raptor. Only with a clearly visible raptor can a redshank make an informed assessment of the risk of staying on the ground. Otherwise it is safest to move to the position of least risk until more information can be obtained. A surprise attacking peregrine may elicit the default response of flight if the redshank is not given sufficient time to identify it. The increased probability of detection of approaching predators accrued by large flocks (Pulliam 1973) may then provide a redshank with enough time to identify the approaching raptor. Lazarus (1979) found that in larger flocks of captive quelea, Quelea quelea, the response of taking flight immediately on sight of a predator, changed to orientation towards the predator, and larger flocks of redshank were less likely to fly immediately on appearance of a sparrowhawk from cover, even when controlling statistically for the probability of detection.

Redshank were less likely to fly on attack by a peregrine as the winter progressed. Juvenile redshank may have been learning which response was better on attack by peregrines, rather than simply the 'bad' respondents being killed. This is possible as even if a redshank responds inappropriately on attack by a peregrine, the probability of capture is still only 14.3% and so the redshank is likely to escape. The data set on which the idea of redshank learning to respond appropriately through the winter is based is small, and lacks controls for variables such as temperature. However as capture rates were low even on inappropriate response, then learning is possible for an individual redshank. There is evidence in fish that early experience can be important in determining adult escape responses (e.g. Goodey & Liley 1986). Melzack (1961) demonstrated that repeated presentations of a hawk model to mallard ducks (Anas platyrhynchos), led to "a virtual disappearance of overt fear responses" which were replaced by coherent and directed vigilance responses. Many waders including redshank remain in the same small area throughout the winter (e.g. Whitfield 1985b) and so it will be possible for an individual to determine the local relative abundance of different raptor species and correspondingly adjust its escape responses. For example in a wintering site where peregrines are the only large raptor, redshank might be expected to fly rarely on attack by an unknown raptor.

The ability to assess the risk of particular escape responses will be crucial to over-winter survival. Redshank are particularly vulnerable to starvation in hard weather (Davidson & Evans 1982), and so in these conditions it will be uneconomic always to flee from a predator (Ydenberg & Dill 1986). Those redshank which select wintering areas such as mud-flat pools will have little risk of attack from cover-using predators such as sparrowhawks (see Newton 1986) and on open attack by peregrines can find refuge very quickly and economically by submerging in the pool. Energetically costly escape flights can then be avoided.

Work on raptor predation on waders has now been carried out in the area since 1982 (Whitfield 1985a; Whitfield et al. 1988). Throughout this time, the most significant agent of mortality for redshank has been raptor predation. Flocking reduces a redshank's risk of attack through the "dilution" effect and so will allow an individual redshank to remain in areas of high raptor activity relatively safely. The vigilance and confusion benefits of flocking will further reduce the probability of capture on attack. Redshank clearly have the ability behaviourally to control a major component of their risk of predation. Decisions such as siting of winter feeding territory must be interpreted in the light of risk of predation as well as the more frequent interpretation of optimal foraging (Lima & Dill 1990; Chapter 5).

CHAPTER 5: CHOICE OF REDSHANK FEEDING LOCATION: PROFITABILITY OR RISK?

5.1 Introduction

A foraging animal must make several decisions concerning the manner in which it feeds. What prey should it select? When and where should it search for food? Which searching method should it use? (Krebs 1978). Animals which collect food efficiently will have a selective advantage over those that forage less efficiently: they will spend less time in energy costly, or risky foraging behaviours, and will take more of a limiting resource. Optimal foraging models make explicit predictions of feeding behaviour based on this assumption, that the more efficient foragers will have greater fitness. There are three main components to an optimality model: the currency, the constraints and the decision variables (Krebs & Kacelnik 1991). The currency is usually maximising the rate of energy intake, but alternatives such as minimising the risk of starvation, or achieving an optimal balance between the risk of predation and starvation can be used. Constraints are fixed properties of the environment or the animal that cannot be behaviourally altered, such as handling time for specific prey, or density of prey. The decision variables are those behavioural components that an animal can alter, such as length of time spent feeding in a patch, or how much time to spend being vigilant. For a chosen currency such as maximisation of energy intake, the currency and decision variables can be measured in order to see if the animal is making the appropriate decisions necessary to maximise the chosen currency. If groups of animals are compared within the same area, at the same time, constraints can be considered as constant, and ignored. If the model fails to account for the observed behaviour, the animal can be assumed to be maximising another currency, and another currency can be tested. Alternatively the parameters of the model may be wrong, or the animal may not be foraging optimally (Gould & Lewontin 1979).

Several field studies of foraging have found support for the currency being net energy maximisation (e.g. Davies 1977, Goss-Custard 1977a, Barnard & Stephens 1981). Other studies, however, have shown that animals do not always feed optimally with respect to energy gain, but are constrained by the risk of predation during foraging (e.g. Milinski & Heller 1978, Sih 1980, Grubb & Greenwald 1982). Most animals in the wild cannot optimise their food intake, as feeding is usually incompatible with anti-predator behaviour. All studies of vigilance show the effects of a risk constraint preventing maximum energy intake (e.g. Caraco 1979, Poysa 1987). An animal must consider the probability of mortality associated with different feeding behaviours: starvation is a gradual process, and multiple sub-optimal foraging decisions will not always lead to death, while a single, poor anti-predation decision will be much more likely to lead to death. Feeding may be just as effectively considered a constraint on anti-predator behaviour (Lima & Dill 1990).

One of the most important decisions a foraging animal can make is where to feed. In most cases, choice of feeding area will be a trade off both between the relative profitability, and relative probability of predation in a patch. Gilliam & Fraser (1987) showed that creek chub (Semotilus atromaculatus) consistently chose the feeding patch which minimised the risk of predation, ignoring the profitability of the patch. Several other studies have also shown choice of non-profitable areas for feeding to minimise the risk of predation, that is risk-averse foraging (e.g. Caraco et al. 1980b, Sih 1980, Dill & Fraser 1984, Caldwell 1986, Holomuzki 1986, Lima & Valone 1986). Risk averse foraging is frequently a function of the condition of the animal. Milinski & Heller (1978) showed that starving sticklebacks would adopt risk-prone foraging, and fed in areas of high profitability despite a high risk of predation, while well fed sticklebacks adopted risk-averse foraging. Other field studies have demonstrated that animals forage primarily according to the risk of predation, but adopt risk-prone foraging as the risk of starvation increases (e.g. Dill & Fraser 1984, Wellborn & Robinson 1987), or as energy needs increase, as during lactation (e.g. Holmes 1991).

Choice of where to feed operates on two broad levels of scale. An animal may choose between separate areas such as wintering sites, and then patches within a site: profitability and probability of predation in a patch will vary over small as well as large areas. For example, a broad area may be relatively safe except in certain sub-areas, which are avoided by an animal: antelopes and marmots avoided feeding close to cover, because bushes and tall vegetation may have obscured and/or harboured predators (Underwood 1982, Carey 1985, respectively). Alternatively, animals may completely abandon areas which have predators: foraging herons moved from mangroves when predators attacked, to feed in habitats, such as reefs, where predators did not occur. The option for an animal of leaving an area of high risk of predation may not always be available (a decision variable becoming a constraint), but other behavioural options such as vigilance and flocking may reduce the individual risk of predation for the area.

At Tyninghame, during winters 1 and 2, it became obvious that adult and juvenile redshank were segregating. Segregation according to age, in different habitats occurs in a wide variety of wader species (Goss-Custard *et al.* 1984, Van der Have *et al* cited in Whitfield 1985b, Whitfield 1985b). Juveniles are frequently of low status and are excluded from the most favoured areas by more experienced adults (Groves 1978, Monaghan 1980, Davies & Houston 1981, Goss-Custard *et al*. 1982, Sutherland & Parker 1985, Whitfield 1985b, Hogstad 1988). Favoured areas have been found to be those of highest feeding profitability (e.g. Goss-Custard 1970b, Sutherland 1982, Thompson & Barnard 1984), although some studies have shown that risk of predation is the main determinant of quality of a area (e.g. Schneider, see also Lima & Dill 1990 for a review). Juvenile marmots (*Marmota*; Holmes 1984, Carey 1985), back-swimmers (*Notonecta hoffmanni*; Sih 1982) and yellow-eyed juncos (*Junco phaeonotus*; Sullivan 1988) were found to use less risky foraging areas and/or adopt more vigilant behaviour compared to adults.

In contrast, at Tyninghame adults appeared to be feeding in areas of low risk, but at a much lower feeding rate than juveniles. Individual risk of predation could be determined as the observed number of kills per redshank, in a fixed time period, in the two areas. Intake rate in the two areas could also be estimated. As very few redshank at Tyninghame starve (Whitfield 1985a, and Chapter 3) it seemed likely that choice of feeding site would be determined by the very high, but variable, risk of predation by raptors, as this would be the main determinant of over-winter survival. Choice of feeding site could be studied on a large scale, comparing adult and juvenile feeding areas (which were separated by a few hundred meters). Choice of feeding site could also be studied on a very small scale, where a few meters difference in the position of a feeding bird in relation to cover would probably make a large difference to the probability of an individual surviving an attack. Redshank feeding in the two areas were studied to determine if they were risk-averse or risk-prone in their foraging.

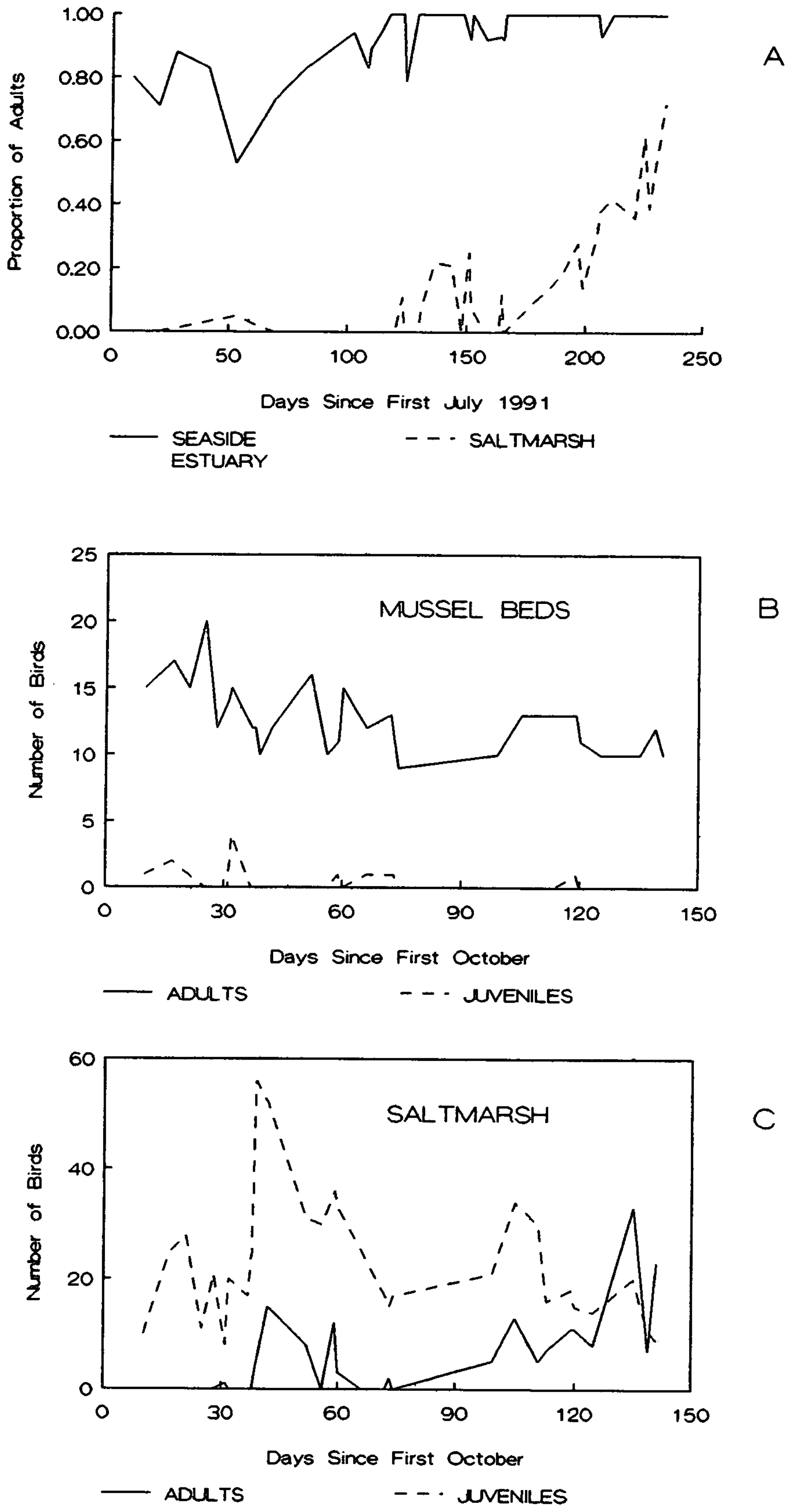
5.2 Results

5.2.1 Distribution According to Age

There were clear differences in the ratio of adult to juvenile redshank between different areas of the estuary. The most pronounced difference was between the mussel beds area of the seaside estuary and the saltmarsh. In 30 scan samples, each involving between 35 and 100 aged individuals, the proportion of adults on the mussel beds was always much higher than the proportion of juveniles (Fig. 1A); conversely the proportion of juveniles was always much higher on the saltmarsh. Figure 1A plots the relative proportions of birds of the two ages in the two areas, from the start of July. Few redshank were present (c20 birds)in July, although numbers rose to over 100 by the start of August. In July both adults and juveniles were present on the mussel beds but by the beginning of October, almost no juveniles were found on the mussel beds (Fig 1B). Almost no adults were

FIGURE 1

RATIO AND NUMBER OF ADULT AND JUVENILE REDSHANK ON THE MUSSEL BEDS AND SALTMARSH WITH TIME OF YEAR

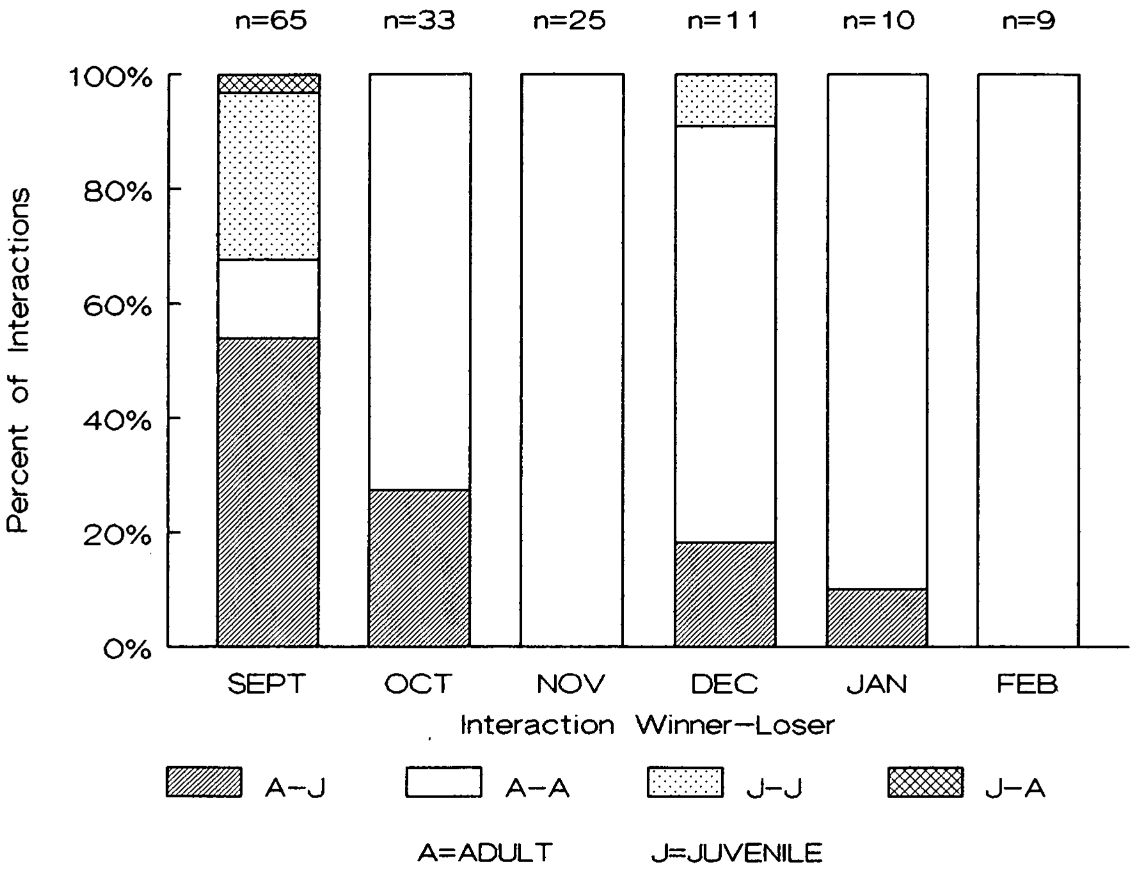


recorded on the saltmarsh until the beginning of November, and the number of adults only rose consistently on the saltmarsh at the end of January (Fig 1C). The proportion of adults on the saltmarsh reflects both the increased number of adults feeding there (Fig 1C) and the decreased number of juveniles due to differential mortality (see Chapter 3). The number and proportion of adults on the mussel beds remained relatively constant from October onwards.

Juvenile redshank were actively excluded from the rocky shore and mussel bed areas by adult redshank. Figure 2 shows the results of 'aggressive' interactions between pairs of redshank on the estuary (94.8% of 153 observed interactions in three winters came from the rocky shore/mussel bed area of the seaside estuary). The winner of an interaction was the bird that displaced and chased off the second bird, preventing it from feeding in the area under dispute. In nearly all cases (96.0%, n=49) of adults interacting with juveniles, the adult was the winner ($x2=41.3$, 1df, $p<0.0001$). Most interactions (57.5%), including nearly all of the adult-juvenile interactions (93.8%), occurred in September and October, and coincided with the maximum number of juveniles on the mussel beds (Fig 1). Juveniles that attempted to feed on the mussel beds at any time were chased off by adults, and could only feed for any length of time on the fringes of the area, adjacent to Sandy Hirst. During September, juveniles that were feeding on the fringe of the mussel beds would attempt to exclude other juveniles by chasing them out of the area.

FIGURE 2

Results of Aggressive Interactions Between Pairs of Redshank of Different Ages 1989–92



5.2.2 Variation in the Risk of Predation

In 126 hours of raptor watching, within two hours of low tide there were 67 sparrowhawk attacks on the seaside estuary, resulting in three redshank kills. In the same time there were 197 sparrowhawk attacks on the saltmarsh, resulting in 21 redshank kills. The success rates of kills for the two areas were not significantly different (G=2.2, 1df, p=0.14) but there was a trend for success rate to be lower on the seaside estuary (4.5%) compared to the saltmarsh (10.7%). The lack of a significant difference was probably due to small sample size. There were significantly fewer attacks on the seaside estuary compared to the saltmarsh (x2=64.0, 1df, p<0.0001). Although there were more redshank on the saltmarsh, compared to the mussel beds, in both areas there were many other potential prey species (up to 400 other waders often on the mussel beds and occasionally up to 300 passerines in the saltmarsh area). Accurate counts of all species present could not be made during raptor watches but in general there were usually c5 times more available prey on the seaside estuary than the saltmarsh.

An individual redshank on the saltmarsh had a much higher probability of death over the winter compared to one on the mussel beds. In 126 hours of raptor watching at low tide (+/-2 hours) only two kills were observed for redshank that were feeding in the mussel bed area, compared to 21 kills within the saltmarsh area (both areas corresponded exactly to the areas scan sampled for numbers of redshank present, data shown in Figs. 1B and 1C). The mean number of redshank, from October to February inclusive, in the mussel bed area was 13.0+/-0.5, and in the saltmarsh area was 28.7+/-2.7. An individual redshank was therefore 4.8 times more likely to be killed by a raptor when feeding on the saltmarsh at low tide, compared to an individual redshank feeding on the mussel beds.

Within the saltmarsh and the seaside estuary, the probability of capture by a sparrowhawk depended significantly on the distance a redshank was from cover (Fig. 3A and see Chapter 3), especially when controlling for flock size (Fig. 3B). Redshank that fed close to cover (<15m) had a very high probability of capture (>50%) in small flocks (<10 birds). Even in large flocks, success rate was dependent on distance from cover.

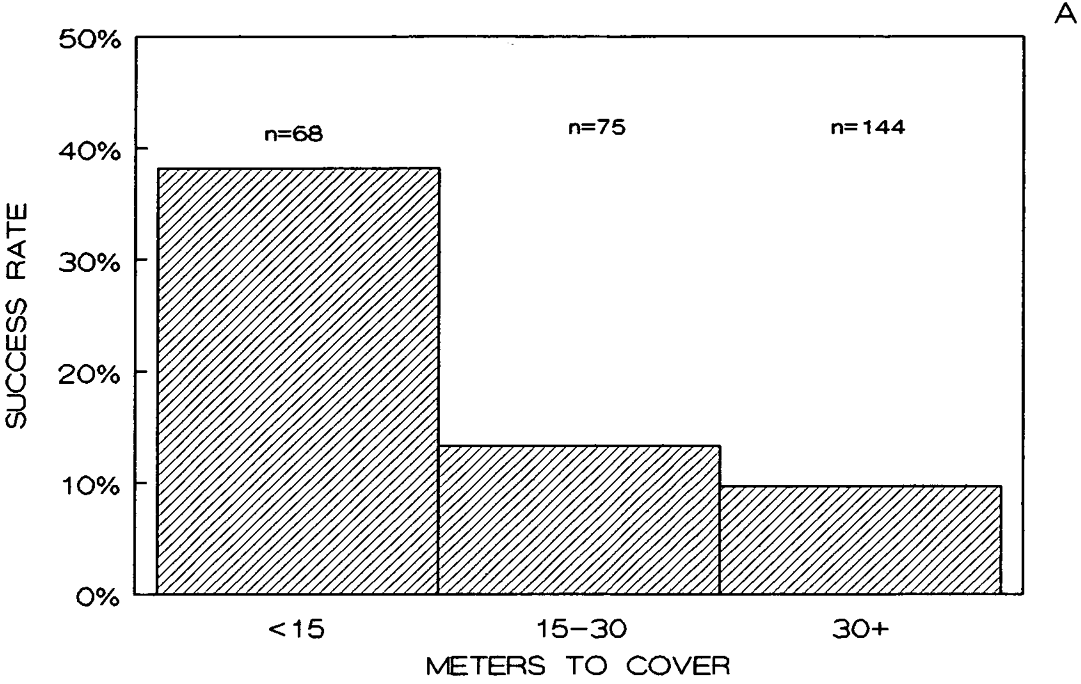
5.2.3 Spacing of Redshank on the Saltmarsh and Mussel Beds

Redshank on the saltmarsh had much lower nearest neighbour distances and fed closer to cover, on average, than redshank on the mussel beds. Scan samples from September to February inclusive (winter 3) were used, taken at the same time for the two areas from October onwards, so providing a direct low tide comparison.

The modal nearest neighbour distance on the saltmarsh was less than 1m, and most redshank (60-83%) in all months had neighbours less then 1m away (Fig. 4A). On the seaside estuary, the modal nearest neighbour distance was greater than 25m, and in all months between 48% and 60% of redshank could be classed as single birds (Fig. 4B). Nearest neighbour distance varied significantly between months in both areas ($G=150.2$, 16df, $p<0.0001$, on the saltmarsh and $G=81.8$, 16df, $P<0.0001$, on the mussel beds; October to February inclusive), but there was no obvious trend for a general increase or decrease in nearest neighbour distance. There was no significant

FIGURE 3

Success Rate of Redshank Attacks by Sparrowhawks with Meters to Cover



Controlling for Flock Size

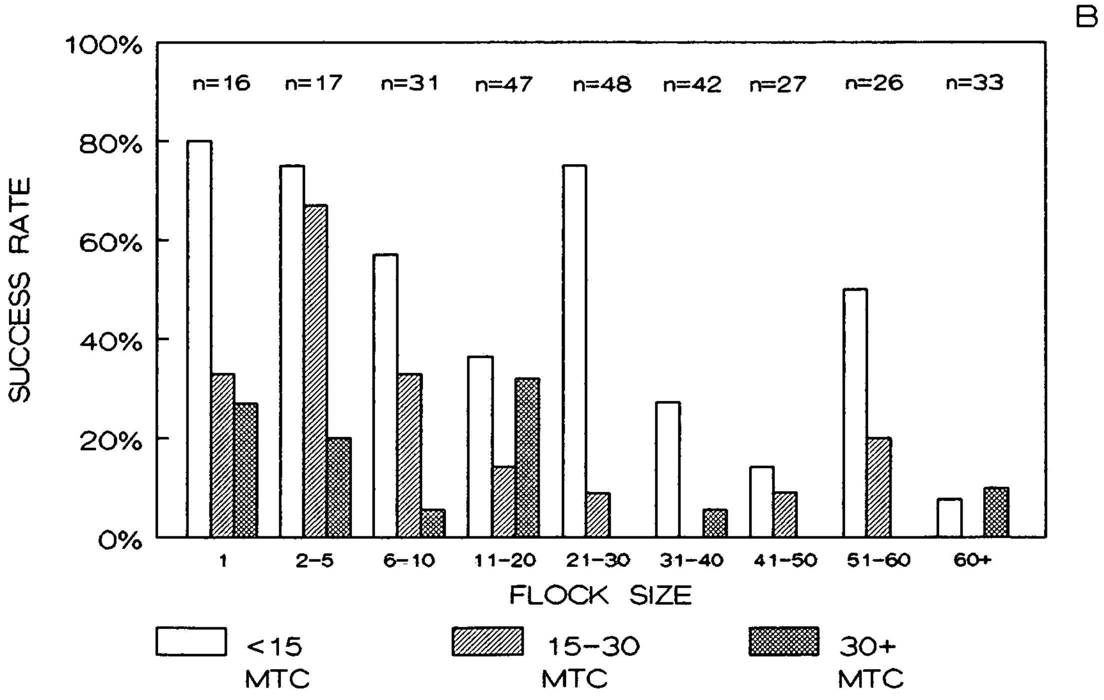
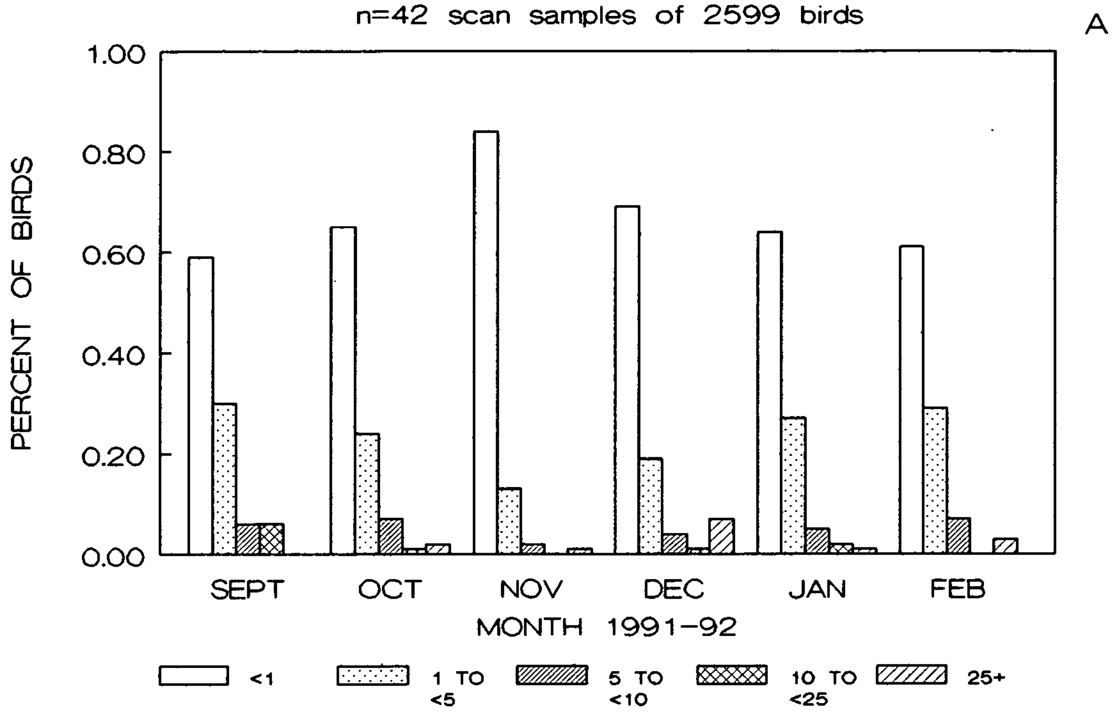


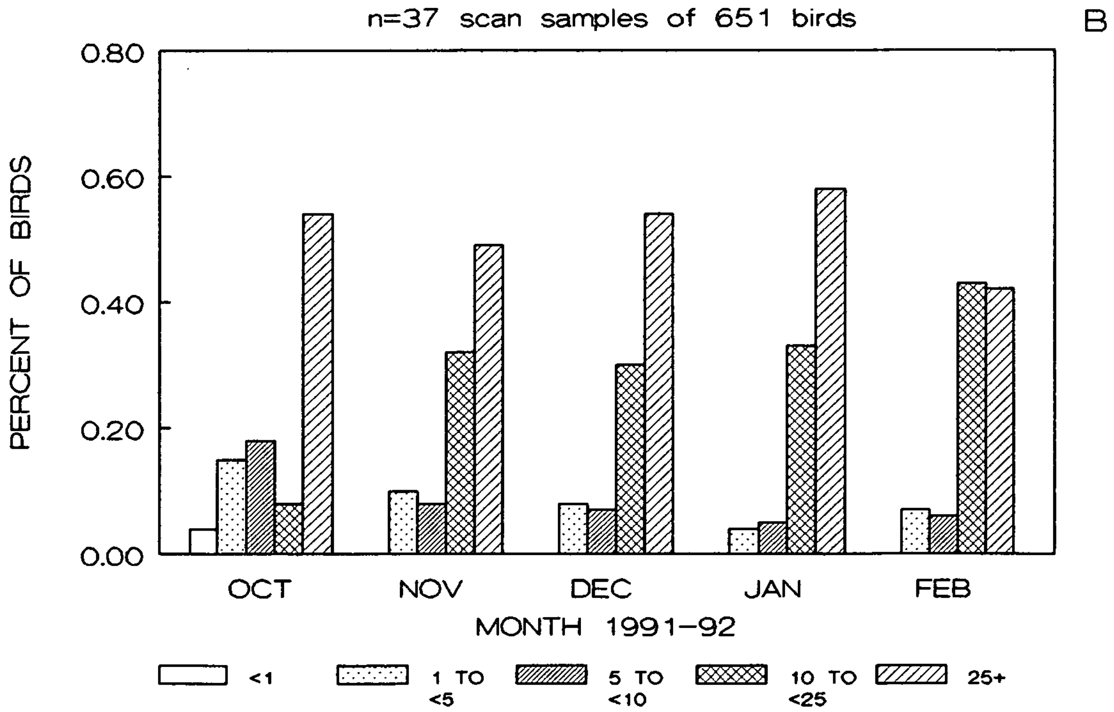
FIGURE 4

NEAREST NEIGHBOUR DISTANCE (METERS) OF REDSHANK

SALTMARSH



SEASIDE ESTUARY



correlation of mean daily temperature and nearest neighbour distance: saltmarsh, e.g., proportion of birds at <1m, T=-0.14, p=0.89; mussel beds, e.g., proportion of birds at >25m, T=1.9, p=0.07; Spearman's Rank Correlation.

The modal distance from cover (either a creek or vegetation) of a redshank on the saltmarsh was 21-50m, with over 20% of birds in all months feeding at less than 20m to cover (Fig. 5A). In December, up to 60% of the redshank fed at less than 20m to cover. On the seaside estuary the modal distance from cover in all months was greater than 100m, with most redshank feeding more than 100m away from cover (Fig. 5B). Only a very small percentage, and these were usually juvenile birds excluded from the main feeding area, were at less than 50m to cover. Distance from cover did not vary significantly by month on the seaside estuary (G=10.9, 8df, p=0.07) but varied significantly by month in the saltmarsh redshank (G=188.2, 10df, p<0.0001). Greater distances from cover were recorded more frequently later on in the winter on the saltmarsh. There was no significant correlation of distance to cover and mean daily temperature: saltmarsh, e.g., proportion of birds at <20mtc, T=0.92, p=0.36; seaside estuary, e.g., proportion of birds at >100mtc, T=0.37, p=0.72; Spearman's Rank Correlation.

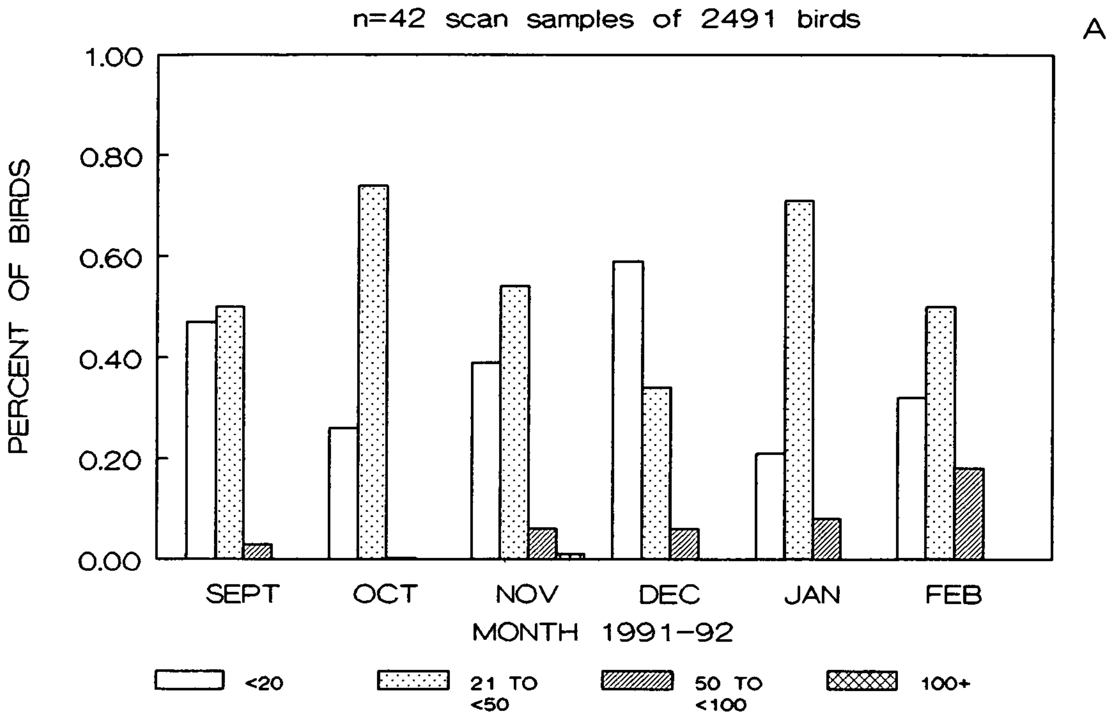
5.2.4 Feeding Rate and Distance to Cover on the Saltmarsh

Redshank on the saltmarsh were almost always juveniles and fed in most areas in a similar manner (shallow probes) on the same prey (Orchestia). Feeding rates at different distances to cover (and therefore different risks of predation) probably represented a

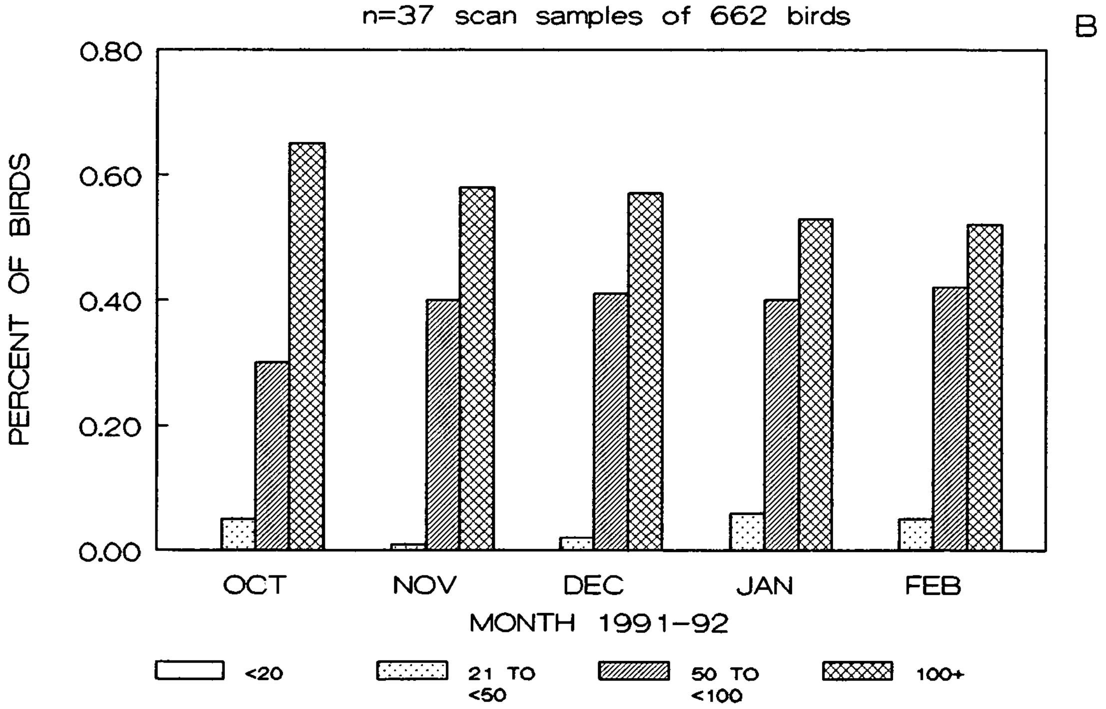
FIGURE 5

METERS FROM COVER OF REDSHANK

SALTMARSH



SEASIDE ESTUARY



comparable measure of energy intake between the different areas. Invertebrates were sampled at different distances to cover to determine if similar prey was available at different distances from cover. Table 1 shows the number of invertebrates per square meter from 60 quadrats, 30 at less than 30m and 30 at greater than 50m to cover, on the same day. Comparing the two sets of quadrats, there were significant differences in the number of prey available per square meter for all types of prey apart from spiders, despite a similar number of prey available overall. More *Orchestia*, insect larvae and beetles were found at less than 30m to cover, and more *Sphaeroma* and molluscs were found at greater than 50m to cover. Table 2 shows the number of invertebrates counted in pairs of quadrats, one taken at less than 15m and one taken between 16-30m to cover. There were no significant differences in the number of prey available per square meter for any of the types of prey at the two different distances to cover.

There was obvious variation in the numbers of invertebrates found on different sampling days (e.g. compare the densities in tables 1 and 2). Pooling data from quadrats taken on different days as in Table 2, may have given a biased result. Number of invertebrates occurring in near (<15mtc) and far (16-30mtc) quadrats were compared in a matched pair format (quadrats were collected in this way, n=24 pairs) using Wilcoxon Matched Pairs Signed Rank Test: *Orchestia*, z=1.1, p=0.20 and non-*Orchestia*, z=-1.7, p=0.09; all prey, z=-1.8, p=0.07. Invertebrate densities were not significantly different at different distances from cover of less than 30m on the same day.

TABLE 1: Prey available on the saltmarsh from n=60 0.01m^2 quadrats, 30 at >50m and 30 at <30m from cover collected over 5 hours on 24/2/92:

Densities/m^2	>50m	<30m	x^2	p	alpha
Orchestia	310	940	317.5	<0.0001	0.008
Sphaeroma	233	33	150.4	<0.0001	0.01
Hydrobia/Littorina	403	7	382.5	<0.0001	0.007
Insect Larvae	33	63	9.4	<0.01	0.02
Beetle	0	7	-	<0.01	0.01
Spider	20	20	0	1	-
TOTAL	999	1070	2.5	0.13	-

Sequential Bonferroni, K=7

TABLE 2: Prey available on the saltmarsh from n=48 0.04m^2 quadrats, 1 at <15m and at 16-30m from cover collected between 17/12/91 to 10/2/92:

Densities/m^2	<=15m	16-30m	x2	p	alpha
Orchestia	455	466	0.13	0.70	-
Sphaeroma	7	12	1.3	0.26	-
Hydrobia/Littorina	24	12	4.0	0.05	0.01
Insect Larvae	50	27	6.9	0.009	0.007
Beetle	25	17	1.5	0.23	-
Spider	29	13	6.1	0.02	0.008
Fly	0	5	-	0.03	0.01
TOTAL	590	552	1.3	0.26	-

Sequential Bonferroni, K=7

Of 2,212 prey items counted in quadrats at less than 30m to cover, 84.1% were Orchestia. During observations of feeding redshank on the saltmarsh grass, it was only possible to see the prey being taken in about 10% of cases: redshank were always seen to take Orchestia when feeding on the saltmarsh grass at low tide and at less than 30mtc. Table 3 shows the relative numbers of different prey types found in 20 fresh redshank gizzards, after they had been killed by sparrowhawks. Hydrobia and Littorina shells remain longer in the gizzard than softer prey such as amphipods, so the absolute numbers of the different prey types were not directly comparable. Despite this, 28.6% of prey recorded in the gizzards was Orchestia and of 9 prey items found in the oesophagus of 4 redshank, just killed after feeding at less than 30mtc on the saltmarsh, 100% were Orchestia. Of the larger prey (greater than 5mm) in all gizzards, 66.3% were Orchestia. The ratio of sizes of Orchestia found in the gizzards of redshank was significantly different to the ratio of sizes of Orchestia available on the saltmarsh (Table 4): $G=31.5$, 2df, $p<0.001$. Orchestia of greater than 10mm represented 24.7% of the total gizzard Orchestia, compared to 5.5% of Orchestia available. The frequency of different sizes of molluscs found in the gizzards of redshank was significantly different to frequency of available sizes of molluscs on the saltmarsh (Table 4): $G=10.2$, 2df, $p<0.01$. Eighty eight percent of gizzard molluscs were less than 6mm, compared to 78.7% of available molluscs: redshank were either preferentially selecting smaller Hydrobia and Littorina, or the presence of molluscs in the gizzards reflects feeding that was not carried out on the saltmarsh at low tide.

TABLE 3: Relative Prey Size Found in Redshank Gizzards

n=20 fresh gizzards

	0-0.5cm	0.6-1.0cm	>1.0cm
Orchestia	20	35	18
Sphaeroma	2	2	1
Littorina	91	15	1
Hydrobia	60	3	0
Corophium	0	2	0
Carcinus	0	0	1
Insect Larvae	2	2	0

Table 4: Data from all saltmarsh quadrats (n=155) from 18/10/91 to 24/2/92 showing relative availability of different size prey (n=3166 prey items).

	Orchestia	Sphaeroma	Litt./Hyd.	Other
0-0.5cm	779	322	531	140
0.6-1cm	717	268	134	135
>1cm	87	18	12	23

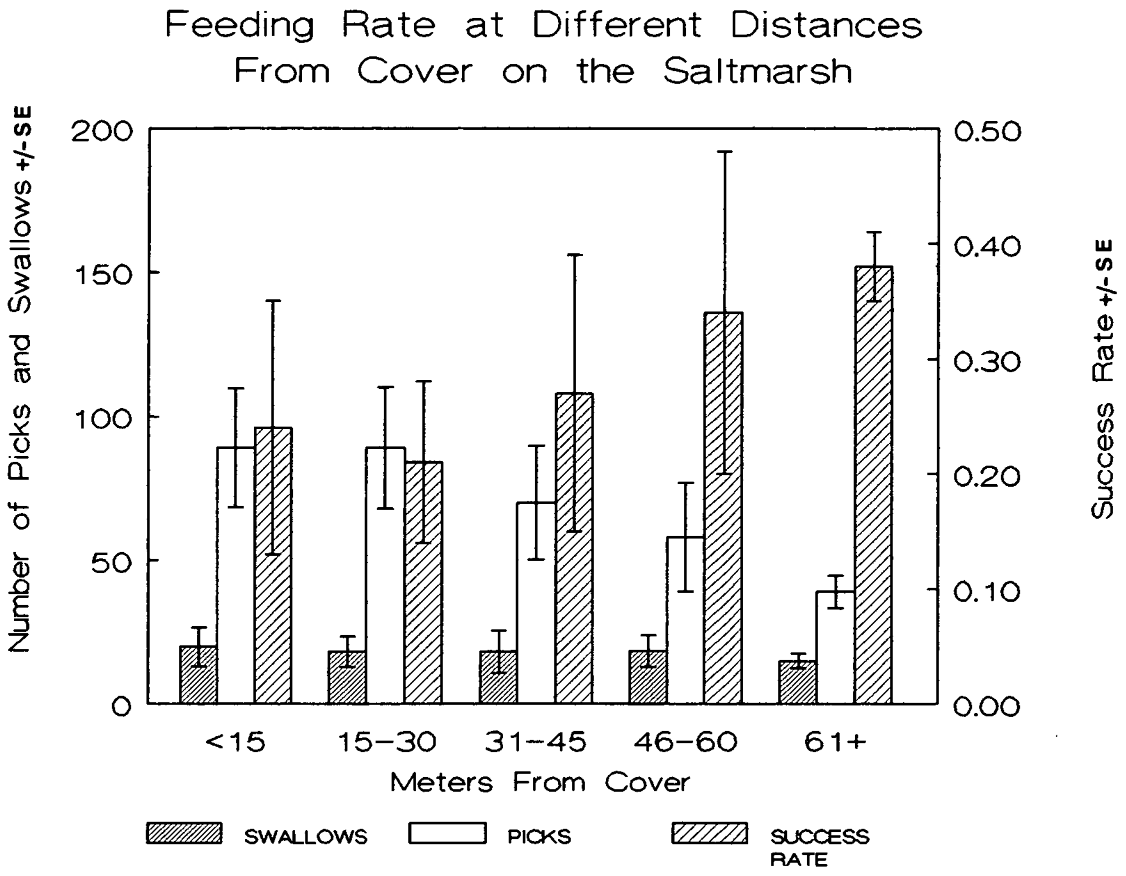
Orchestia were the most important prey for redshank feeding at low tide on the saltmarsh. The occurrence of different sized _Orchestia_ with respect to distance to cover may therefore have been important. There was no significant difference in the relative sizes of _Orchestia_ at greater than 50m and less than 30m to cover: G=0.57, 2df, p=0.74, using quadrat data in Table 1, collected at the same time. There was no significant difference in the numbers of _Orchestia_ in any of the three different size classes at less than 15m and 16-30m to cover: 1-5mm, Z=-0.63, p=0.53; 6-10mm, z=-1.5, p=0.14, and >10mm, Z=-0.31, p=0.75; Wilcoxon Matched-Pairs Signed-Rank Test, using matched pair quadrat data in Table 2.

Feeding rate at different distances to cover was compared for 117 matched pairs collected from October to February inclusive (winter 3). The number of swallows, picks and percent of picks that led to a swallow (success rate) were compared for a redshank feeding close to cover, and a second bird feeding 5-30m further from cover (86% of pairs were separated by c10m). Both birds sampled had nearest neighbours 0.5-5m away (70% of the pairs came from birds with nearest neighbour distances of 0.8-1.8m). Matched pairs were compared using Wilcoxon Matched-pairs Signed-rank Tests. For all cases (n=117) the number of swallows and success rate were significantly higher closer to cover: swallows, z=-2.9, p<0.005, and success rate, z=-4.2, p<0.0001. The number of picks for close and far birds was not significantly different: z=-1.03, p=0.30. Overall a redshank which fed closer to cover had a higher intake rate. Considering the similar sizes of _Orchestia_ available at different distances to cover, a redshank feeding closer to cover probably had a greater energy intake.

The magnitude of the differences in redshank feeding rate at different distances to cover was fairly small. Figure 6 shows the mean feeding rate (+/- one standard error) at different distances to cover on the saltmarsh, using all focal sampling cases collected during winter 3. Intake rates were not therefore strictly directly comparable, as cases were collected unequally by month, and the pattern of invertebrate variation between months was not known. Swallow rates were highest closer to cover (20.0+/-6.8 at <15mtc and 15.0+/-2.6 at 60+mtc), but the number of picks declined rapidly further away from cover (89.1+/-20.6 at <15mtc and 39.0+/-5.6 at 60+mtc). Success rate was therefore much greater further away from cover (24% at <15mtc and 38% at 60+mtc).

A multiple regression analysis was carried out on all focal feeding cases collected on the saltmarsh, at low tide, during winter 3 (n=364, 2 minute samples). The number of picks had an approximately normal distribution (Z=0.93, Kolmogorov-Smirnov comparison to a normal distribution, p=0.35); the number of swallows was transformed by a square root function to form an approximately normal distribution (Z=1.3, Kolmogorov-Smirnov comparison to a normal distribution, p=0.06), and success rate was transformed by a Log10 function to form an approximately normal distribution (Z=1.2, Kolmogorov-Smirnov comparison to a normal distribution, p=0.09). The effect of the distance the redshank being sampled was from me (as observation distance increases, the ease of seeing a redshank swallow decreases) and success rate was checked by a regression of

FIGURE 6



Feeding Rate at Different Distances From Cover on the Saltmarsh the two variables. There was no significant correlation between the distance a redshank was from me and the success rate ($T=0.46$, $p=0.65$, $n=142$).

A multiple regression analysis was carried out on the transformed number of swallows as dependent variable with meters to cover and nearest neighbour distance. After backwards deletion of variables the equation remaining included meters to cover only ($y=-0.005x + 4.4$, $T=-2.0$, $p<0.05$): as distance to cover increased the number of swallows decreased slightly. There was no effect of spacing on the number of swallows ($T=1.4$, $p=0.16$). A multiple regression analysis was carried out on the number of picks as dependent variable with meters to cover and nearest neighbour distance. Both independent variables were significantly correlated with the number of picks (nnd, $0.02x$, $T=3.0$, $p<0.005$; mtc, $-0.73x$, $T=-9.3$, $p<0.0001$, constant=101.8): as birds fed further apart and further from cover there were more picks. A multiple regression analysis was carried out on the transformed success rate as dependent variable with meters to cover and nearest neighbour distance. After backwards deletion of variables the equation remaining included meters to cover only ($y=0.004x - 0.75$, $T=5.9$, $p<0.0001$): as distance to cover increased success rate increased. There was no effect of spacing on success rate ($T=-0.72$, $p=0.47$).

A second series of multiple regression analyses was carried out with the feeding variables, each as dependent variables, with spacing and distance to cover, including only a subset of cases collected from redshank feeding at less than 30m to cover ($n=275$). The results agreed with the matched pair results. Success rate was greater closer to cover (in the equation, mtc, T=-2.1, p=0.04; not in the equation, nnd, T=-0.25, p=0.80). The number of picks increased as birds fed further apart (in the equation, nnd, T=0.25, p=0.01; not in the equation, mtc, T=-0.27, p=0.79). The number of swallows increased when birds were closer to cover and spaced further apart (in the equation, nnd, T=1.7, p=0.08 and mtc, T=-2.5, p=0.01).

5.2.5 Feeding Rates on the Mussel Beds

Redshank on the mussel beds were almost always adults and fed in a variety of ways, on a wide range of prey. The commonest feeding method was wading up to the mid leg level and making rapid picks at moving prey in the water below, or shallowly probing at the bottom of the mussel pool. Redshank also waded to their bellies and fed commonly with their head completely submerged while picking (the head was raised to swallow prey and between picks). Redshank also fed by walking rapidly along the edge of the pools, picking on the surface of the mud and between the mussels.

Redshank took a variety of prey while feeding around the mussel beds. In 344, 2 minute focal samples, 1,010 prey items were recorded (Table 5), although few could be specifically identified. Invertebrates were sampled from the mud (from cores) and from the water column (by netting) to attempt to identify what prey was being taken (Table 6). Most prey was unidentified small prey: this was classified into mobile prey (46.7%) and non-mobile prey (29.8%). Mobile small prey were actively chased by the redshank in the water and caught, often, by a rapid heron-like plunge of the bill into the

TABLE 5: Prey items recorded during focal samples of redshank feeding on the mussel pools.

n=1010 items from 344 focal samples

	Length of Prey (cm)						
	0-0.5	0.6-1	1.1-2	2.1-3	3.1-4	4.1-5	5.1-6
Mobile Small Prey	472	-	-	-	-	-	-
Non-mobile Small Prey	301	-	-	-	-	-	-
Carcinus	4	52	23	1	0	0	0
Worm Diameter<0.5cm	0	2	11	2	1	0	0
Worm Diameter>0.5cm	0	0	3	3	9	0	2
Arenicola	0	0	0	0	0	0	1
Nereis	0	0	1	1	1	0	0
Fish	0	0	0	2	1	0	0
Corophium	0	2	0	0	0	0	0
Mollusc	0	3	2	0	0	0	0
Unknown	-	104	5	0	1	0	0
TOTAL	777	163	45	9	13	0	3

TABLE 6: Prey Available on the Mussel Pools

M=Mud Samples, n=20 cores 675cm^2, 5 on 14/10/91, 28/10/92, 22/10/92, and 26/1/92.

S=Sieve Samples, n=100 sweeps, 50 on 16/12/91 and 26/1/92.

		Size (cm)					
		0.1-1	1.1-2	2.1-3	3.1-4	4.1-5	5.1-6
Littorina sp.	M	31	27	3	0	0	0
	S	0	0	2	0	0	0
Insect Larvae	M	0	1	0	0	0	0
	S	0	1	0	0	0	0
Nereis sp.	M	0	4	0	1	6	1
	S	0	0	0	0	1	1
Arenicola sp.	M	0	0	1	0	1	0
Carcinus sp.	M	0	1	0	0	0	0
	S	1	0	0	0	0	0
Venus sp.	M	1	1	0	0	0	0
	S	0	0	4	0	0	0
Venerupis sp.	M	3	5	0	0	0	0
Lepidochiton sp.	M	2	0	0	0	0	0
	S	1	0	0	0	0	0
Nemertine sp.	M	0	0	0	0	1	0
Gammarus sp.	M	0	2	0	0	0	0
	S	14	4	0	0	0	0
Nototropis sp.	M	1	0	0	0	0	0
	S	20	0	0	0	0	0
Schistomysis sp.	S	6	11	0	0	0	0
Crangon sp.	S	14	19	0	0	0	0
Gobius sp.	S	0	0	4	1	0	0

water. These prey were probably small individuals of crustacean species such as Gammarus, Schistomysis, Nototropis and Crangon. Larger individuals observed being taken in focal samples were recorded as Corophium (i.e. a generalised, common amphipod). Small non-mobile prey were picked up from the bottom of pools or on the surface of the mud without a 'chase'. These prey were probably small individuals of mollusc species such as Littorina, Venus, Venerupis or Lepidochiton, or non-mobile amphipods. Crabs could always be identified, even when very small and were taken frequently (7.9%). Worms were taken less frequently (3.9%); thin worms were probably Nemertine and larger worms were Nereis and less commonly Arenicola. Occasionally fish were taken (0.3%); these were small Gobius. Redshank were occasionally seen to catch larger fish (>3cm) but handling time was frequently in excess of 1 minute because redshank seemed unable to swallow such large prey. Large fish were usually discarded uneaten. Some prey (10.9%) were classified as unknown larger prey; these were almost certainly larger amphipod individuals.

Feeding rate at different distances to cover and nearest neighbour distance was analysed for redshank feeding on the mussel pools, using the 344 focal samples. The number of picks had an approximately normal distribution (z=1.1, Kolmogorov-Smirnov comparison to a normal distribution, p=0.16); success rate was transformed by a Log10 function to form an approximately normal distribution (z=0.7, Kolmogorov-Smirnov comparison to a normal distribution, p=0.63) and number of swallows was analysed non-parametrically as the distribution could not be easily normalised.

The effect of observer distance on success rate was checked by a regression. There was no significant correlation between the distance a redshank was from me and the success rate during the focal sample ($T=0.12$, $p=0.91$, $n=175$). A multiple regression analysis was carried out with transformed success rate as dependent variable, with meters to cover and nearest neighbour distance. After backwards deletion of variables, the equation remaining included meters to cover only ($y=-0.004x - 1.0$, $T=-3.3$, $p<0.001$): success rate was slightly higher closer to cover. There was no effect of spacing on success rate ($T=1.2$, $p=0.21$). A multiple regression analysis was carried out on the number of picks as dependent variable with meters to cover and nearest neighbour distance. Both independent variables were significantly correlated with the number of picks (mtc, $-0.2x$, $T=-2.0$, $p<0.05$; nnd, $0.42x$, $T=2.0$, $p<0.05$, constant=77.3): as birds fed further apart and closer to cover there were more picks. The number of swallows decreased as redshank fed closer together ($T=2.9$, Spearman's Rank Correlation, $p<0.005$), and the number of swallows increased as redshank fed closer to cover ($T=-4.7$, Spearman's Rank Correlation, $p<0.0001$). There was no significant correlation between distance to cover and nearest neighbour distance ($T=2.0$, Spearman's Rank Correlation, $p=0.052$).

Between the 4th and 19th of September, focal samples in a matched pair format were taken to compare adult and juvenile feeding rates on the mussel beds. Two different feeding types were compared separately for the two ages: shallow wading feeding involved rapid picks on the surface of wet mud around the mussel beds, deep wading feeding involved wading up to the belly in mussel pools, with slow deliberate steps and picks. Matched pairs were compared using Wilcoxon Matched-pairs Signed-rank tests in all cases. For shallow wading, 35 pairs were collected: adults made significantly more swallows ($x=12.6$) and picks ($x=128.3$), compared to juvenile swallows ($x=9.8$) and picks ($x=95.9$); $z=-2.6$, $p<0.01$ for swallows, and $z=-4.4$, $p<0.0001$ for picks. Success rates were not significantly different (10% for adults, 11% for juveniles): $Z=-0.87$, $p=0.39$. For deep wading, 20 pairs were collected: adults had a significantly greater success rate ($x=9.4\%$) and made significantly more swallows ($x=4.7$) compared to juvenile success rate ($x=6.3\%$) and number of swallows ($x=2.7$); $z=-3.1$, $p<0.005$ for success rate, and $z=-2.8$, $p<0.01$ for swallows. There was no significant difference in the number of picks ($x=52.9$ for adults, $x=47.4$ for juveniles). Overall adult intake rates were higher in the mussel bed area than juvenile intake rates (compare the similar intake rates for adults and juveniles on the saltmarsh in Area 2, in Chapter 4.2.3.5).

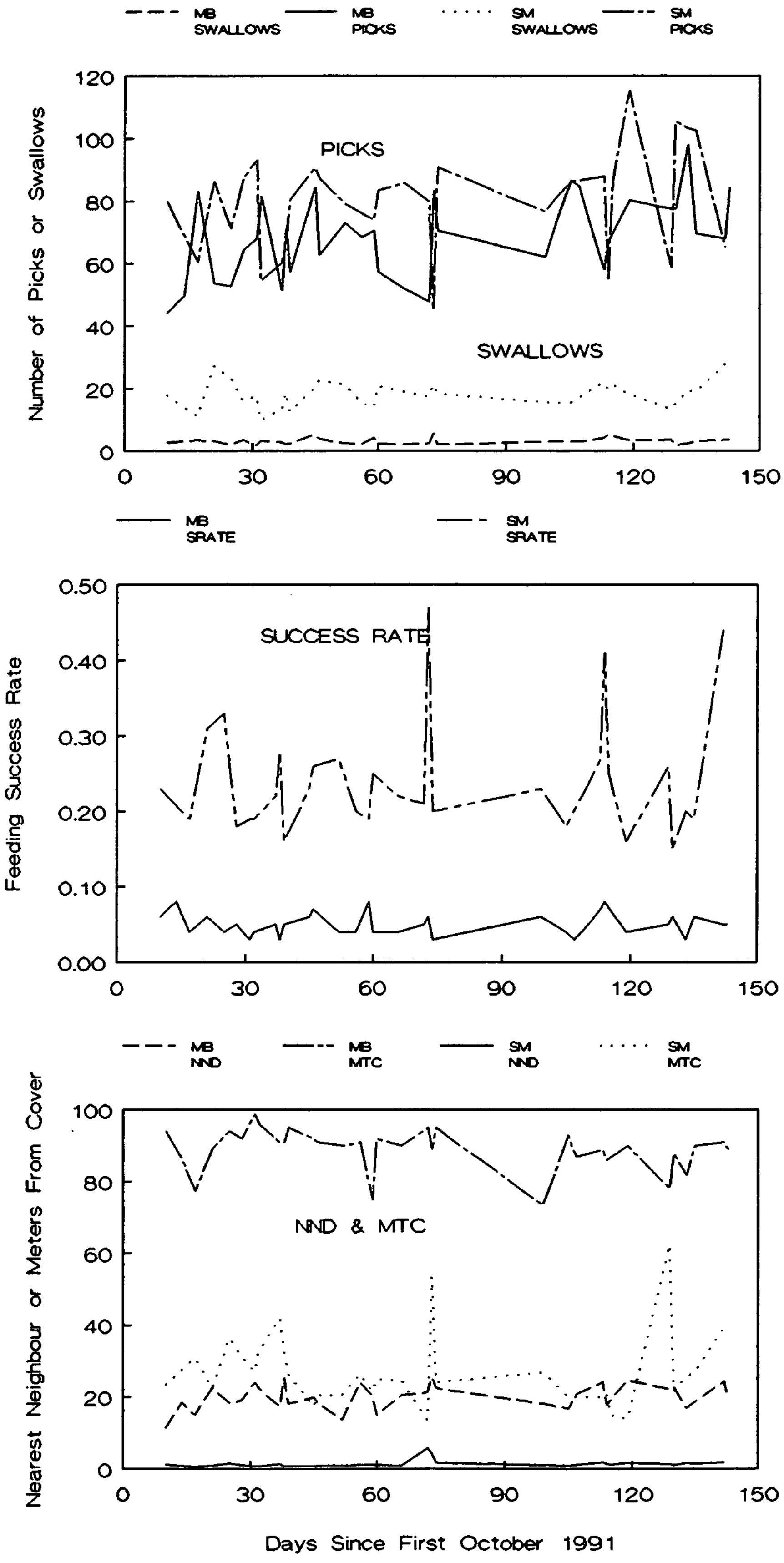
5.2.6 A Comparison of Feeding Rates on the Saltmarsh and Mussel Beds

Feeding data from the mussel beds and saltmarsh, collected in winter 3, were compared using Mann-Whitney U-tests ($n=650$ cases). The number of swallows, number of picks and success rate were lower for mussel-bed-feeding birds, compared to saltmarsh-feeding birds: swallows, $z=-21.7$, $p<0.0001$; picks $z=-6.3$, $p<0.0001$ and success rate, $z=-21.4$, $p<0.0001$. Comparison of aggregated data was subject to bias, as an unequal number of cases was collected at different times, and there was significant variation by sampling period in each of the areas. On the mussel beds, all variables measured, except for number of swallows, varied significantly between sampling periods: picks, $x^2=80.9$, $p<0.0001$; swallows, $x^2=41.0$, $p=0.09$; success rate, $x^2=53.4$, $p<0.01$; nearest neighbour distance, $x^2=69.9$, $p<0.0005$ and meters to cover, $x^2=46.1$, $p<0.05$; Kruskall-Wallis 1-way ANOVA. On the saltmarsh, all variables measured varied significantly between sampling periods: picks, $x^2=114.0$, $p<0.0001$; swallows, $x^2=88.4$, $p<0.0001$; success rate, $x^2=127.0$, $p<0.0001$; nearest neighbour distance, $x^2=122.0$, $p<0.0001$ and meters to cover, $x^2=133.0$, $p<0.0001$; Kruskall-Wallis 1-way ANOVA. The variability in feeding and spacing data over the sampling period is shown in Figure 7. Despite significant variation, the magnitude of the differences between the variables between the mussel beds and the saltmarsh remained fairly constant. Redshank on the saltmarsh had consistently higher numbers of swallows (c6 times), but number of picks was similar, although usually slightly higher, than for mussel bed feeding redshank. Success rate was, as a result, consistently much higher (c5 times) on the saltmarsh. Redshank feeding on the mussel beds were much more widely spaced (c20 times) and much further away from cover (c3-4 times).

Feeding and spacing data were collected in a matched pair format, at low tide, to compare the two areas. Focal samples were taken from one area, immediately followed by the other area, with the order of sampling reversed on each sampling day. In total, 30 matched pairs were taken from October to February inclusive, containing 650 focal samples of feeding data (n=306 from the saltmarsh and n=344 from the mussel beds), 250 focal samples of pacing data (n=125 from each area) and 30 scan samples from each area of nearest neighbour

FIGURE 7

Feeding and Spacing Data Comparing Mussel Beds (MB) and Saltmarsh (SM)



distance, meters from cover and adult to juvenile ratio. Matched pairs were analysed using Wilcoxon Matched-pairs Signed-rank tests. Redshank made significantly more swallows on the saltmarsh (mean difference 15.1+/-4.2, the mean number of swallows on the mussel beds was 16.8% of the number of swallows on the saltmarsh): z=-4.8, p<0.0001. Redshank made significantly more picks on the saltmarsh (mean difference 11.6+/-20.3, the mean number of picks on the mussel beds was 85.1% of the number of picks on the saltmarsh): z=-2.8, p<0.01. Redshank had a significantly higher proportion of picks which led to swallows (success rate) on the saltmarsh (mean difference 0.19+/-0.08, the mean success rate on the mussel beds was 21.2% of the mean success rate on the saltmarsh): z=-4.8, p<0.0001. Nearest neighbour distance between redshank was significantly greater on the mussel beds (mean difference 18.7+/-3.6m, the mean nearest neighbour distance on the saltmarsh was 7.0% of the mean nearest neighbour distance on the mussel bed): z=-4.8, p<0.0001. Redshank fed at significantly greater distances to cover on the mussel beds (mean difference 61.5+/-13.4m, the mean distance to cover on the saltmarsh was 30.6% of the mean distance to cover on the mussel beds): z=4.8, p<0.0001. The mean age of redshank (where adults scored 2 and juveniles scored 1) was significantly greater on the mussel beds (mean difference 0.97+/-0.09, data were collected almost entirely from juveniles on the saltmarsh and adults on the mussel beds): z=-4.8, p<0.0001. The number of paces used by a feeding redshank was significantly higher on the mussel beds (mean difference 24.6+/-3.1, the mean number of paces on the saltmarsh was

71.9% of the mean number of paces on the mussel beds): $z=-4.1$, $p<0.0001$.

5.2.7 Estimation of Energy Intake Comparing a Redshank Feeding on the Mussel Beds and on the Saltmarsh at Low Tide

Average energy intake per hour was calculated for a redshank feeding on the saltmarsh and for a redshank feeding on the mussel beds, at the same time (at low tide). There was no significant variation in the number of swallows in either area by month (saltmarsh, $x^2=3.2$, $p=0.53$ and mussel beds, $x^2=6.8$, $p=0.15$, Kruskall-Wallis 1-way ANOVA). Intake data from October to February inclusive were therefore pooled, to obtain a representative intake rate per hour at low tide at any time, midwinter. Mean intake rate per two minute focal sample was 18.5 for the saltmarsh and 3.2 for the mussel beds. The mean time per hour in which no feeding could occur due to raptor disturbance was 4.2 minutes for the saltmarsh and 0.9 minutes for the mussel beds. Therefore, in an average hour, a redshank feeding on the saltmarsh took 516.2 prey items, and a redshank on the mussel beds took 94.6 prey items.

Energy intake was estimated by using the calorific values of prey, given in Table 7, obtained from other studies, and from observations of the size and type of prey seen taken during focal samples (Table 5) and found in redshank gizzards (Table 3). The calorific content per milligram of amphipods taken was assumed to be similar to that obtained from *Corophium*; all molluscs taken were assumed to have similar calorific values per mg to *Macoma*; *Carcinus* crabs were assumed to have similar calorific values to *Uca* crabs;

Table 7: Energy content of prey used in estimating energy intake on the mussel beds and the saltmarsh. AFDM=ash free dry mass.

	Prey Item	Energy Content KJ.g AFDM^{-1}	Source
1	Corophium	25.6	Speakman 1984
2	Macoma	19.1	Speakman 1984
3	Uca	21.0	Zwarts & Bloomert 1990
4	Nereis	26.8	Speakman 1984
5	Fish	23.4	Mean of 8 studies values given in Zwarts & Bloomert 1990

Conversion factors from length of prey to mg AFDM:

1.	Log(AFDM)=-2.21 + 2.42Log(Length in mm)	Goss-Custard 1977b
2.	5mm=2 AFDM 10mm=7.5 AFDM 15mm=17 AFDM	Speakman 1984
3.	Ln(AFDM)=2.9Ln(Carapace Width in mm)+3.2	Zwarts & Bloomert 1990
4.	A 1 bill length worm=30mg dry weight AFDM=-0.004 + 0.78(Dry Weight)	Goss-Custard 1977b
5.	AFDM=Dry Weight	Zwarts & Bloomert 1990
	Mean of 5 Gobius: Length=27mm+/-3 Total Dry Weight=0.26g =52mg AFDM per 27mm fish	This study

all worms were assumed to be Nereis, and the calorific value per mg of fish (taken from several studies, see Table 7) was assumed to be representative for Gobius. Overall, estuarine invertebrates have similar calorific values per mg of ash free dry mass (AFDM), (McLusky 1981). The major potential source of error in this estimation was the accurate relationship of length of prey to its AFDM content.

On the saltmarsh, redshank were assumed to be taking entirely amphipods. The ratio of the different size classes of amphipods selected by a feeding redshank was taken to be the ratio of the sizes of amphipods found in the freshly killed redshank gizzards (Table 3, taking size values as 5, 10 and 15mm). On the mussel beds, all mobile small prey taken were assumed to be 10mm amphipods (taking size values as the maximum of a particular size class), mobile large prey were assumed to be 20mm amphipods. Non-mobile small prey were assumed to be 5mm molluscs, and non-mobile large prey as 15mm molluscs. For crabs, worms and fish, the mean size of all individual prey taken was used. The average rate of energy intake per hour for the two areas was calculated for the saltmarsh as 21.2 KJ/hour, and for the mussel beds as 14.6 KJ/hour (Table 8). In calculating energy intake the relative digestabilities of different prey were ignored. The percentage digestability of various redshank prey are reasonably similar, e.g. crab 65.1%, fish 82.6%, hydrobia 64.5%, fly larvae c90% (Speakman 1987), and the main prey type taken was similar between the two habitats. The amount of energy expended per prey item was greater on the mussel beds (27.3 paces and 21.8 picks) compared to the saltmarsh (3.4 paces and 4.3

Table 8: Calculation of mean hourly energy intake rate for redshank feeding at low tide (+/- 2 hours) on the saltmarsh and the mussel pools.

Prey	Swallows per Hour	Prey Size mm	AFDM per Prey Length	Total AFDM mg		Energy Intake KJ/HR
SALTMARSH 516 Swallows per Hour						
Amphipod	137.5	5	0.3	41.3		
	254.4	10	1.6	254.4		
	123.8	15	4.3	532.3		
				828.0	=	21.2
				TOTAL	=	21.2
MUSSEL BEDS 95 Swallows per Hour						
Amphipod	45	10	1.6	72.0		
	11	20	8.7	95.7		
				167.7	=	4.3
Mollusc	28.4	5	2.0	56.8		
	0.3	10	7.5	2.3		
	0.2	15	17.0	3.4		
				62.5	=	1.3
Crab	5	7.5	14.1	70.5		
	2	15.0	105.0	210.0		
				280.5	=	5.9
Worm	0.5	1.5	7.8	3.9		
	3	2.4	30.0	90.0		
	0.1	3.5	62.9	6.3		
				100.2	=	2.7
Fish	0.3	2.8	52.0	15.6	=	0.4
				TOTAL	=	14.6

picks). Considering the mean energy value per prey item taken on the saltmarsh was 0.041 KJ and on the mussel beds was 0.152 KJ, then the mean amounts of energy gained per pace and per pick on the mussel beds were 0.0056 and 0.0070 KJ respectively, compared to 0.012 and 0.010 KJ on the saltmarsh. There was no significant difference in the wind speed between the two areas (z=-1.9, Wilcoxon Matched-pairs Signed-rank test, n=22 pairs of the mean of 5 wind speed measurements taken directly after focal feeding sampling, p=0.06: the trend was for the mussel beds to be windier than the saltmarsh). Temperature in the two areas was assumed to be the same in both areas as these were separated by only 800m. Overall a redshank, feeding at low tide, on the mussel beds probably used more energy during feeding, and took in less energy per hour than a redshank on the saltmarsh.

5.3 Discussion

Adult redshank on the mussel beds at low tide were risk averse foragers, choosing to feed in a relatively poor area in terms of energy intake, but with a much greater probability of escaping raptor predation. Juvenile redshank were actively excluded from the mussel beds, so could not be considered to be risk-prone foragers with respect to the saltmarsh or mussel beds: the decision variable of where to feed over the whole estuary for the adults was a constraint for the juveniles. Within the saltmarsh however, juveniles could decide where to feed with respect to cover. Juvenile redshank on the saltmarsh were risk-prone foraging, choosing to feed close to cover, in a relatively richer area in terms of energy intake, but with a much greater probability of being killed by a raptor.

Feeding territories were being held by adult redshank on the mussel beds, but not by juveniles on the saltmarsh. Individual redshank on the mussel beds excluded other redshank from defined areas during low tide (including two individually recognisable colour-ringed birds over several weeks). Redshank on the saltmarsh fed in large, dense flocks and no aggressive interactions were seen in these flocks. Defence of a resource has costs (through energy expenditure of chasing, and potential injury in fights - witnessed on two occasions between adults on the mussel beds) as well as benefits of priority of access to the resource (Brown 1964). Gill & Wolf (1975) showed the tradeoffs that occur in resource defence in sunbirds (Nectarinia reichenowi): birds defended territories only over a narrow range of nectar availabilities in the flowers within the territories. At low nectar levels, the costs of excluding intruders outweighed the gains in undepleted nectar, and at high nectar levels there was enough for the resident as well as intruders, without the resident having to use energy in intruder-exclusion.

Redshank on the mussel beds would appear to be defending territories to prevent depletion of limited resources. Energy values per prey item were much higher on the mussel beds, and prey appeared to occur at much lower density compared to the saltmarsh. Several feeding redshank could probably have rapidly depleted the area of prey. Rates of aggression in waders should increase with the patchiness of prey distribution (Recher & Recher 1969). This was found to be the case with short-billed dowitchers (Limnodromus griseus, Mallory & Schneider 1979). Redshank may have been excluding other redshank because of interference competition; intake rate was dependent on the spacing between feeding birds. The number of swallows increased as nearest neighbour distance increased. Redshank fed mostly by sight on the mussel beds, particularly when feeding on the larger, more profitable prey during wading in the mussel pools. Much prey was caught by heron-like surprise lunges, and would be consequently subject to disturbance by other redshank nearby. Territories were probably not being held on the saltmarsh, as prey was probably at a high enough density that a redshank could feed continuously and without depletion with near neighbours. There was no effect of spacing on the intake rate on the saltmarsh. Large flocks of redshank could therefore form to maximise anti-predation benefits without a large cost in reduced feeding (see also Goss-Custard 1976).

In both saltmarsh and mussel bed areas, there was no effect of spacing on success rate, and the number of picks increased as spacing increased, which suggested that interference competition, where it was occurring, was affecting the visibility of the prey. A redshank would probably only pick when prey was sighted, and a constant proportion of picks were then successful. On the saltmarsh, the difference between the pick rate of a bird with nearest neighbour distance of 1 and 25m was only 0.5% of the bird with the greater pick rate (102.0 picks for the 25m nnd bird). On the mussel beds the difference between the pick rate of a bird with nearest neighbour distance of 1 and 25m was 11.0% of the bird with the greater pick rate (87.3 picks for the 25m nnd bird). Interference competition was a much more significant factor on the mussel beds, and it was much more beneficial for a redshank to exclude others from its vicinity in order to increase its intake rate significantly.

If the net rate of energy intake within several areas is equal to, or greater than the net energy expenditure in a given time, then according to the hypothesis of optimality, if energy gain is not being maximised, an animal should choose the area that maximises its fitness with respect to the most important currency remaining. At Tyninghame, adult redshank on the mussel beds apparently did not starve, despite selecting lower quality feeding areas. Adult redshank could therefore afford to choose low tide feeding areas with respect to risk of predation. If energy intake rates fell below energy requirements and redshank feeding on the mussel beds started to starve, it would be expected that the territory-holders would abandon their territories and start to feed on the more profitable saltmarsh (e.g. Davies and Houston 1981). This appeared to be the case, as the number of adults feeding on the saltmarsh increased as the winter progressed, despite the redshank population of the estuary falling through the winter (Chapter 3). On three occasions in winter 3, an individually colour-ringed redshank, which usually maintained a territory around the mussel beds, fed on the saltmarsh at low tide, coincident with a late winter cold weather period.

Given that some adult redshank appeared able to survive the winter with a much lower energy intake at low tide than juveniles feeding on the saltmarsh, why did saltmarsh feeding redshank adopt risk-prone foraging? Redshank which fed close to cover (<15mtc) compared to those which fed further from cover (16-30m) were approximately three times more likely to be caught on attack, but the increase in feeding rate for a redshank feeding at less than 15mtc was 9.9% of that for a redshank feeding at 16-30mtc. Juvenile redshank may have been more likely to starve, due to smaller body size. Juvenile redshank were significantly smaller than adults at Tyninghame (see Chapter 3 and Prater et al. 1977), and therefore would be more prone to starvation in shorter periods of cold weather (Davidson & Evans 1982), and so would have to adopt risk-prone foraging more frequently than adults.

Low-tide-foraging may represent the major foraging period for juvenile birds, and energy intake during low tide represents a greater proportion of their daily energy budget than for adults. Juveniles were found to have lower intake rates compared to adults when feeding by wading (although these data were only collected in September and the differences may not have been maintained throughout the winter, e.g. Groves 1978, Whitfield 1985b). Juvenile and adult redshank had similar intake rates when feeding on the saltmarsh (see Chapter 4). At mid- and high-tides, when most feeding areas are at the tide edge, juveniles were probably unable to feed as well as adults. Age-related foraging differences have been found in a number of wader species (Groves 1978, Burger 1980, Whitfield 1985b) as well as in other bird species (e.g. Dunn 1972, Siegfried 1972). One problem with the argument that juvenile redshank were less efficient foragers when not feeding on the saltmarsh than adults was that the saltmarsh was available as a feeding area except during spring tides. The saltmarsh was only completely covered at most for 3 hours in any one spring tide, for only at most around 8 days in every month. An adult would have to feed very much more efficiently on spring tides to make up the energetic deficit of a juvenile, that had been feeding on the saltmarsh when conditions permitted.

There was limited space on the rocky shore and mussel beds for redshank, and there appeared to be strong competition for feeding areas. Possession of a feeding area (with exclusion of other redshank from that area) on the mussel beds greatly increased the probability of over-winter survival. Feeding on the saltmarsh may have allowed those surviving juveniles to have a high body weight at the end of the winter. Fat reserves gained before migration to the breeding grounds may be used, in part, for reproduction, as well as for fuel during migration (e.g. Davidson 1981a). High body weight would probably allow a redshank to lay eggs earlier in the season, with a higher probability of fledging more young earlier, and so allow it to return to its wintering site early enough to find a vacant territory. Failed breeders, however, tend to return earliest to the wintering grounds (e.g. Nettleship 1973, Whitfield 1985b), but the optimum strategy to maximise reproductive fitness (particularly in a relatively short-lived species such as a redshank) is likely to be a tradeoff between successful reproduction in all years as well as the earliest possible return to the wintering site. The redshank's young would also arrive at their wintering site early and so have a greater probability of finding a vacant, 'safe' area in which to feed and possibly in which establish a territory. Prior possession of a territory is frequently the determinant of the winner in territorial fights (Krebs & Davies 1987). Of those juvenile redshank colour-ringed in winter 2, and which fed on the saltmarsh throughout that winter, none returned to feed regularly on the saltmarsh, and several were observed winning territorial interactions as adults on the rocky shore during the following winter. Although feeding close to cover on the saltmarsh was a very risky strategy for juvenile redshank, it may have had a very high pay-off in future reproductive fitness, by establishing a pattern of early successful breeding, and early claiming of a winter territory.

The data presented in this chapter provide a reasonable indication that juveniles adopt a risk-prone and adults adopt a risk-averse winter feeding strategy. Ideally all redshank at Tyninghame would have been colour-ringed and the faithfulness to feeding sites, and acquisition of feeding areas on the mussel beds by second-winter-birds recorded. If possible, measures of body condition (through weight and size measurements) of adults on the mussel beds and juveniles on the saltmarsh would have been taken. Body condition, in conjunction with movements of individuals from the mussel beds to the saltmarsh, and vice-versa would have demonstrated whether adults were definitely adopting risk-averse foraging except when risk of starvation increased. The numbers of juveniles maintaining territories on the rocky shore and mussel beds in winters of low adult numbers would also have allowed testing of the hypothesis of age dependent risk-averse or risk-prone foraging.

CHAPTER 6: SPARROWHAWK WINTER HUNTING BEHAVIOUR

6.1 Introduction

Sparrowhawks are one of the commonest and most widespread raptor species in Britain (Sharrock 1976, Lack 1986). They are one of the major predators of birds, with nearly every British bird species of less than about 500g being recorded as prey (Newton 1986). Despite this, sparrowhawks are rarely seen and then usually only for a few seconds at a time due to their almost continual use of cover and preference for wooded habitats. Any observational study of hunting sparrowhawks must take account of the severe problems of sampling bias: only the small fraction of behaviour which occurs out of cover will be recorded. Sparrowhawks are well studied (see Newton 1986) but much of the data are for the breeding season. A complete description of sparrowhawk winter hunting behaviour is impossible using only observational methods. This chapter concentrates therefore on the factors which affect prey selection by sparrowhawks. These could be reasonably assessed based even on a sample of hunting observations because of the good recovery of sparrowhawk kills and ease of censusing the availability of prey. The main information necessary to determine why sparrowhawks select particular prey would be:

6.1.1 Diet: The range and variation in diet; which species are being taken?

6.1.2 Numerical Availability and Vulnerability of Prey: How do sparrowhawks respond to the relative numbers of different species of prey? How do individual prey species vary in conspicuousness and ease of capture, and so modify the availability of that species to sparrowhawks?

6.1.3 Raptor Interactions, Mobbing and Non-hunting Constraints: How is prey choice constrained by intra- and interspecific competition? How do activities other than hunting constrain the time available for hunting, and possibly limit prey choice?

6.1.4 Hunting Strategies: To what extent is prey choice controlled by the range of hunting strategies available to a sparrowhawk?

6.1.1 Diet

Sparrowhawk diet is almost entirely birds, with more than 120 bird species recorded (Cramp & Simmons 1980, Newton 1986). There are few British studies of sparrowhawk diet in the non-breeding season, e.g., Whitfield (1985a), Newton (1986). Winter diet is varied, for example, six species formed more than 5% of the diet in a study in south Scotland (Newton 1986). The ten most frequent species from September to March inclusive provided 78% of all items and 68% of food by weight, and sparrowhawks took all species that commonly occurred in the study area (Newton 1986). Whitfield (1985a) found that coastal wintering sparrowhawks took a wide variety of wader species, with redshank most frequently taken.

Sparrowhawks are strongly sexually size-dimorphic: female sparrowhawks are up to 25% larger than males (Cramp & Simmons 1980). Correspondingly, the different sexes show a difference in mean size of prey taken, with males regularly taking prey up to 40g and females regularly up to 150g (Tinbergen 1946, in Newton 1986, Cramp & Simmons 1980, Newton & Marquiss 1982). Mueller & Berger (1970) and

Toland (1986) found similar prey preferences, with the male preferring smaller prey in the similarly sexually size-dimorphic sharp-shinned (Accipiter striatus) and Coopers hawk (A. cooperii) respectively. Sexual size dimorphism in birds of prey is hypothesised to reduce intraspecific competition for food (Lack 1954, and reviewed by Newton 1979, Andersson & Norberg 1981), and is most pronounced in bird-eating raptors due to the difficulties of capture of flying prey, leading to unavailability and increased levels of intraspecific competition (Temeles 1985). Marquiss & Newton (1981) showed that female sparrowhawks occurred in more open habitats and hunted more in the open, so that differences in the diet of the two sexes will reflect habitat differences as well as size differences.

6.1.2 Numerical Availability and Vulnerability of Prey

If all prey species have a similar profitabilty to a sparrowhawk then it will be expected to show a functional response to the relative availability of different types of prey (e.g. Holling 1959a). The proportions of attacks and kills should exactly reflect the proportions each species represents in the total prey population. Prey species however, differ markedly in factors such as size, conspicuousness, use of cover, and escape ability. For example, larger prey will be the most profitable, in terms of energy gained per unit of energy used in hunting, but as prey gets larger, costs increase as chase lengths may get longer, and handling times in subduing large, struggling prey increase. The risk of injury also increases as prey gets larger (Newton 1986). Sparrowhawks will be expected to take the largest prey which can be killed easily. Species within the optimal size range of prey will vary in their vulnerability to predation by sparrowhawks (Tinbergen 1946, in Newton 1986, Newton 1986), as expressed by the percentage that a species occurred in the sparrowhawks' diet compared to the species' percentage occurrence in the population. The vulnerability index of a species has been interpreted as reflecting the time a predator spent hunting within the species' micro habitat, the conspicuousness of the prey (a composite of colouration and ecological habits, see Baker & Parker 1979), and the ability to elude capture on attack. Credible explanations of why different species have differing vulnerabilities to sparrowhawk predation require data on attack rate, success rate and detailed information of sparrowhawk use of hunting methods and areas, otherwise explanations are only reasoned guesses (Gould & Lewontin 1979, Newton 1986). The relative vulnerability of a prey species is likely to account for more of the variation in sparrowhawk choice of prey than simple numerical availability.

A major component of a species' vulnerability is how often it is attacked. Consequently the daily pattern of hunting will be important, particularly with respect to sparrowhawks hunting waders, because their availability will vary with the tidal cycle. Another major component of a species' vulnerability will be its ability to escape when attacked. The efficiency of sparrowhawk hunting has been little studied, particularly interspecific variation. Rudebeck (1950) calculated the percentage of attacks which resulted in capture as 12%, and Lindstrom (1989) calculated a success rate of

8%. Studies of bird feeding raptors have generally shown a low success rate of capture for the non-breeding season (see Temeles 1985 for a review), but this needs to be related to the daily pattern of hunting. A success rate of 1%, for example, may be more than sufficient if hunts are very brief, use little energy and the prey caught is very large. Many factors will affect the hunting efficiency of sparrowhawks, and will correspondingly have major effect on the winter behaviour, and population of both predator and prey species. Redshank, for example, respond to the presence of sparrowhawks by flocking (Whitfield 1988) and becoming more vigilant (Chapter 4), these behaviours reduce the success rate of attack by the sparrowhawk. The use of different sparrowhawk attack strategies, and choice of species to attack should reflect the behavioural responses of the prey. Choice of prey is further complicated by the fact that not all individuals within a species respond (or can respond) in the same way to a predator (Chapters 4 and 5). Certain sections of a population of a species may be more vulnerable and consequently more available than others. Rare inconspicuous species may also become very vulnerable through association with very vulnerable conspicuous species.

6.1.3 Raptor Interactions, Mobbing and Non-hunting Constraints

There have been few comprehensive studies of over winter sparrowhawk behaviour which quantify the possible effects of competition between sparrowhawks or other raptor species hunting in the same area, the effects of mobbing or any other constraints which may act on hunting and consequently prey choice. Marquis & Newton (1981) radio-tracked sparrowhawks in the winter in Scotland. Ranges of adult sparrowhawks were centred around winter roosts, with wide overlaps between individual home ranges. Several sparrowhawks would hunt in the same area during a day, although at different times. Ranging behaviour was related to hunting success: an unsuccessful bird moving until it made a kill. Sparrowhawks were found to be inactive for most of the day. Despite the biases in collecting observational data for sparrowhawks, it is the only way to collect data on the occurrence of specific behaviours during the winter, such as mobbing, interactions with other raptors and kleptoparasitism.

Much of sparrowhawk feeding behaviour appears to be the result of kleptoparasitism pressure (Newton 1986), but this has not been quantified. Kleptoparasitism between raptors and between raptors and crows (both opportunistic feeders on large prey) is common (Brockmann & Barnard 1979), and has been widely documented (e.g., Rudebeck 1950,1951, Sage 1963, Boyle 1966, Fischer 1985, Newton 1986, Temeles 1990). Temeles (1990) found a relationship in northern harriers (Circus cyaneus) between body size and territoriality towards other raptor species based on kleptoparasitism. Smaller raptor species were allowed into the area and kleptoparasitised while larger species, which were potential kleptoparasites, were chased off. The risk of kleptoparasitism may influence choice of prey: smaller prey may be selected to minimise handling time.

6.1.4 Hunting Strategies

Data on the hunting behaviour of sparrowhawks is largely anecdotal due to the large amount of time necessary to accumulate sufficient observations of hunting birds. Observational studies on wild hunting sparrowhawks include Owen (1930), Rudebeck (1950), Morse (1973), Barnard (1979), Newton (1986), Lindstrom (1989), and Wilson & Weir (1989). Of these only Rudebeck, Lindstrom and Wilson & Weir present quantitative data on attack types and success rates, although the results of falconry studies on hunting goshawks (Fox 1981, Kenward 1982) are probably very relevant to sparrowhawks. The main hunting strategy used by sparrowhawks is surprise (Owen 1932, Rudebeck 1950). The main hunting techniques of sparrowhawks were described as mainly short-stay-perch hunting (short flights between perches in dense cover), high soaring followed by stooping, contour-hugging flight, still hunting (followed by an ambush attack) and low quartering, although the last two were used much less frequently (Cramp & Simmons 1980, Newton 1986). Within a hunt, a hawk may attack prey by a direct flight at the quarry or an indirect flight which uses cover to conceal the sparrowhawks approach as much as possible (Newton 1986). Sparrowhawks have been recorded occasionally using other hunting methods (e.g Owen 1932, Morse 1973, Naunton 1973, Barnard 1979, Kemp 1992). Sparrowhawks, in general, appear to be very flexible predators, adopting a wide variety of hunting and attack types to varying conditions. Although they are predominantly woodland species, they use several hunting methods which allow surprise approaches of prey in open habitats.

There are significant aerodynamic differences between adult and immature _Accipiters_ which allow adults to fly faster (Mueller _et al._ 1981) so that choice of prey may be relatively constrained in juvenile sparrowhawks. Several studies have shown that there is a trend for hunting behaviour and hunting success to be related to the age of the raptor (Mueller & Berger 1970, Marr & McWhirter 1982, Toland 1986, Dekker 1988). Acquisition of effective hunting skills in the first winter is probably very important for future fitness (e.g Whitfield 1985b). Choice of prey may therefore be constrained by previous experience. Other studies have recorded a negligible effect of age on raptor hunting. For example Toland (1986) recorded no significant differences in attack success for adult and immature _Accipiter_ species and Fox (1981) found no difference in the success rate of attacks between adult and immature falconry goshawks (_A. gentilis_).

6.1.5 Prey Choice

Sparrowhawks are generalist predators, with a wide range of potential prey to choose from at any one time. Foraging theory is based on many assumptions about prey choice, and studies of hunting sparrowhawks could provide much information about these assumptions. For example, each species of prey will be uniquely vulnerable due to its specific habits, while within that species, behaviours such as flocking or concealment will vary the risk of predation. An individual sparrowhawk may have had much experience with a particular species, and so be more successful at finding and/or capturing it, but only within a very local area due to ranging habits. The resulting complicated interaction of intra- and interspecific prey vulnerability, coupled with individual sparrowhawk differences provides much opportunity for determining the factors which influence instantaneous prey choice decisions as well as the longer term evolutionary trends of predators and prey.

Sparrowhawks at Tyninghame hunted frequently in the open so allowing for many observations to be accumulated of hunting and attacking birds. The woods around the estuary could be easily searched allowing for the identification of much of the prey taken. Despite the problems of observing sparrowhawks and the biases of only being able to observe behaviour when they were out of cover, it was possible to obtain a reasonable idea of their ecology, as well as an indication of the factors probably influencing the prey choice decisions made by hunting sparrowhawks.

6.2 Results

6.2.1 Number of Sparrowhawks

Estimation of the number of sparrowhawks hunting at Tyninghame is important: for example an increase in observed attack rates may simply be a consequence of more individual sparrowhawks attacking at the same rate. As most sparrowhawk sightings were very short (54% of sightings were of a minute or less), and few of the sparrowhawks were individually marked, it was difficult to determine the exact number present in the study area at any one time. The pattern of sightings was similar in all three winters: there was no significant difference in the lengths of sightings between winters (x2=1.2, n=1802 sightings, Kruskall-Wallis 1-way ANOVA, p=0.54). Total number present was estimated daily in three ways: the total number of differently plumaged or aged birds seen; the maximum number of birds seen during one sighting and the relative frequency of sightings of individually recognisable sparrowhawks.

The total number of different individuals seen in any one day varied from 0 to 5. It was impossible to judge the efficiency of this estimate as an index of the total number of sparrowhawks present, but as the number of sparrowhawks increased the index will have become less accurate. Using plumage and age characteristics it will always be possible to record 4 different birds (male, female, adult and juvenile) per day without concurrent sightings of same plumage/age individuals. The time period of observation necessary to see all identically plumaged individuals at the same time (and therefore establish how many are present) will increase exponentially with the number of identical individuals present: all identically plumaged birds will have to be visible at the same time, an increasingly unlikely event as n increases.

p=probability of seeing any sparrowhawk in any one minute

n=number of sparrowhawks present

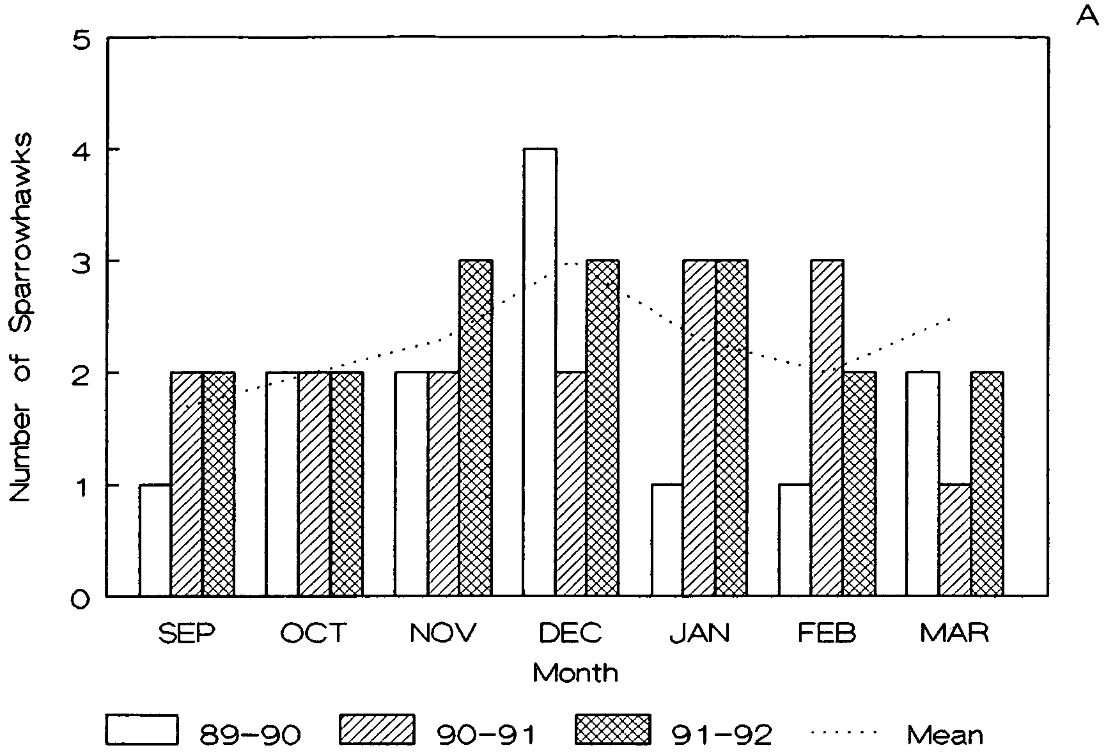
p_q=probability of seeing q specific individual sparrowhawks in the same sighting

$p_q=(p/n)^q$

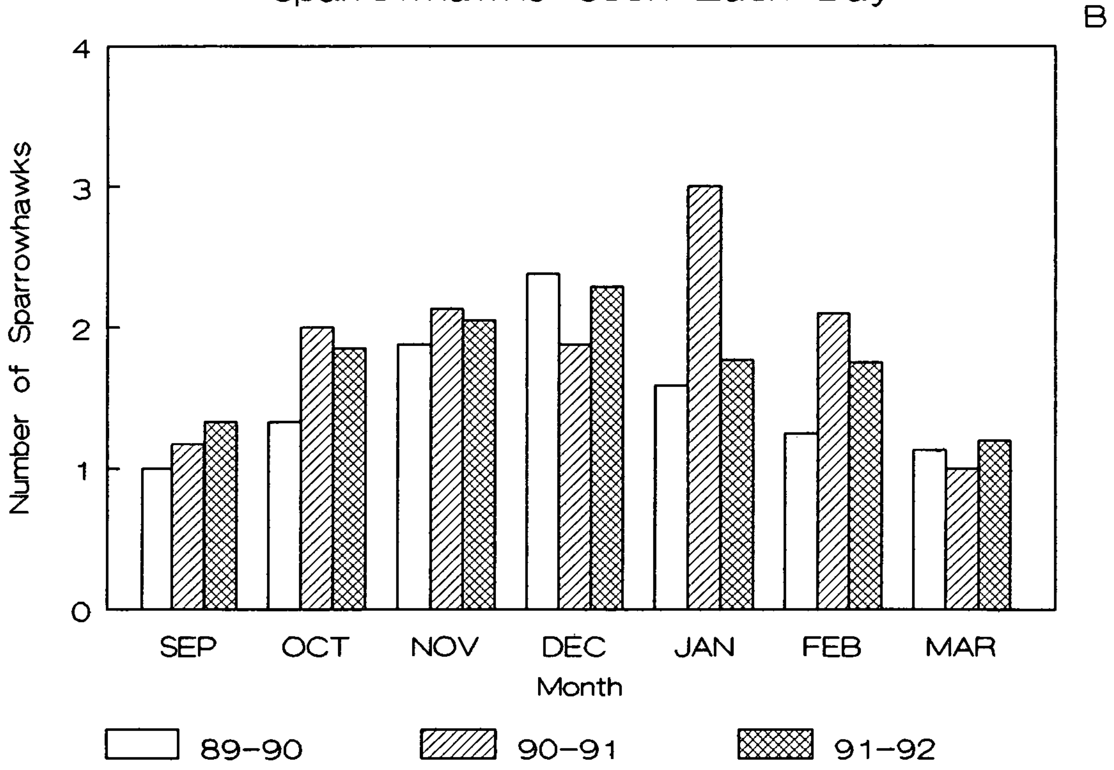
The mean maximum number of birds seen together in any one sighting reached a peak of three in any one month (mean calculated from the maximum number of birds in one sighting for each day of observation for a month; Fig. 1A). The number of sparrowhawks seen together peaked mid-winter with a second smaller peak in march. Two identically plumaged birds, e.g. two immature females were seen on several occasions, but there were no observations of three identical

FIGURE 1

Maximum Number of Sparrowhawks Seen Together in Any Month



Monthly Mean Total Number of Different Sparrowhawks Seen Each Day



birds. Observation periods may not have been sufficiently long to observe such rare events. For example assuming 9 sparrowhawks in the study area of which 3 are identical, and using frequency of sighting data from January 1991 (when the frequency of multiple sightings was greatest), then the time period (T) of observation necessary on average to see the three identically plumaged birds together (p_3) will be:

$$p=\frac{524 \text{ total minutes sparrowhawk sighting}}{2580 \text{ total minutes raptor watching}}$$

$$p_3=\{(0.203)/9\}^3 = 1.14 \times 10^{-5}$$

$$T=1/p_3 = 1{,}450 \text{ Hours}$$

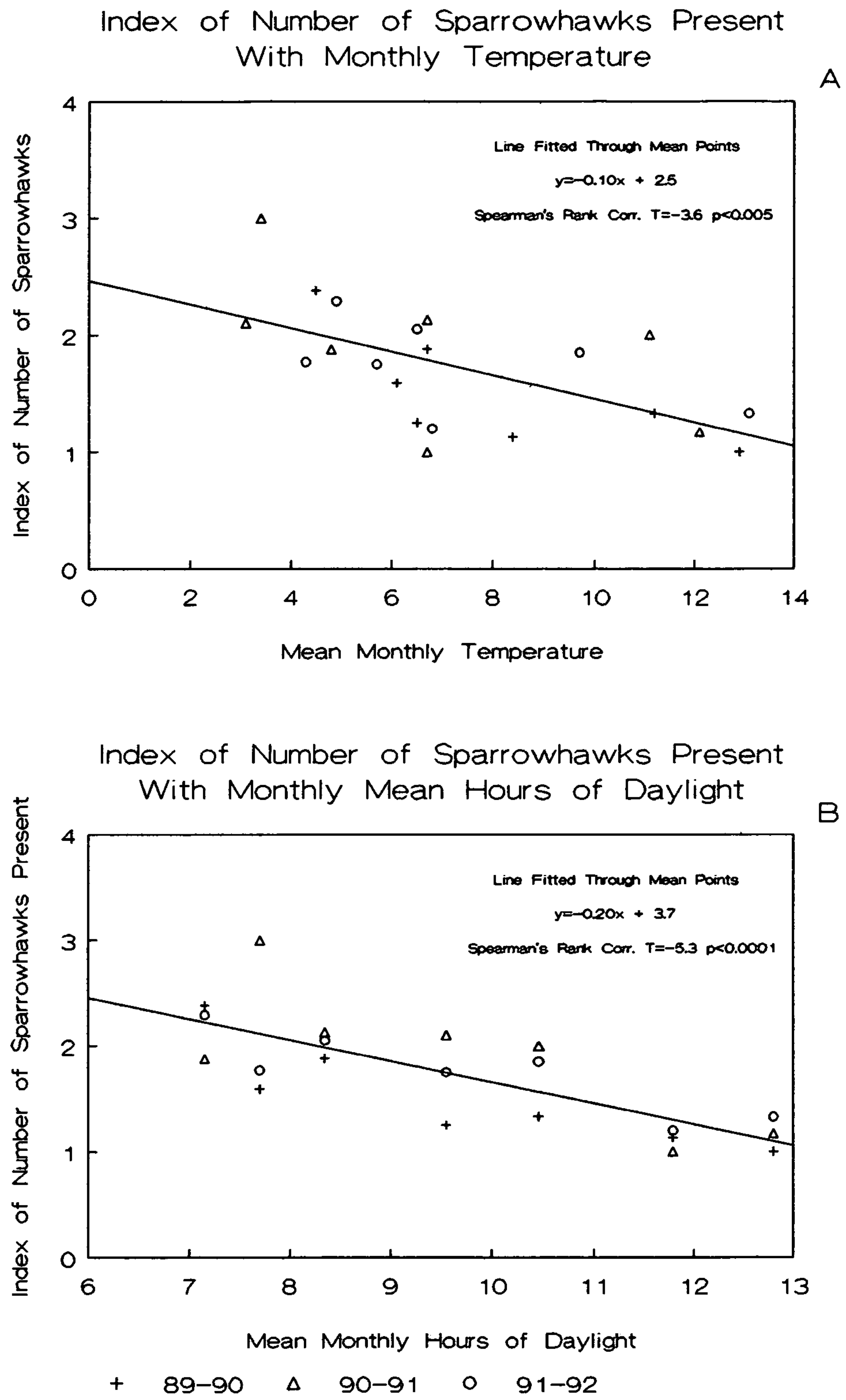
The calculation above assumes that sparrowhawks behave independently of each other which may not the case; a displaying sparrowhawk may attract one or more sparrowhawks and a sparrowhawk carrying prey often attracts other sparrowhawks, but both of these events were rare. The example above is useful as it demonstrates the limitations of attempting to estimate the actual number of sparrowhawks within an area from simultaneous sightings.

The total number of different sparrowhawks seen each day was averaged for each month to give an index of number of sparrowhawks present in the study area (Fig. 1B). The number of different sparrowhawks recorded daily peaked in December and January. This index was also dependent on the length of observation period but was probably not significantly affected by variation in observation effort. The daily number of hours spent at Tyninghame varied little (6.9 hours +/-1.0). There was also no strong relationship between the mean length of daily observation per month and the number of birds seen in that month (T=-1.6, n=21, Spearman's rank correlation, p=0.13).

During winter 2, one adult female sparrowhawk (LW) became individually recognisable due to the conjunction of a very bright (male type) plumage and by losing an outer primary from its left wing. There was no way to check the reliability of these characters, but it was frequently possible to count which primary was missing (the fourth) and so check with reasonable certainty that only one bird was involved. The ratio of sightings of LW compared to other or unknown sparrowhawks was not significantly different by month (G=0.81, G test, 2 df pooling Oct and Nov, and Jan and Feb to build sample sizes, p=0.68). Of three males radio-tagged, there were only two subsequent visual sightings after capture within the study area.

Overall the number of sparrowhawks in the study area was probably between 4 and 8 on any one day. Some individuals, such as LW, were resident at least for the winter, while some were very irregular visitors, such as the males that were radio-tagged. The monthly mean of daily estimates of the number of different sparrowhawks in the study area was used in subsequent analysis as an index of the actual number of sparrowhawks present. The index of number of sparrowhawks present was found to correlate (Spearman's Rank Correlation) negatively with mean monthly temperature (T=-3.6, n=21, p<0.005; Fig.2A) and mean monthly daylength (T=-5.3, n=21, p<0.0001; Fig 2B); there were more birds present in the study area at low temperatures and during short daylengths. The index also correlated (Spearman's Rank Correlation) positively with attack rate (T=4.0, n=21, p<0.001), number of prey taken (T=4.3, n=21, p<0.0005)

FIGURE 2


Index of Number of Sparrowhawks Present With Monthly Temperature
A
Line Fitted Through Mean Points
y=-0.10x + 2.5
Spearman's Rank Corr. T=-3.6 p<0.005
Index of Number of Sparrowhawks
0
1
2
3
4
0
2
4
6
8
10
12
14
Mean Monthly Temperature
Index of Number of Sparrowhawks Present With Monthly Mean Hours of Daylight
B
Line Fitted Through Mean Points
y=-0.20x + 3.7
Spearman's Rank Corr. T=-5.3 p<0.0001
Index of Number of Sparrowhawks Present
0
1
2
3
4
6
7
8
9
10
11
12
13
Mean Monthly Hours of Daylight
+ 89-90
Δ 90-91
O 91-92

and total weight of prey taken (T=5.1, n=21, p<0.0001); when there were more birds present in the study area more attacks were seen per hour and more prey was taken.

6.2.2 Diet

Sparrowhawks took a wide variety of prey at Tyninghame; an average of 14.9+/-0.8 species of prey were found per month. Overall, 43 species of bird and 2 species of mammal were recorded as prey (Table 1), the majority being redshank and dunlin (Fig. 3). Passerine species were commonly taken but contributed little to the amount of prey by weight, except in the cases of thrushes and starlings. Woodpigeons (Columba palumbus) and pheasant (Phasianus colchicus) were rarely killed, but formed a significant proportion of sparrowhawk diet due to their large masses. Waders typically formed 40-60% of sparrowhawk diet by number and about 60% by weight (Fig. 4). The total number of prey taken, the number of species taken, the total weight of prey found and the mean weight of prey was found to vary by month.

6.2.2.1 Total Number of Prey

The total number of prey taken (NOP) increased through the winter, peaking December to February with relatively similar low numbers of prey taken in both September and March (Fig 5B). The total number of prey taken correlated negatively with both mean monthly temperature (T=-5.6, Spearman's Rank Correlation, n=21, p<0.0001) and mean monthly daylength (T=-4.9, Spearman's Rank Correlation, n=21, p<0.001). The correlation with daylength disappeared when total

TABLE 1: Prey Found Killed By Sparrowhawks

	Kills	% by No.	Weight g.	% by Wgt
Pheasant	3	0.2%	1127	2.9%
Ringed Plover	3	0.2%	55	0.1%
Grey Plover	7	0.6%	246	1.5%
Lapwing	5	0.4%	200	0.9%
Knot	7	0.6%	146	0.9%
Purple Sandpiper	2	0.2%	63	0.1%
Dunlin	214	17.5%	51	9.3%
Ruff	3	0.2%	158	0.4%
Snipe	7	0.6%	115	0.7%
Woodcock	7	0.6%	325	1.9%
Redshank	356	29.1%	142	43.0%
Greenshank	3	0.2%	174	0.4%
Turnstone	27	2.2%	111	2.6%
Little Auk	3	0.2%	116	0.3%
Woodpigeon	30	2.5%	515	13.2%
Green Woodpecker	1	0.1%	194	0.2%
Great Spotted Woodpecker	1	0.1%	89	0.1%
Skylark	37	3.0%	40	1.3%
Meadow Pipit	4	0.3%	19	0.1%
Rock Pipit	23	1.9%	25	0.5%
Pied Wagtail	2	0.2%	24	0.0%
Wren	13	1.1%	9	0.1%
Dunnock	19	1.6%	22	0.4%
Robin	48	3.9%	20	0.8%
Blackbird	65	5.3%	103	5.7%
Song Thrush	23	1.9%	81	1.6%
Mistle Thrush	6	0.5%	129	0.7%
Redwing	22	1.8%	68	1.3%
Fieldfare	22	1.8%	116	2.2%
Goldcrest	28	2.3%	6	0.1%
Blackcap	1	0.1%	17	0.0%
Long-tailed Tit	2	0.2%	6	0.0%
Coal Tit	37	3.0%	9	0.3%
Blue Tit	45	3.7%	11	0.4%
Great Tit	10	0.8%	20	0.2%
Treecreeper	2	0.2%	9	0.0%
Rook	1	0.1%	532	0.5%
Starling	55	4.5%	89	4.2%
Chaffinch	36	2.9%	22	0.7%
Greenfinch	18	0.1%	31	0.5%
Goldfinch	3	0.2%	17	0.0%
Bullfinch	5	0.4%	25	0.1%
Linnet	9	0.7%	20	0.2%
Rabbit	7	0.6%	-	-
Vole	2	0.2%	-	-
Total	1224			

FIGURE 3

Prey Found Killed by Sparrowhawks
(Species which were recorded > 2%)

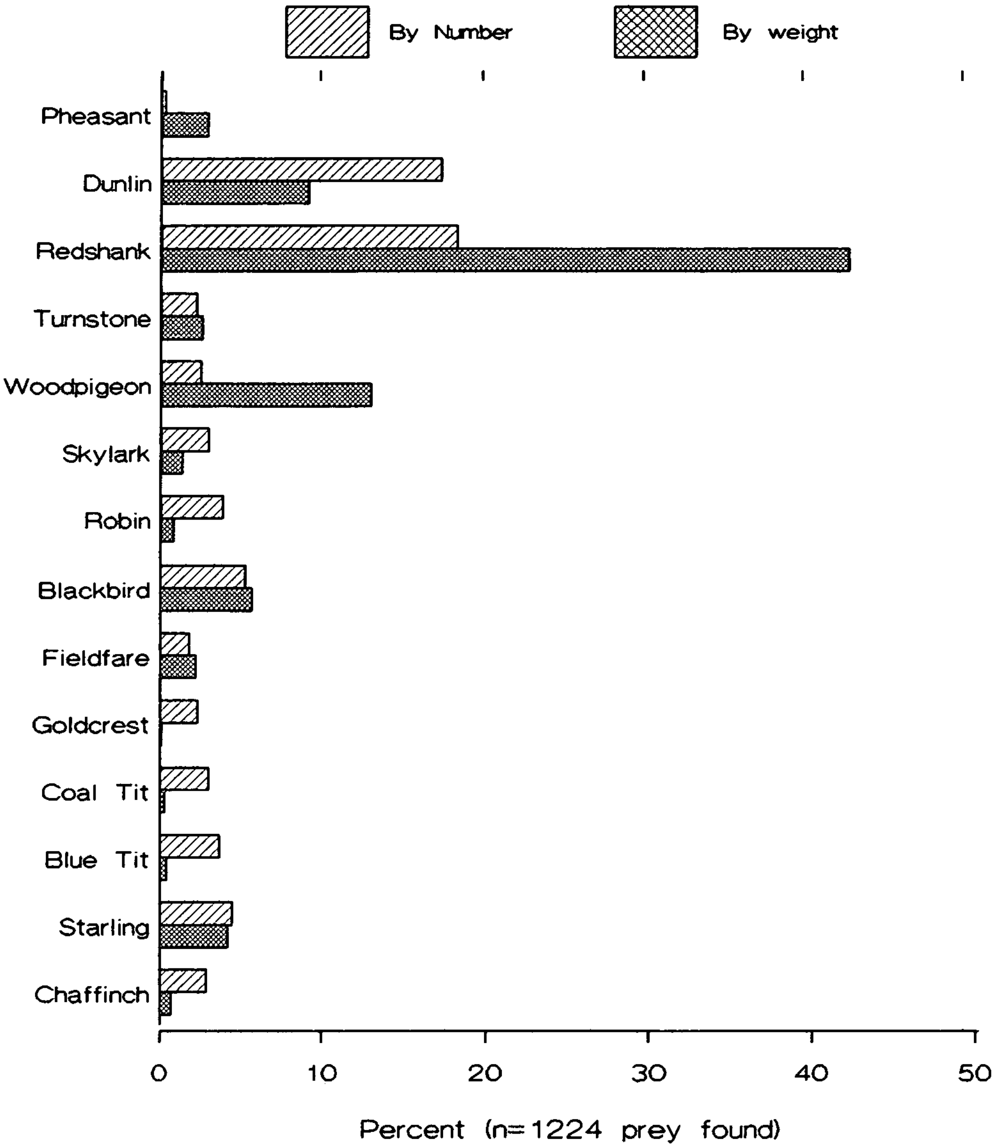
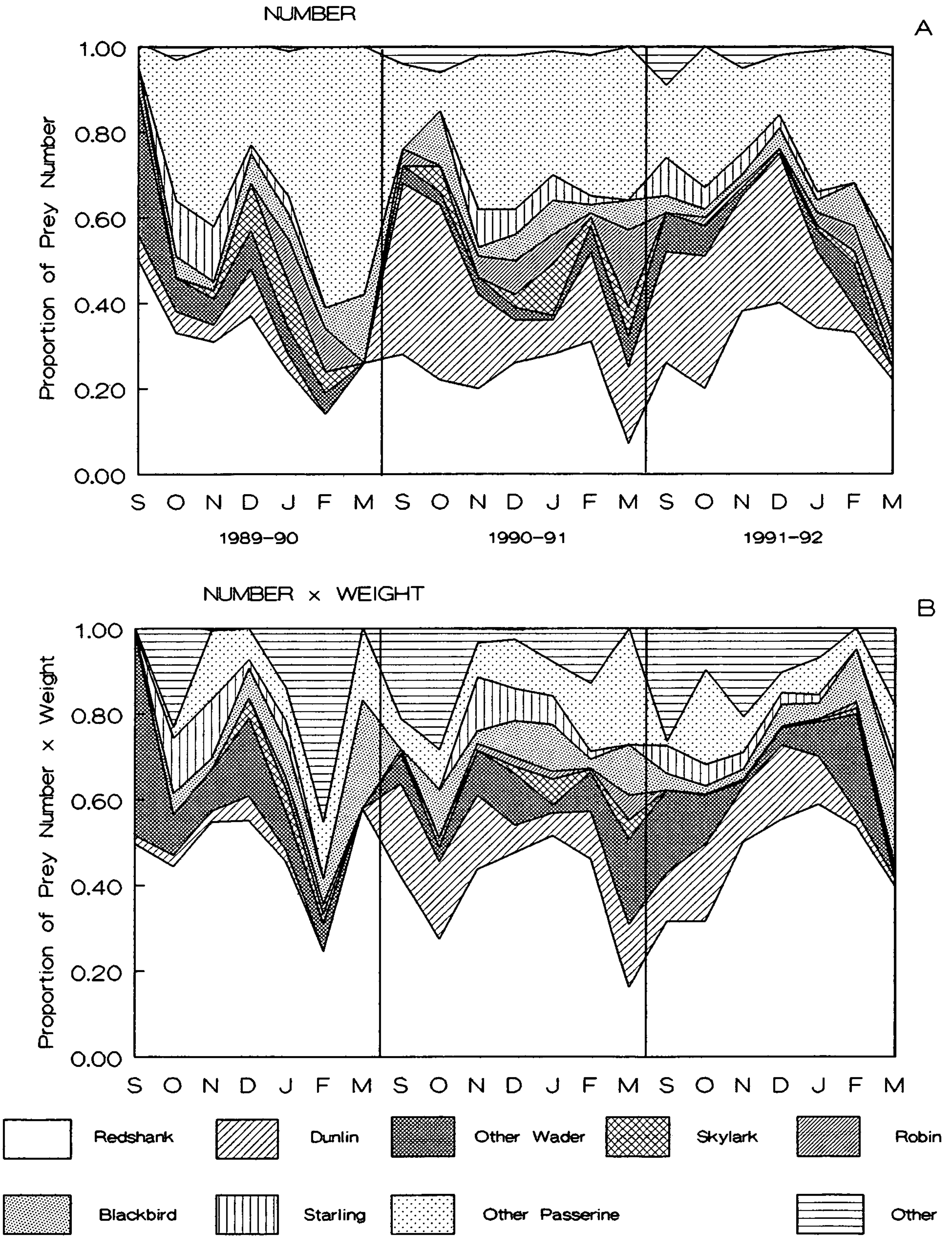


FIGURE 4

Variation in Sparrowhawk Prey By Month



number of prey was divided by the daily index of the number of sparrowhawks present ($T=-2.1$, Spearman's Rank Correlation, $p=0.05$). There was still a strong negative correlation between the number of prey/index of the number of sparrowhawks and temperature ($T=-3.3$, Spearman's Rank Correlation, $p<0.005$). At low temperatures sparrowhawks probably ate significantly more prey.

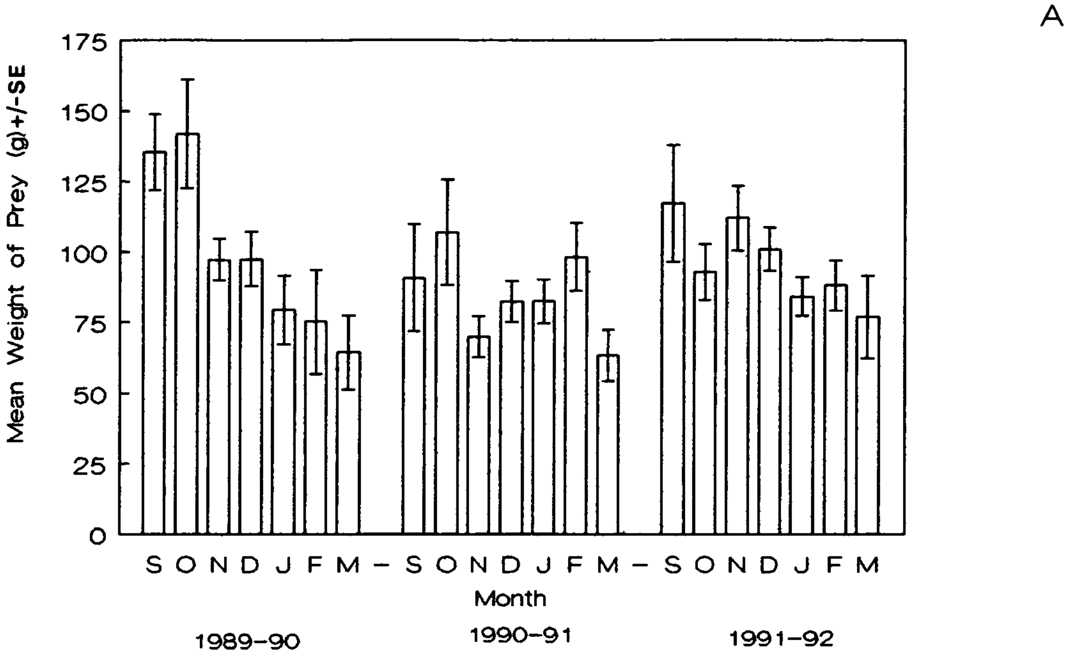
The number of species killed in each month increased as the number of prey increased ($T=5.4$, Spearman's Rank Correlation, $n=21$, $p<0.0001$). The number of species killed starts to become more constant at higher numbers of prey (as would be expected as the number of species available was finite) although the decrease in the rate of addition of new species at relatively high numbers of prey is not significant ($G=31.0$, 20 df, $p>0.05$). Due to the association between number of prey and number of species in each month there were strong correlations of number of species with temperature and daylength.

6.2.2.2 Total Weight of Prey

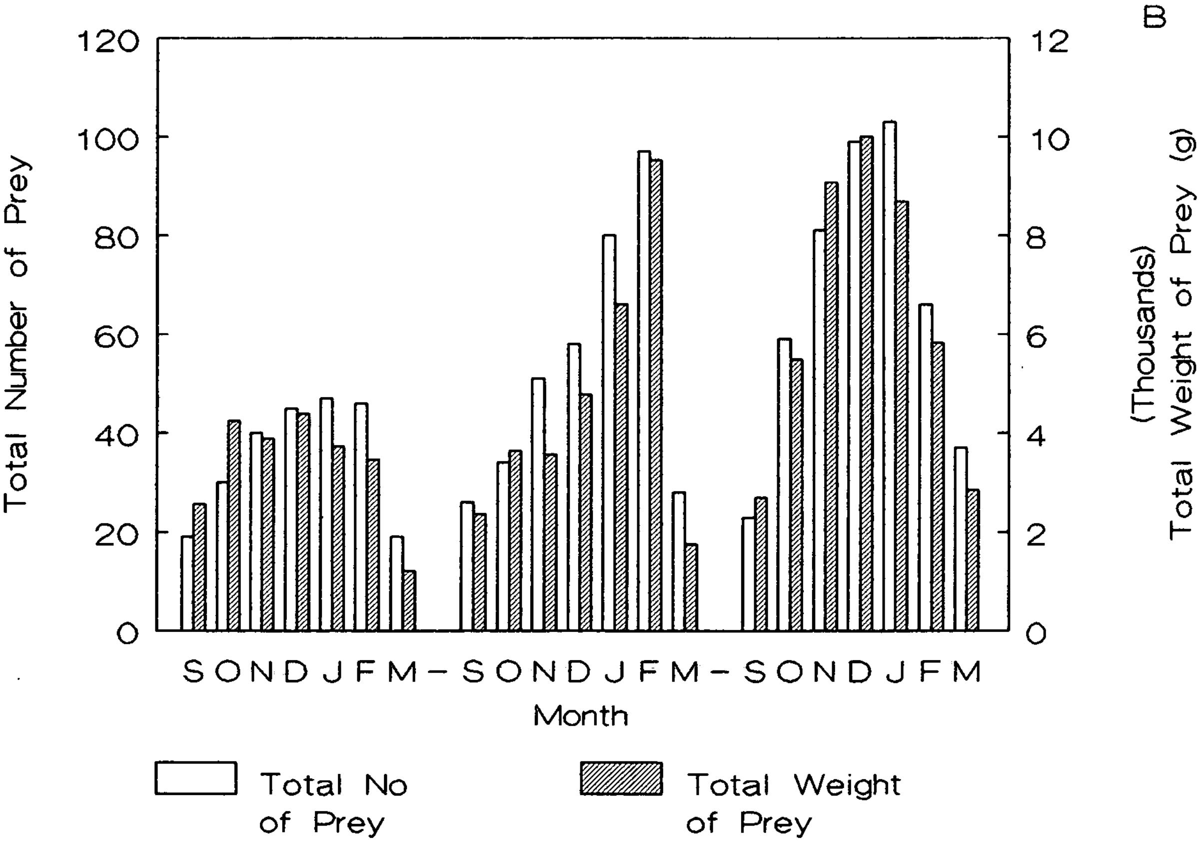
The total weight of prey taken increased approximately in accordance with the total number of prey taken (Fig. 5B), but the mean weight of prey taken per month varied significantly (Fig. 5A). There was no significant variation in the mean or variance of weight of prey between years (Between year: analysis of homogeneity of variance, Bartletts-Box, $F=0.82$, $p=0.44$; pairwise comparisons between years, no two groups were significantly different at the 5% level, Scheffe procedure; 1989-90, $x=94.7$g+/-5.6; 1990-91, $x=86.1$g+/-4.5 and 1991-92, $x=95.1$g+/-3.8). Within each year there was significant

FIGURE 5

Mean Weight of Sparrowhawk Prey by Month



Total Number and Weight of Sparrowhawk Prey Found in each Month



heteroscedasticity (Bartletts-Box: 1989-90, $F=8.6$, $p<0.0001$; 1990-91, $F=3.7$, $p<0.0001$; 1991-92, $F=3.4$, $p<0.005$), attributable to the varying number of species killed in each month. There was significant variation in the mean weight of prey by month ($x^2=36.2$, Kruskall-Wallis 1-way ANOVA, years pooled) and the mean weight of prey was found to decrease significantly from September to March ($T=-5.6$, Spearman's Rank Correlation, years pooled, $n=21$, $p<0.0001$; e.g. September $x=112.2$g+/-11.0, March $x=69.6$g+/-7.9).

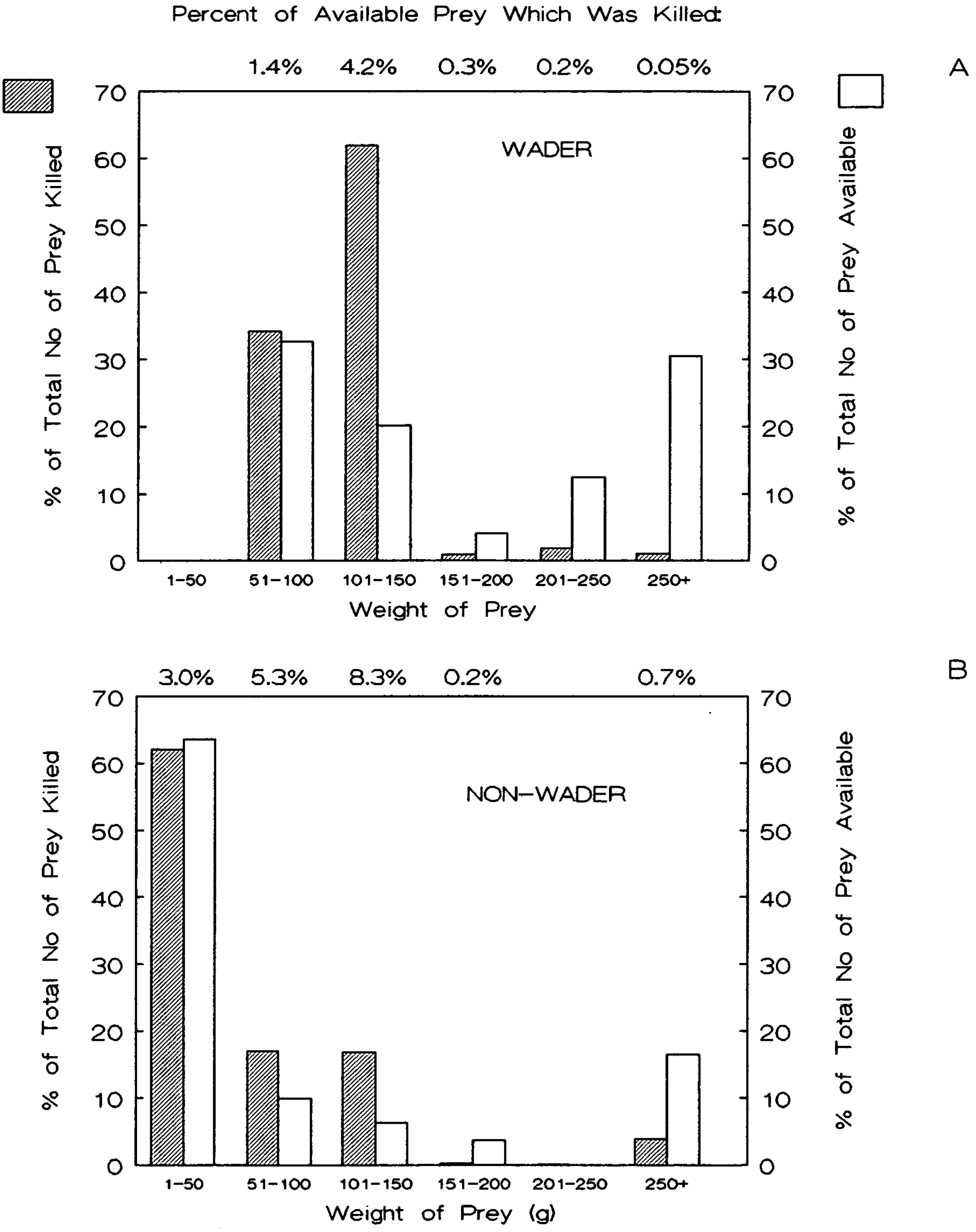
The total weight of prey found in each month was significantly correlated with mean monthly temperature ($T=-4.3$, Spearman's Rank Correlation, $n=21$, $p<0.0005$) and mean monthly daylength ($T=-4.5$, Spearman's Rank Correlation, $n=21$, $p<0.0005$). Both of these correlations were lost when the total weight of prey was adjusted (divided) by the index of the number of birds present (temperature: $T=-1.7$, $p=0.10$; daylength: $T=-1.2$, $p=0.24$). The high numbers of prey and correspondingly high total weight of prey found for months of low temperature and short daylength were probably a consequence of more individual sparrowhawks hunting around the estuary.

6.2.2.3 Selection of Prey

The weight of prey preferentially selected by sparrowhawks was between 51-150g: much more of this weight class was taken than would be expected from its relative occurrence in the population (Fig. 6). Small prey (1-50g) were taken approximately in accordance to their relative occurrence in the population. Prey of greater than 150g was rarely taken.

Weight of Prey Available and Selected by Sparrowhawks

FIGURE 6



Certain species of prey were more vulnerable to sparrowhawk predation than others as measured by the percentage a species represented in the total number of prey killed relative to the species' percentage occurrence in the population (vulnerability index). Waders and passerines were considered separately due to the different census methods employed; data from September to March inclusive were used. Most large wader species (grey plover and larger) were not vulnerable to sparrowhawk predation (indexes of less than 1), while the smaller waders (redshank and smaller) with the exception of knot were more vulnerable (indexes of greater than 1; Table 2). Many wader species had vulnerability indices of 0 due to their rarity in the population; a longer study would have been needed to determine their actual vulnerability. The relative vulnerability of the different wader species was reasonably constant between years - species remained consistently vulnerable or invulnerable. Analysis of concordance of vulnerability indices was restricted to those species that were either killed or commonly occurring, because multiple indices of 0 caused by rarity rather than invulnerability would lead to a meaninglessly high degree of concordance, as would the inclusion of species too large ever to be taken by sparrowhawks. The relative vulnerabilities between wader species commonly occurring and/or killed (see Table 2) were significantly similar between years ($w=0.71$, $x^2=34.1$, 17 df, Kendall's Coefficient of Concordance, $p<0.01$, alpha=0.025, Sequential Bonferroni, $K=2$). The relative vulnerabilities between wader species which were commonly killed (see Table 2) were significantly similar between years ($w=0.67$, $x^2=18.0$, 9 df,

TABLE 2: Wader Vulnerability Indices

		1989-90	1990-91	1991-92	1989-92
2	Oystercatcher	0.0	0.0	0.0	0.0
1	Avocet	-	0.0	-	0.0
	Ringed Plover	0.0	0.6	0.3	0.4
	Grey Plover	0.9	0.1	0.1	0.2
2	Golden Plover	0.0	0.0	0.0	0.0
	Lapwing	0.1	0.3	0.0	0.1
	Knot	0.2	0.5	0.5	0.4
2	Sanderling	0.0	0.0	0.0	0.0
1	Little Stint	-	-	0.0	0.0
2	Curlew Sandpiper	0.0	0.0	0.0	0.0
	Purple Sandpiper	0.0	2.1	3.3	2.0
	Dunlin	0.5	1.0	1.3	1.1
2	Ruff	-	0.0	52.5	28.7
1	Jack Snipe	-	0.0	0.0	0.0
	Snipe	10.7	9.6	3.8	6.7
2	Bar-tailed Godwit	0.0	0.0	0.0	0.0
2	Whimbrel	0.0	0.0	0.0	0.0
2	Curlew	0.0	0.0	0.0	0.0
1	Spotted Redshank	0.0	0.0	0.0	0.0
	Redshank	4.1	4.0	3.5	3.8
	Greenshank	4.3	0.0	0.0	1.2
1	Green Sandpiper	0.0	-	0.0	0.0
1	Common Sandpiper	0.0	0.0	0.0	0.0
	Turnstone	7.9	1.3	1.5	2.3

Comparing vulnerability indices between years using Kendall's Coefficient of Concordance:

1. Species excluded from analysis 1. Analysis 1 included all species found killed in at least 1 year and/or occurring in census at numbers of > 10 in any one month: w=0.71, x^2=34.1, 17 df, Kendall's Coefficient of Concordance, p<0.01, alpha=0.025, Sequential Bonferroni, K=2.

1. and 2. Species excluded from analysis 2. Analysis 2 included all species regularly killed (kills found in > 1 month): w=0.67, x2=18.0, 9 df, p<0.05, alpha=0.05, Sequential Bonferroni, K=2.

Kendall's Coefficient of Concordance, $p<0.05$, alpha=0.05, Sequential Bonferroni, K=2). 'Passerines' (with woodpigeons, pheasants and woodpeckers) showed a similar wide variety of vulnerability to sparrowhawk predation (Table 3). Jackdaws (Corvus monedula) and carrion crows were the only commonly occurring species that were not recorded as sparrowhawk prey. As most species of passerine are less than 175g, most were potentially available to sparrowhawks and correspondingly only one species, the siskin (Carduelis spinus), recorded a vulnerability index of 0 over the three winters. Siskins were the rarest species regularly recorded on the censuses, and so this index probably represents that rarity, rather than a true vulnerability. There were no obvious family trends for vulnerability, for example chaffinches were relatively invulnerable while greenfinches (Carduelis chloris) were highly vulnerable. The relative vulnerabilities between 'passerines' that commonly occurred (see Table 3) were significantly similar between years ($w=0.67$, $x^2=56.5$, 30 df, Kendall's Coefficient of Concordance, $p<0.01$).

There was a significant relationship between body weight and vulnerability index. Using passerine species (from Table 3) of weight of less than 150g, there was a significant positive correlation between body weight and mean winter vulnerability index ($T=2.7$, Spearman's Rank Correlation, $p<0.02$); larger prey up to the modal prey weight class (see Fig. 6) were more vulnerable to predation by sparrowhawks. At prey weights of greater than 150g vulnerability declined as body weight increased.

One of the major components of a species' vulnerability index is the degree of conspicuousness to a hunting sparrowhawk. This is very

TABLE 3: Passerine Vulnerability Indices

	1989-90	1990-91	1991-92	1989-92
Pheasant	0.0	0.5	0.0	0.2
Woodpigeon	0.3	0.3	0.3	0.3
Woodpecker Sp.	0.0	0.0	3.2	1.4
Skylark	0.6	1.1	0.6	0.8
Meadow Pipit	0.8	0.0	0.5	0.5
Rock Pipit	0.0	3.3	1.2	1.5
Pied Wagtail	0.0	0.0	0.0	0.0
Wren	1.0	0.6	0.3	0.6
Dunnock	0.8	1.3	1.5	1.3
Robin	1.6	2.3	0.9	1.5
Blackbird	4.3	3.4	4.2	3.9
Song Thrush	4.9	2.4	6.5	4.4
Mistle Thrush	0.0	0.3	4.0	1.0
Redwing	16.3	5.0	9.6	6.8
Fieldfare	3.6	0.8	4.8	1.2
Goldcrest	1.9	0.5	0.3	0.8
Warbler Sp.	0.0	0.0	4.8	3.1
Coal Tit	2.1	0.4	1.1	1.0
Blue Tit	0.7	1.3	2.0	1.6
Great Tit	1.7	0.6	0.6	0.8
Long-tailed Tit	0.0	0.0	0.4	0.2
Treecreeper	0.0	0.8	0.7	0.6
Jackdaw	0.0	0.0	0.0	0.0
Carrion Crow	0.0	0.0	0.0	0.0
Starling	1.0	0.8	0.9	0.9
Chaffinch	0.5	0.7	0.3	0.5
Greenfinch	2.1	1.9	3.7	2.2
Siskin	0.0	0.0	0.0	0.0
Goldfinch	1.6	0.0	3.0	1.3
Bullfinch	-	0.0	7.2	7.0
Linnet	0.4	0.4	0.2	0.4

Comparing vulnerability indices between years using Kendall's Coefficient of Concordance:

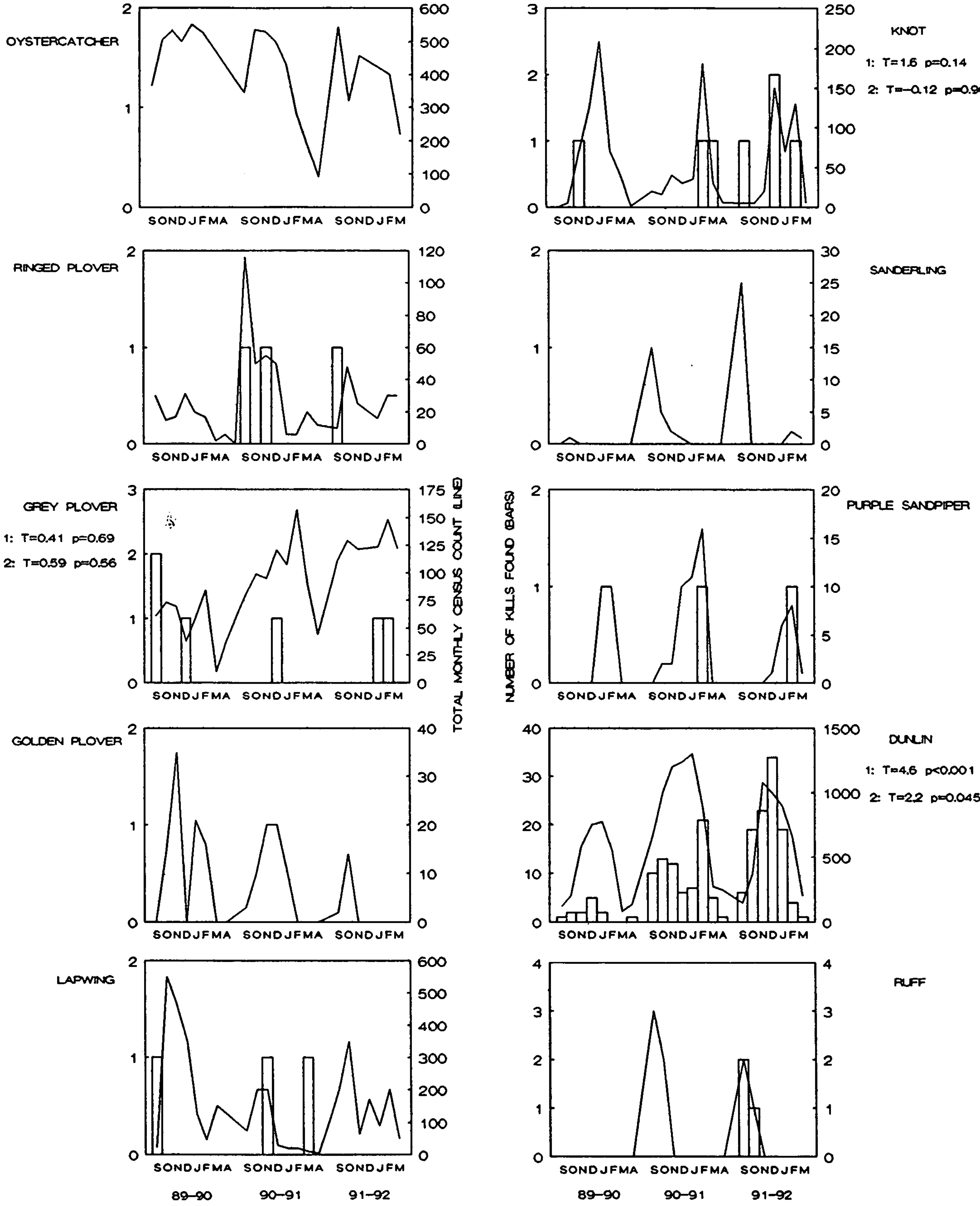
1. Species found killed in at least 1 year and/or occurring in census at numbers of > 10 in any one month: w=0.67, x^2=56.5, 30df, $p<0.005$.

difficult to quantify objectively across species, but within a highly sexually dimorphic species such as a chaffinch it was possible to determine whether the more conspicuous males were more vulnerable to predation than females. The ratio of female to male kills for chaffinches and female (including the similar plumaged immature males) and male blackbirds were compared to the relative occurrence of females and males within the population (with data pooled for the three winters to obtain sufficiently large sample sizes of kills found). For blackbirds there was no significant difference in the ratio of female plumage to male plumage kills (38:23) from that expected if sparrowhawks were selecting at random with respect to their occurrence in the population (262:112); $x^2=1.7$, 1df, p=0.20. For chaffinches the ratio of female to male kills (7:19) was not significantly different from the occurrence of females and males within the population (232:278); $x^2=3.6$, 1df, p=0.06. The trend is for the more brightly coloured male chaffinches to be selected in preference to the females, and the lack of a significant result may be due to small sample sizes.

The number of a prey species available and the number of a species killed each month were only significantly positively correlated in a small number of species (Figs 7A-7E). Where sufficient kills (>5) for a species were recorded, the number of kills was correlated with the census numbers for that particular month and the previous month. Among the wader species, grey plover, knot, turnstone and snipe showed no significant correlations with the current or previous month's census number; dunlin showed a highly significant correlation with the current month's census

FIGURE 7A

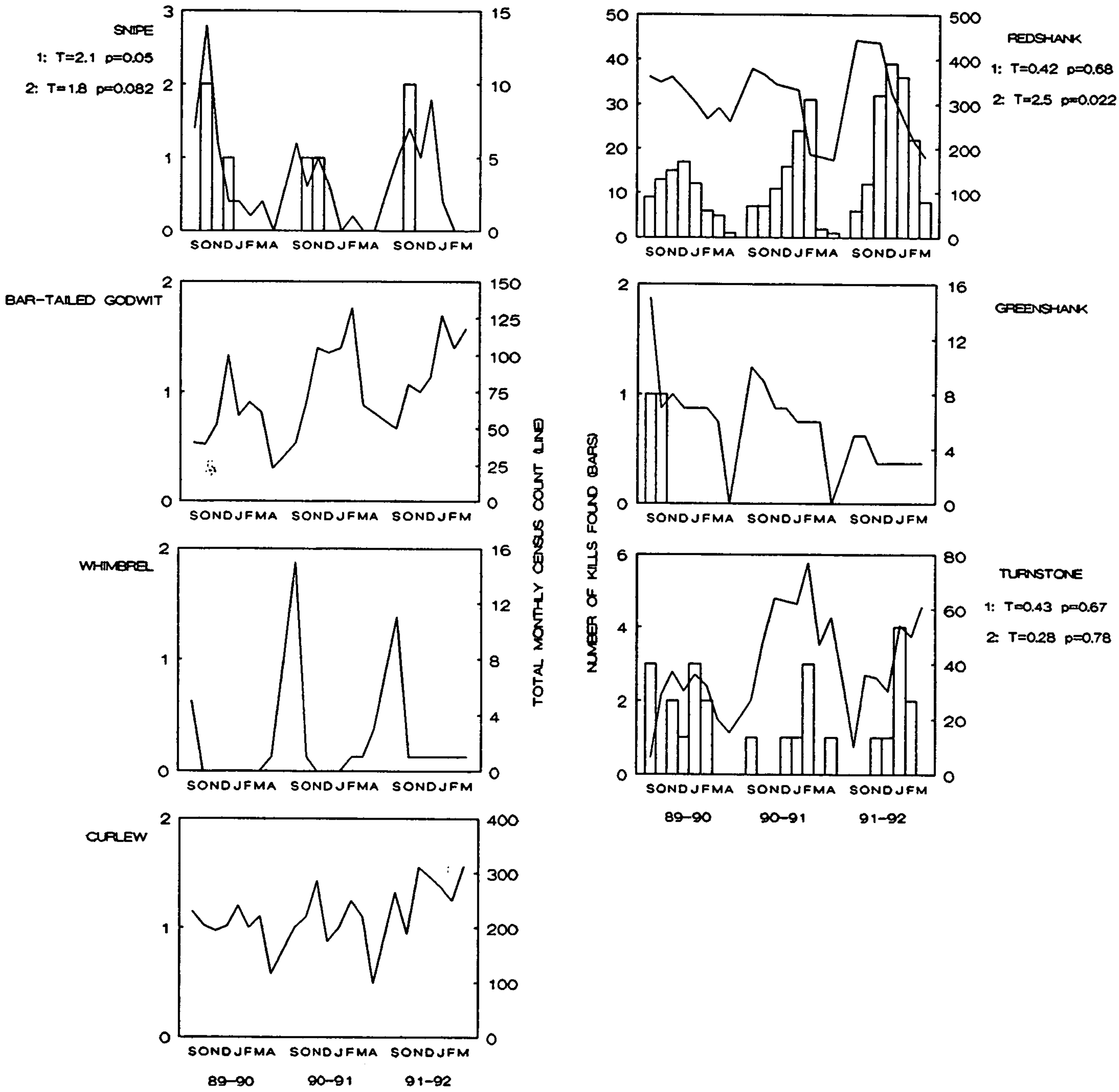
NUMBER OF WADERS CENSUSED (RIGHT AXIS, LINE) AND FOUND KILLED BY SPARROWHAWKS (LEFT AXIS, BAR) IN EACH MONTH



Spearman's Rank Correlation: No. of Kills with 1:Current Month and 2: Previous Month's Census Count

FIGURE 7

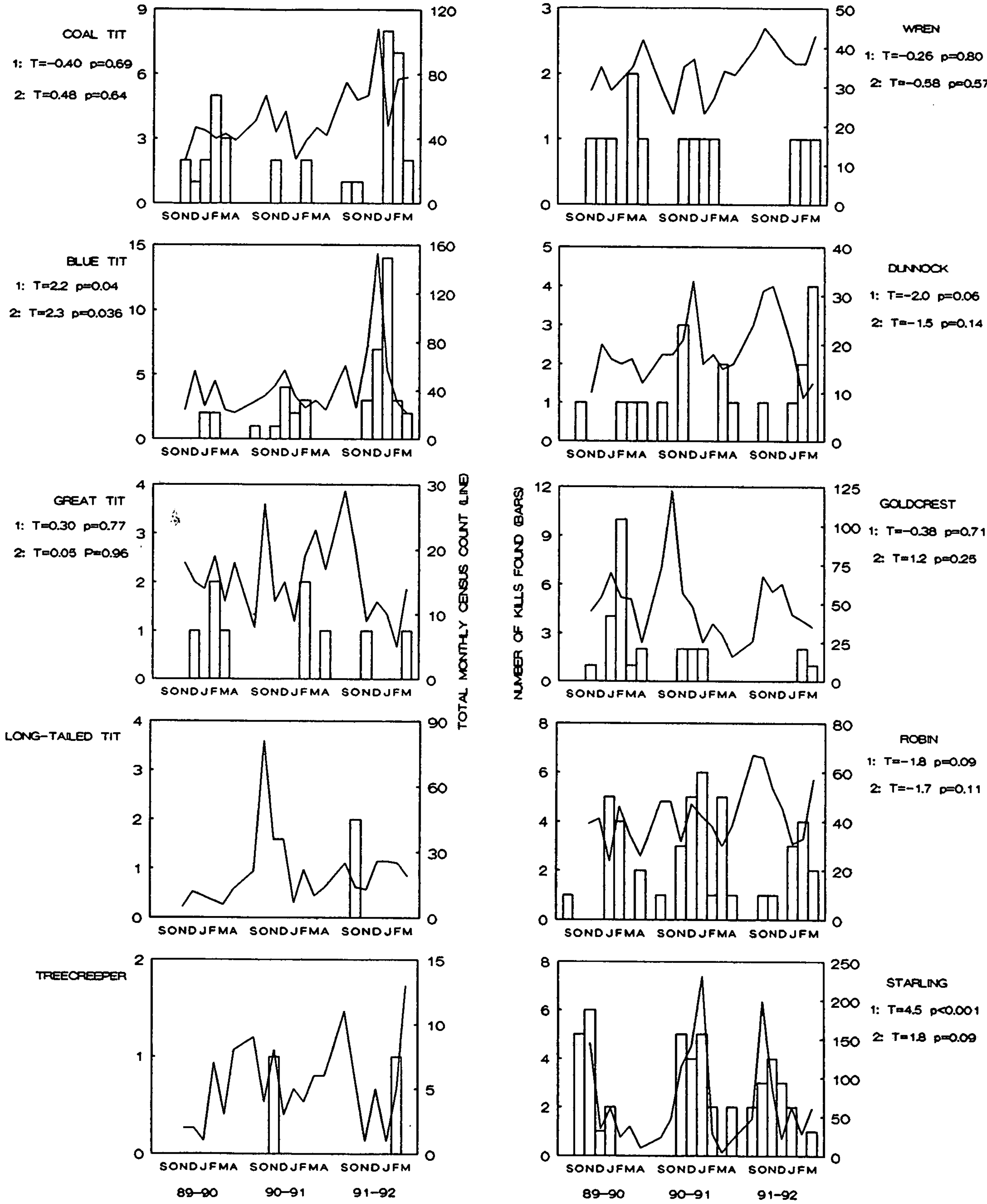
NUMBER OF WADERS CENSUSED (RIGHT AXIS, LINE) AND FOUND KILLED (LEFT AXIS, BARS) BY SPARROWHAWKS IN EACH MONTH



Spearman's Rank Correlation: No. of Kills with 1: Current Month and 2: Previous Month's Census Count

FIGURE 7

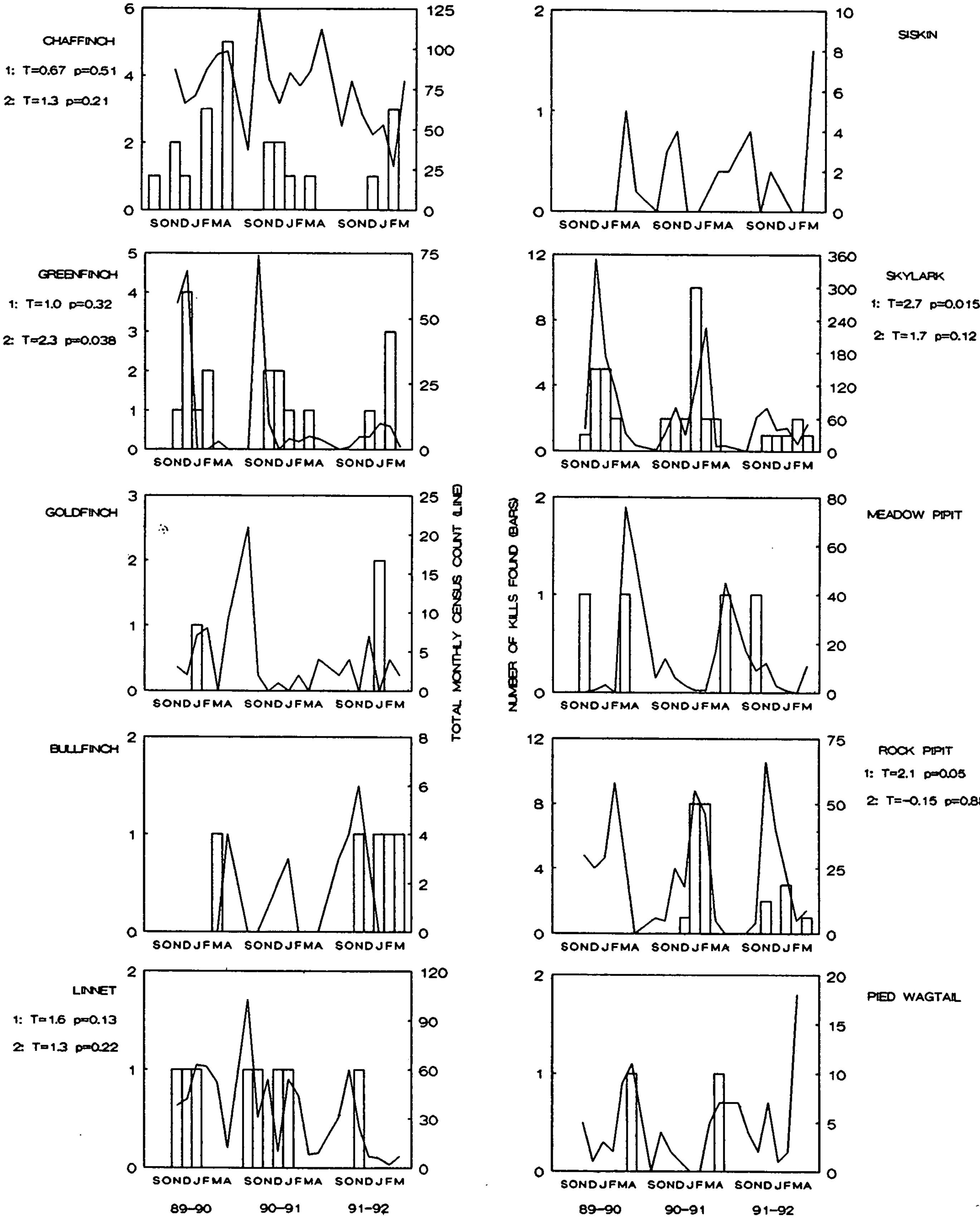
NUMBER OF NONWADERS CENSUSED (RIGHT AXIS, LINE) AND FOUND KILLED (LEFT AXIS, BARS) BY SPARROWHAWKS IN EACH MONTH



Spearman's Rank Correlation: No. of Kills with 1: Current Month and 2: Previous Month's Census Count

FIGURE 7

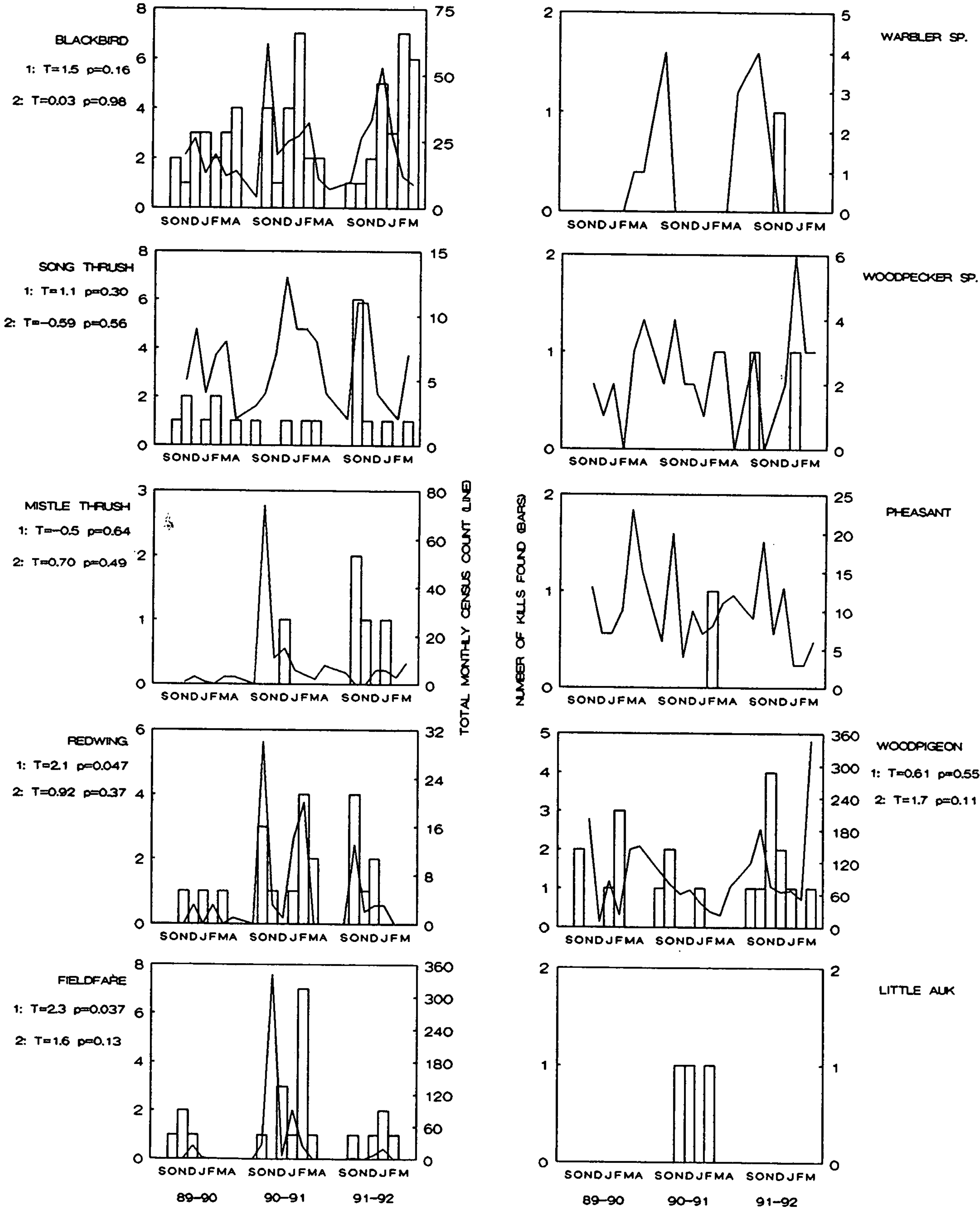
NUMBER OF NONWADERS CENSUSED (RIGHT AXIS, LINE) AND FOUND KILLED (LEFT AXIS, BARS) BY SPARROWHAWKS IN EACH MONTH



Spearman's Rank Correlation: No. of Kills with 1: Current Month and 2: Previous Month's Census Count

FIGURE 7

NUMBER OF NONWADERS CENSUSED (RIGHT AXIS, LINE) AND FOUND KILLED (LEFT AXIS, BARS) BY SPARROWHAWKS IN EACH MONTH



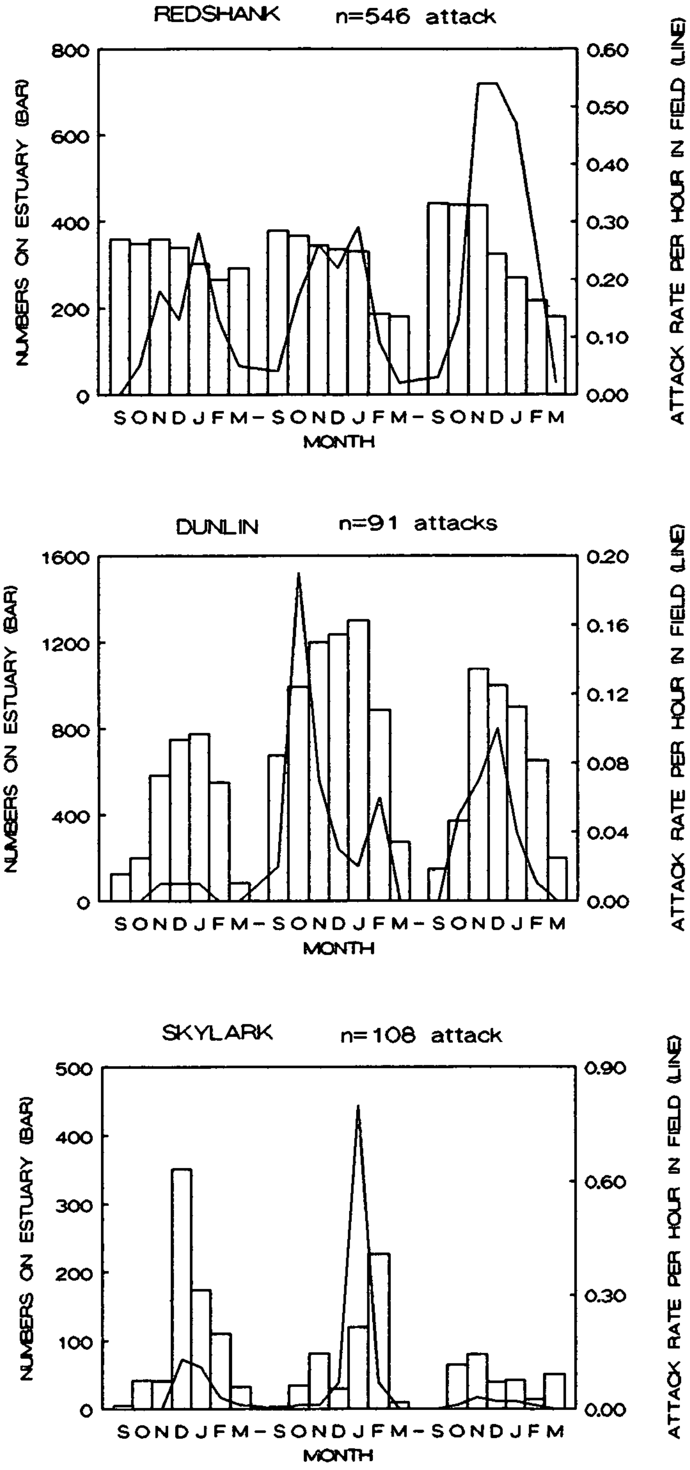
Spearman's Rank Correlation: No. of Kills with 1: Current Month and 2: Previous Month's Census Count

figure (e.g. more dunlin in a month, more kills in that month; T=4.6, Spearman's Rank Correlation, n=21, p<0.001, alpha=0.025, sequential Bonferroni, K=2) and redshank showed a significant correlation with the previous month's census count (e.g. more redshank in one month, more kills in the following month; T=2.5, Spearman's Rank Correlation, n=21, p<0.025, alpha=0.025, sequential Bonferroni, K=2). Of the 'passerines' only two species showed significant correlations between monthly number of kills and census counts: skylark kills were significantly positively correlated with the current month's census figure (T=2.7, Spearman's Rank Correlation, n=21, p<0.02, alpha=0.025, sequential Bonferroni, K=2); and starling kills were significantly positively correlated with the current month's census figure (T=4.5, Spearman's Rank Correlation, n=21, p<0.001, alpha=0.025, sequential Bonferroni, K=2). Blue tits (Parus caeruleus), rock pipits (Anthus spinoletta), dunnocks (Prunella modularis), redwings (Turdus iliacus) and fieldfares showed a trend for number of kills to reflect the current month's census figure, and greenfinches showed a trend for kills to reflect the previous month's census figure.

Where data were sufficient there were strong positive correlations between attack rate and the census counts for that species, matching the correlations between number of kills and census counts (Fig 8). For redshank, monthly attack rate correlated significantly with the previous month's census (T=-3.8, Spearman's Rank Correlation, n=21, p<0.005, alpha=0.025, Sequential Bonferroni, K=2); for dunlin, attack rate correlated most significantly with the current month's census (T=5.7, Spearman's Rank Correlation, n=21,

FIGURE 8

SPARROWHAWK ATTACK RATE (RIGHT AXIS, LINE) COMPARED WITH NUMBERS OF A PREY SPECIES AVAILABLE (LEFT AXIS, BAR)



Spearman's Corr.

1: T=0.20 p=0.85

2: T=3.8 p<0.005

Spearman's Corr.

1: T=5.7 p<0.0001

2: T=2.1 p<0.05

Spearman's Corr.

1: T=4.4 p<0.005

2: T=1.4 p=0.19

Spearman's Rank Correlation: Attack Rate with 1: Current Month and 2: Previous Month's Numbers of Birds

$p<0.0001$, alpha=0.025, Sequential Bonferroni, K=2); and for skylark, attack rate correlated with the current month's census (T=4.4, Spearman's Rank Correlation, n=21, $p<0.005$, alpha=0.025, Sequential Bonferroni, K=2).

Time budget data were analysed using a hierarchical loglinear analysis, in order to determine which variables were affecting sparrowhawk choice of prey. Sightings which contained an attack (n=490) were simplified into wader or non-wader attacks (choice, 2 levels) and analysed with mean daily temperature (4 levels; <3, 3.1-6, 6.1-9 and >9^{o}C), month (7 levels; September to March inclusive), time (4 levels; 6-9am, 9.01am-12pm, 12.01-3pm, 3.01-6pm), daylength (3 levels; 6-8, 8.1-10, >10 hours), tide state (2 levels; high or low tide +/-3 hours) and sex (2 levels; male and female). Only six factors were included per partial association analysis to reduce computing time; analysis 1 excluded month and analysis 2 excluded tide state. Month and tide state were not analysed together as the variation in tide state was a constant for each month.

In analysis 1, the highest significant level of interaction for the 6 factors was at the 3-way level (x^2=245, 106df, $p<0.0001$). There were no significant 3-way interactions involving choice of wader or non-wader. There were several significant 2-way interactions involving choice; choice and temperature (partial x^2=21.7, 3df, $p<0.0005$); choice and time (partial x^2=9.1, 3df, $p<0.05$) and choice and sex (partial x^2=58.4, 1df, $p<0.0001$). Significantly more non-waders were taken at low temperatures, e.g., 26.2% (43/121) of sightings with attacks at temperatures of less than 3^{o}c were on non-waders compared to 17.2 % (16/77) of sightings at temperatures of greater than 9^{o}C. Significantly more non-waders were taken earlier in the day, e.g., 20.5% (8/31) of sightings with attacks were on non-waders at 6-9am compared to 9.7% (11/102) of sightings at 3-6pm. Significantly more non-waders were taken by male than female sparrowhawks, e.g., 70.0% (28/12) of sightings of males making attacks were on non-waders compared to 11.8% (53/398) of female sightings. In analysis 2, month was included and tide state was excluded. There were no significant interactions between month and choice of wader or non-wader prey at either the 2- or 3-way level.

The sex of the sparrowhawk was further shown to influence choice of prey by direct observation of attacks. Male sparrowhawks showed a higher ratio of attacks on skylarks to attacks on redshank compared to female sparrowhawks (G=116.6, 1 df, n=595 attacks, p<0.001, alpha=0.01, Sequential Bonferroni, K=5), and a higher ratio of attacks on passerines to attacks on waders (G=123.1, 1 df, n=888 attacks, p<0.001, alpha=0.01, Sequential Bonferroni, K=5). Age of sparrowhawk did not appear to influence choice of prey: comparing adult and juvenile birds controlling for sex; males only, passerine vs. wader attacks (G=1.5, 1df, n=56, p>0.05); females only, passerine vs. wader attacks (G=0.83. 1df, n=224, p>0.05) and redshanks vs. skylarks (G=1.0, 1df, n=234, p>0.05).

6.2.3 Attack Rate

6.2.3.1 Directly Observed Attack Rate

Attack rate, as estimated from direct observation, was very variable. Attack rate on all species varied significantly between winters ($x^2=41.5$, 2df, $p<0.001$, alpha=0.05, Sequential Bonferroni, K=2) as did attack rate on redshank only ($x^2=52.9$, 2df, $p<0.001$, alpha=0.025, Sequential Bonferroni, K=2). Changes in attack rate measured from direct observation may simply be a consequence of changes in the number of sparrowhawks within the study area. Attack rates between winters were divided by the average of the monthly indices of number of sparrowhawks present for each winter; adjusted attack rate on all species remained significantly different between winters ($x^2=15.0$, 2df, $p<0.001$, alpha=0.05, Sequential Bonferroni, K=2) as did attack rate on redshank ($x^2=27.9$, 2df, $p<0.001$, alpha=0.025, Sequential Bonferroni, K=2). The attack rate for all species and redshank only, respectively, per hour RW was: in winter 1, 0.5 and 0.24; winter 2, 0.98 and 0.33; and winter 3, 0.98 and 0.62. The adjusted attack rate for all species and redshank only, respectively, per hour RW was: winter 1, 0.32 and 0.16; winter 2, 0.52 and 0.17; and winter 3, 0.56 and 0.36. For attack rate on all species winters 2 and 3 were very similar to each other, while for attack rates on redshank only, winters 1 and 2 were similar.

Attack rate varied significantly between month and hour of the day; there was much less variation between time of day controlling for month than between months controlling for time of day (Table 4). There was significant variation across all months during the same time of day for both winter 2 and winter 3, but significant variation between different times of day only in winter 2 in September and October, though there was a similar non-significant trend in the data for winter 3 (winter 1 data was not analysed due to blank cells). The pattern of attack rate split by time of day and

TABLE 4: Variation in Directly Observed Attack Rate By Hour and By Month

Attacks (A), Hour RW (RW), Attack Rate (A/RW)

1990-91

		SEP-OCT	NOV	DEC	JAN	FEB-MAR	x^2
6-10am	A	12	19	9	30	7	15.5
	RW	19.3	15.0	10.6	16.3	10.7	*$p<0.004$
	A/RW	0.62	1.3	0.85	1.8	0.66	a=0.005
10-2	A	8	5	7	22	5	23.4
	RW	20.4	16.6	11.3	13.8	8.2	*$p<0.001$
	A/RW	0.39	0.30	0.62	1.6	0.61	a=0.004
2-6pm	A	17	13	6	25	10	12.8
	RW	8.6	15.1	7.5	11.8	9.7	$p<0.02$
	A/RW	2.0	0.86	0.80	2.1	1.0	a=0.006
x^2		20.8	9.4	0.43	1.0	1.3	
		* $p<0.001$	$p<0.01$	$p=0.81$	$p=0.61$	$p=0.52$	
		a=0.005	a=0.005				

1991-92

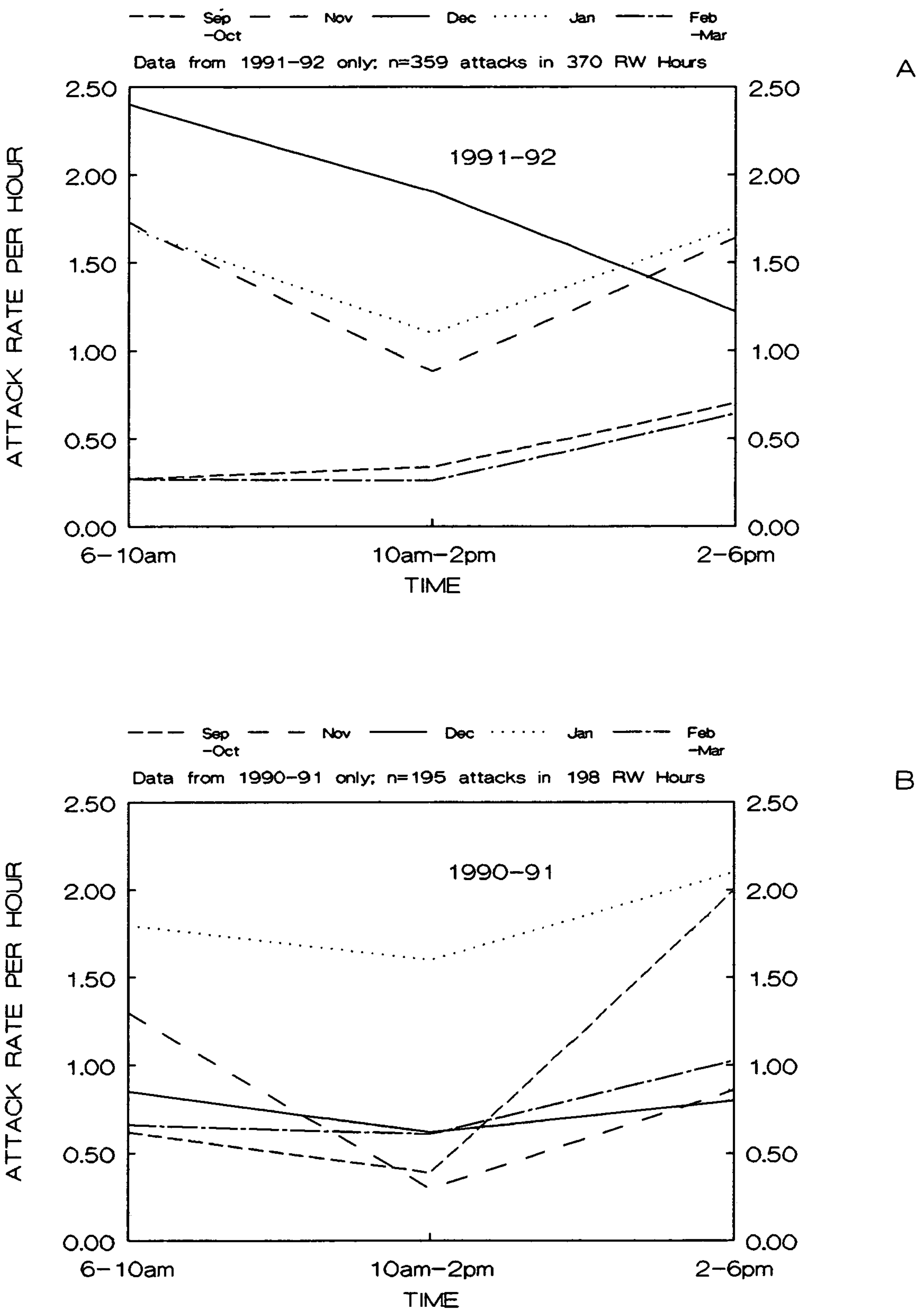
		SEP-OCT	NOV	DEC	JAN	FEB-MAR	x^2
6-10am	A	5	30	33	31	5	51.7
	RW	18.3	17.3	13.5	18.3	18.8	*$p<0.001$
	A/RW	0.27	1.7	2.4	1.7	0.27	a=0.003
10-2	A	12	22	51	30	6	53.2
	RW	35.5	25.1	27.5	28.5	22.9	*$p<0.001$
	A/RW	0.39	0.30	0.62	1.6	0.61	a=0.003
2-6pm	A	20	33	20	42	19	22.0
	RW	28.4	20.1	16.4	25.4	29.7	*$p<0.001$
	A/RW	2.0	0.86	0.80	2.1	1.0	a=0.004
x^2		6.3	7.2	6.2	4.6	5.9	
		$p<0.05$	$p<0.05$	$p<0.05$	$p=0.10$	$p=0.054$	
		a=0.007	a=0.007	a=0.008			

a=alpha, Sequential Bonferroni, K=16, at the 5% level month was different between winters 2 and 3 (Fig. 9). In winter 2 attack rate peaked in the morning in December; attack rate peaked equally morning and afternoon in January and November and only rose in the afternoon with little change in September, October, February and March. This consistent pattern, of a peak in December, did not occur the following winter. In winter 3 variation with time of day was less pronounced with only very slight peaks in attack rate in the morning compared to the afternoon in most months.

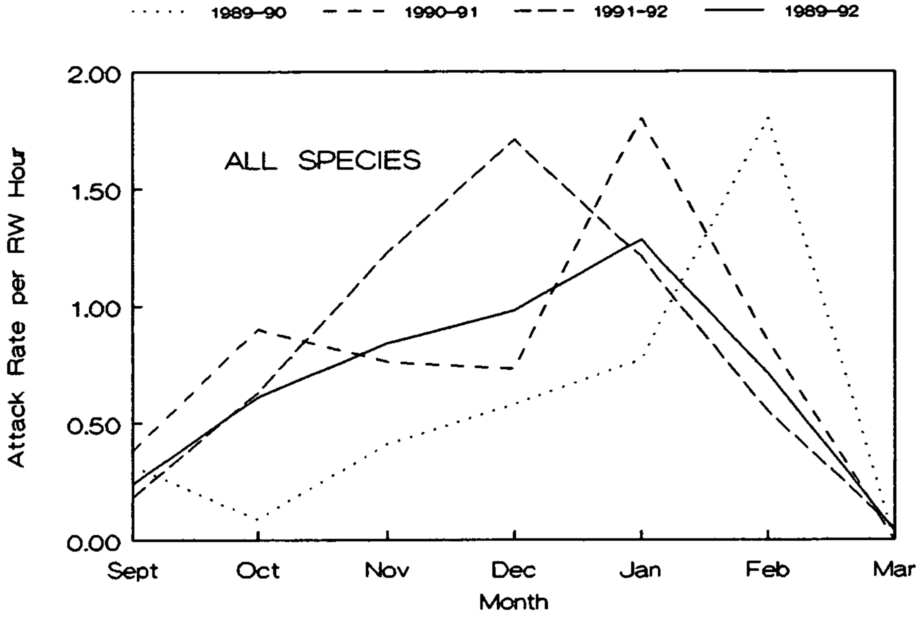
Attack rate over each winter showed a broadly similar pattern with a peak mid winter and similar low rates of attack at the start and end of each winter (Fig. 10). The peak attack rate occurred in a different month for each of the winters, February in winter 1, January in winter 2, and December in winter 3. The monthly peaks in observed attack rate coincided with the monthly peaks in the index of number of sparrowhawks present (compare Figs. 10 and 1B). Early in each winter, attack rate with time of day showed two significant peaks in the morning and evening, but these become less defined by December or January. When all months are pooled this pattern becomes very definite (Fig. 11): attack rate at 10am and 4pm is approximately double that of between 12am and 3pm inclusive. The number of birds hunting in the study area may have varied with time of day and month, causing these differences in observed attack rate. Confirmation of an increased midwinter attack rate per individual sparrowhawk came during winter 2, when an individually recognisable sparrowhawk (LW) was observed to attack more per sighting in December and January, 47.8% (11 attacks out of 23 sightings),

FIGURE 9

Sparrowhawk Attack Rates At Different Times of Day and Year



Variation in Sparrowhawk Attack Rate by Month



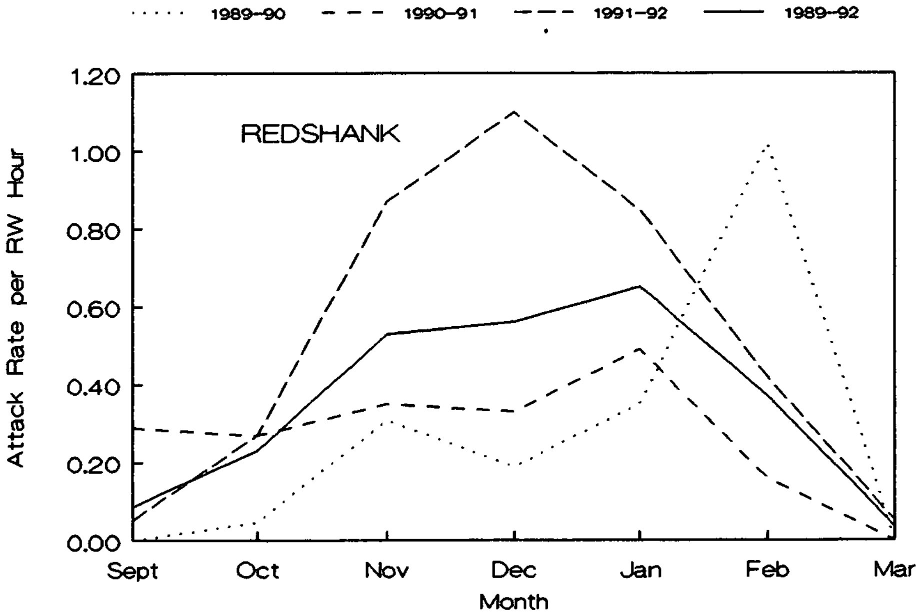
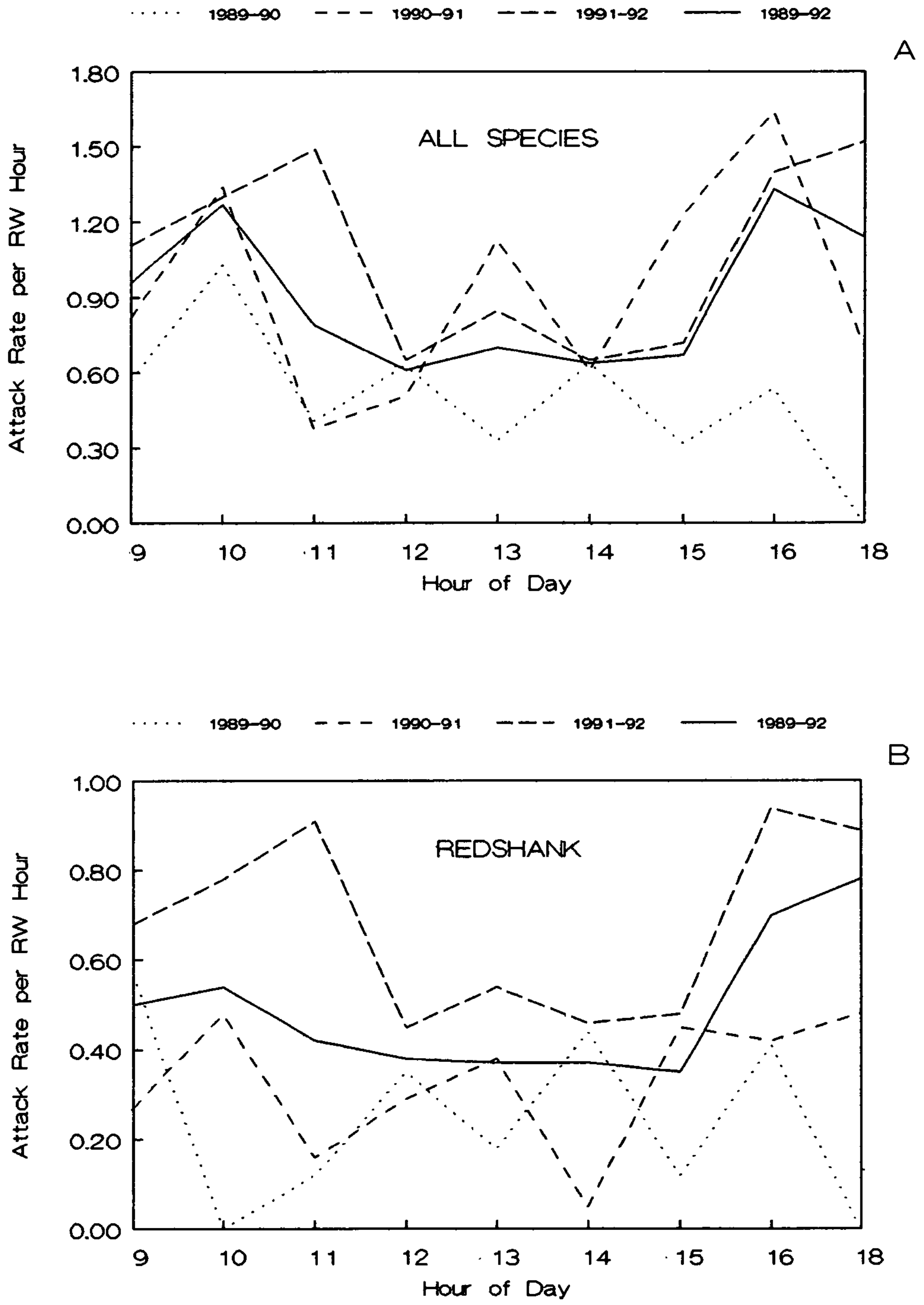


FIGURE 11

Variation in Sparrowhawk Attack Rate With Time of Day



compared to all other months, 20% (5 attacks out of 25 sightings); $G=4.1$, 1df, $p<0.05$.

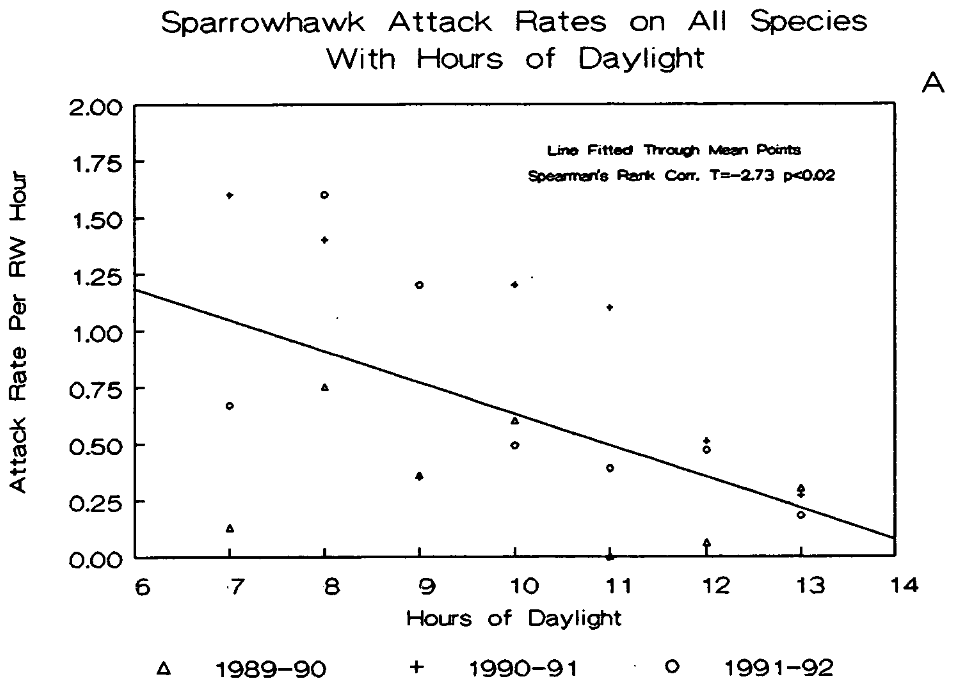
Attack rate (x) on all species correlated significantly with both mean monthly temperature (z) and daylength (y), ($t=-0.40$ and $t=-0.48$ respectively, Kendall's Rank Correlation, $n=21$). Attack rate and temperature were found to be independent when controlling statistically for daylength ($T_{xz.y}=0.125$, Kendall's Partial Correlation Coefficient, $p>0.05$) while attack rate and daylength were not found to be independent when controlling statistically for temperature ($T_{xy.z}=0.301$, Kendall's Partial Correlation Coefficient, $p<0.05$). Attack rate on all species therefore correlated most significantly with daylength; as daylength decreased the attack rate increased (Fig 12). When attack rate was adjusted by the index of number of sparrowhawks present, there was still a significant correlation between attack rate on all species and daylength ($T=-3.0$, Spearman's Rank Correlation, $n=21$, $p<0.01$) and between attack rate on redshank and daylength ($T=-2.9$, Spearman's Rank Correlation, $n=21$, $p<0.01$).

Directly observed attack rate was generally higher at low tide than at high tide except for attacks on non-waders which were higher at high tide (Table 5). Attack rates on waders were significantly higher at low tide.

6.2.3.2 Attack Rates From Time Budget Data

In order to remove the effects of number of sparrowhawks within the study area on the directly observed attack rate, time budget data were analysed scoring whether an attack occurred during a sighting,

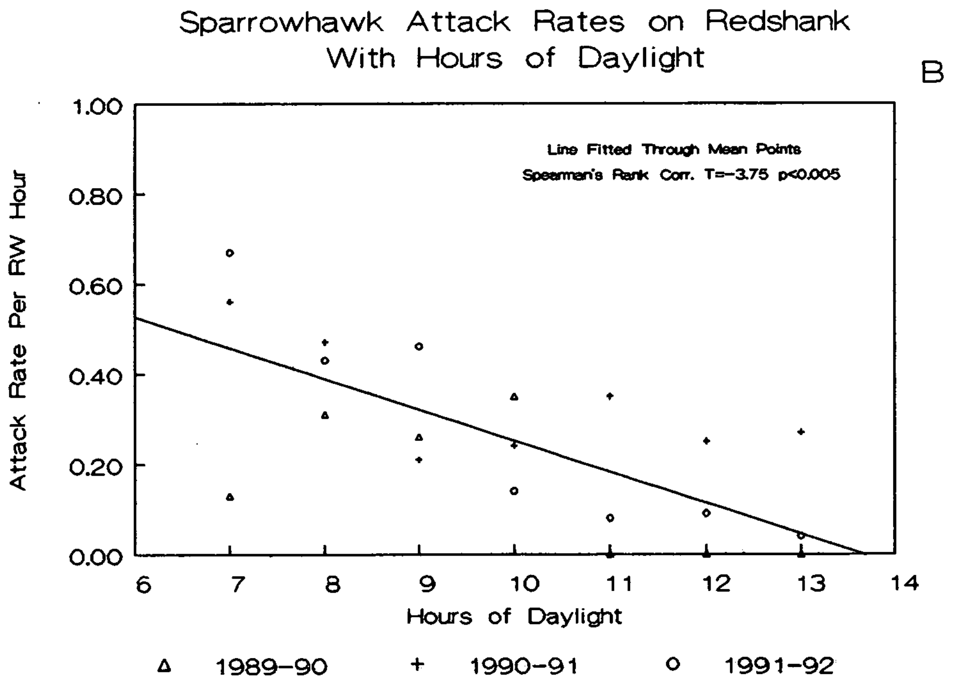
FIGURE 12



Sparrowhawk Attack Rates on All Species With Hours of Daylight

A

Line Fitted Through Mean Points
Spearman's Rank Corr. T=-2.73 p<0.02



Sparrowhawk Attack Rates on Redshank With Hours of Daylight

B

Line Fitted Through Mean Points
Spearman's Rank Corr. T=-3.75 p<0.005

TABLE 5: Directly Observed Attack Rate With State of Tide

Data from raptor watch periods completely within 1.5 hours of high or low tide.

	No. RW Hours	No. Attacks: All Species	Waders	Non-wader	Redshank
Low Tide+/-1.5	52	58	50	8	39
Attack Rate		1.12	0.96	0.15	0.75
High Tide+/-1.5	34	25	16	9	13
Attack Rate		0.73	0.47	0.26	0.38

High tide compared to Low Tide:

Wader Attacks: $x^2=6.5$ $p=0.012$, $a=0.025$

Non-wader Attacks: $x^2=1.3$ $p>0.05$

a=alpha, Sequential Bonferroni, K=2

and the variables correlated with this. Only sightings of less than 6 minutes were used in analysis as the probability of seeing an attack within a sighting was not significantly different across this range of sighting lengths (G=2.92, 4df, p=0.55; attack rates per sighting for 1 to 5 minute sightings was 0.43, 0.44, 0.57, 0.50, and 0.46 respectively). In total, 84.1% of sightings (n=1803) were of less than 6 minutes in length and contained 67.0% of attacks (n=1011).

The analysis was independent of the number of sparrowhawks but may have been subject to other sampling biases. If sparrowhawks move out of cover and so become visible more often in response to low temperatures, while the attack rate per bird remains constant, the number of sightings without an attack will increase and so attack rate will have appeared to decrease at low temperatures. The average length of sighting of a sparrowhawk will reflect the visibility of a sparrowhawk and so allow this type of sampling bias to be accounted for. The variation in the length of sparrowhawk sightings (of less than 6 mins, as used in the final analysis) was analysed across a variety of variables which appear to affect attack rate (using Kruskall-Wallis 1-way ANOVA): mean daily temperature in 12 classes (x^2=8.6, p=0.66), daylength in 3 classes (x^2=3.3, p=0.19), month in 7 classes (x^2=15.1, p=0.02), tide state in 2 classes (x^2=1.4, p=0.24), time of day in 4 classes (x^2=8.1, p=0.04) and sex of sparrowhawk (x^2=5.0, p=0.03). Where there was significant variation in the length of sightings for a variable, the variation in the probability of seeing an attack within sightings of different lengths was analysed. If, for example, there were relatively more sightings of 5 mins in December and the probability of seeing an attack was greater in a 5 min sighting then the attack rate will appear to be greater in December. There was no significant variation in the probability of seeing an attack in sightings of different lengths by: month (e.g. the highest value of $x^2=6.8$, 4df, $p=0.15$, for October); time of day (e.g. the highest value of $x^2=6.2$, 4df, $p=0.19$ for 6-9am); and sex (e.g., the highest value of $x^2=5.9$, 4df, $p=0.21$ for females). Therefore, within the analysis, the variation in the probability of seeing an attack within one sparrowhawk sighting of less than 6 minutes was not a consequence of variation in the length of that sighting.

Some variation in the probability of an attack occurring during a sighting may have been due to the variation in the amount of time spent raptor watching (which varied with time of day and by month). The probability of any length sighting containing an attack was not significantly different between raptor watch and non-raptor watch sightings ($x^2=2.1$, 1df, $p=0.14$), but was significantly different for sightings of less than 6 minutes. Thirty six percent (230/397) of non-raptor watch sightings had attacks in them, compared to 42% of raptor watch sightings (374/515); $x^2=4.2$, 1df, $p<0.05$. As raptor watching involved more intensive observation, very brief sightings were probably made more frequently, and these invariably were attack dashes out and straight back into cover. The variation in the probability of seeing an attack between raptor watch and non-raptor watch sightings was largely non-significant across the variables used in subsequent analysis of attack rate. There were no significant differences in the probability of seeing an attack within a raptor watch and a non-raptor watch sighting of less than 6 minutes by month, temperature, tide difference and sex. There were significant differences in the relative probabilities by time of day: e.g. at 3-6pm, 52% (98/90) of raptor watch sightings had an attack in them compared to 25% (22/67) of non-raptor watch sightings (x^2=17.4, 1df, $p<0.0001$); at 12-3pm, 42% (114/159) of raptor watch sightings had attacks in them compared to 50% (105/105) non-raptor watch sightings (x^2=2.9, 1df, $p=0.09$). There were also significant differences in the relative probabilities by daylength: e.g., at 6-8 hours daylength 45% (223/269) of raptor watch sightings had attacks in them compared to 37% (223/269) of non-raptor watch sightings (x2=4.6, 1df, $p<0.05$); at 8-10 hours daylength there were no significant differences (x^2=0.34, 1df, $p=0.56$). The variation in the probability of observing an attack within a sighting due to the two methods of sampling (raptor watch and non-raptor watch periods) was ignored during initial analysis so that large sample sizes appropriate for loglinear analysis could be maintained (pooling the two samples; analyses 1 and 2 below). Subsequent analyses attempted to discount this variation (analysis 3 below).

Hierarchical loglinear analysis was used to determine the variables which were determining the probability of attack (as a measure of attack rate). The factors which were used were attacks (2 levels, sightings with no attacks, or one or more), mean daily temperature (4 levels), time of day (4 levels), daylength (3 levels), sex (2 levels) and month (7 levels); 7 factor analysis used 1111 cases. Only six factors were included per partial association analysis to reduce computing time; analysis 1 excluded tide state and analysis 2 excluded month. Month and tide state were not analysed together as the variation in tide state was a constant for each month. Both 6 factor analyses used 1503 cases. The highest significant level of interaction for all 7 factors was at the 3-way level (x^2=431, 394 df, p<0.0001).

In analysis 1 there were two significant 3-way interactions: attack rate, temperature and daylength (partial x^2=13.5, 6df, p<0.05), and attack rate, time of day and month (partial x^2=32.9, 18 df, p<0.05). At short daylengths, for example, there were no significant differences in the probability of attack with temperature: (6-8 hours) 43% (92/121) of sightings had attacks in them at low temperatures (<3°C), compared to 54.5% (18/15) at high temperatures (>9°c). At longer daylengths (>8 hours) there was a significantly greater probability of attack at low temperatures: 49.1% (79/82) of sightings had an attack in them at less than 3°C, compared to 32.0% (80/170) of sightings at greater than 9°C. In most months there was no significant difference in the attack rate with time of day except in October and November which had significantly higher rates of attack later in the day (e.g., November 15.3% (3/23) of sightings had attacks in them at 6-9am compared to 41.5% (22/31) of sightings at 3-6pm). There were several significant 2-way interactions: attack rate and time of day (partial x^2=25.8, 3df, p<0.0001); attack rate and sex (partial x^2=38.0, 1df, p<0.0001) and attack rate and month (partial x^2=17.5, 6df, p<0.01). Attack rate increased significantly through the day, e.g., 24.4% (41/127) of sightings at 6-9am had attacks in them compared to 43.3% (120/157) at 3-6pm. Attack rate was significantly higher for female sparrowhawks, 49.1% (472/489) sightings of females had attacks in them compared to 25.6% (41/119) of sightings of males. Attack rate was significantly higher mid-winter: 26% (11/31) of September sightings had attacks in them; October, 32% (74/156); November, 40% (125/187); December, 39% (118/186); January, 50% (200/204); February, 39% (71/113); and March, 15% (5/28).

In analysis 2 where month was excluded and tide state added, there were two additional 3-way interactions: attack rate, temperature and tide state (partial x^2=11.6, 3df, $p<0.01$) and attack rate, time of day and tide state (partial x^2=9.3, 3df, $p<0.05$). At high tides, attack rate was similar across all temperatures (46.4%, 353/407 of sightings had an attack in them) but at low tides attack rate is higher at low temperatures, e.g., 45.4% (84/101) of sightings had an attack in them at less than 3°C compared to 29.1% (37/90) of sightings at greater than 9°C. The difference in attack rate at high and low tide became greater later in the day, e.g., at 6-9am, 24.7% (18/55) of sightings at low tide had an attack in them compared to 24.2% (22/69) at high tide; at 9am-3pm, 34.3% (190/362) of sightings at low tide had attacks in them compared to 49.3% (252/259) at high tide. There was one additional 2-way interaction: attack rate and state of tide (partial x^2=20.7, 1df, $p<0.0001$). At high tides there were significantly more attacks than at low tides, e.g., at high tide 46.4% (353/407) of sightings had attacks in them compared to 33.5% (249/494) sightings at low tide.

Analysis 3 was carried out to determine whether the significant interactions remained when the effects of the two different sampling methods (raptor and non-raptor watching) were removed. Raptor watch sightings only were used in the analysis of the factors influencing attack rate. The factors that showed significant variation in the probability of seeing an attack within a sighting and that gave significant interactions in analyses 1 and 2 were time of day, daylength and month. The 4 factor analysis had no significant 3-level interactions; the interaction between attack rate , time of day and month was not significant (partial $x^2=20.4$, 18df, $p=0.31$). The result contrasts with the significant interaction in analysis 1 for the three factors, suggesting that it was a consequence of the distribution of raptor watch periods and subsequent sampling bias. Both of the two factor interactions, time of day and attack rate (partial $x^2=12.2$, 3df, $p<0.01$), and month and attack rate (partial $x^2=12.9$, 6df, $p<0.05$) remained significant, suggesting that the variations in sparrowhawk behaviour may have been due to these factors and not biased sampling.

6.2.4 Success Rate of Attacks

Overall 877 sparrowhawk attacks were observed including 86 kills and 100 captures. Most of these were on redshank, allowing the factors which affect success rate to be analysed for a single species so removing a lot of variation. Success rate of capture of redshank did not vary significantly between years comparing the direct estimate (averaging 12.4%, n=537 attacks) or indirect estimate of success rate (Tables 6 and 7 respectively). The indirect estimate of success rate was based on the attack rate per raptor watch hour and the number of kills found, the assumption being that the number of kills per attack rate would reflect success rate. The direct estimate of

TABLE 6: Direct Estimate of Sparrowhawk Success Rates Hunting Redshank

$$\text{Success Rate}=\frac{\text{Number of Observed Captures}}{\text{Number of Observed Attacks}}$$

		1989-90	1990-91	1991-92	Total Success Rate
SEPTEMBER	Captures	0	1	0	
	Attacks	0	5	3	12.5
OCTOBER	Captures	1	1	2	
	Attacks	4	18	19	9.8
NOVEMBER	Captures	1	3	10	
	Attacks	21	36	86	9.8
DECEMBER	Captures	0	3	14	
	Attacks	11	26	70	15.9
JANUARY	Captures	5	9	11	
	Attacks	38	49	86	14.5
FEBRUARY	Captures	1	6	1	
	Attacks	15	12	32	13.6
MARCH	Captures	0	0	1	
	Attacks	4	1	1	16.7
TOTAL SUCCESS RATE		8.6	15.6	13.1	

Kruskall-Wallis 1-way ANOVA:

Comparing success rate by year: $x^2=2.5$ $p=0.29$

Comparing success rate by month: $x^2=2.9$ $p=0.82$

TABLE 7: Indirect Estimate of Sparrowhawk Success Rates Hunting Redshank

$$\text{Index of Success Rate} = \frac{\text{No. Redshank/Sparrowhawk Kills Found}}{\text{Attack Rate per Raptor Watch Hour}}$$

$$= \frac{\text{No. Kills Found} \times \text{No. Hours Raptor Watch}}{\text{No. Attacks During Raptor Watch}}$$

		1989-90	1990-91	1991-92	Index
SEPTEMBER	No. Attacks	0	3	2	
	RW Hours	9.4	10.5	38.2	255
	Kills Found	9	7	6	
OCTOBER	No. Attacks	1	10	13	
	RW Hours	21.8	36.7	48.0	143
	Kills Found	13	7	12	
NOVEMBER	No. Attacks	19	17	57	
	RW Hours	60.4	48.6	65.2	109
	Kills Found	15	11	32	
DECEMBER	No. Attacks	12	10	64	
	RW Hours	64.3	30.1	60.4	130
	Kills Found	17	16	39	
JANUARY	No. Attacks	11	21	71	
	RW Hours	31.0	43.0	84.0	110
	Kills Found	12	24	36	
FEBRUARY	No. Attacks	5	4	23	
	RW Hours	4.9	25.8	54.4	164
	Kills Found	6	31	22	
MARCH	No. Attacks	0	0	1	
	RW Hours	8.2	1.0	19.4	435
	Kills Found	5	2	8	
TOTAL	No. Attacks	48	65	231	
	RW Hours	204	198	370	
	Kills Found	77	98	155	
	Total Winter Index	327	299	248	

Index of success rate compared by year: $x^2=3.8$ $p=0.15$ 2df

Index of success rate compared by month: $x^2=45.2$ $p<0.0001$ 6df

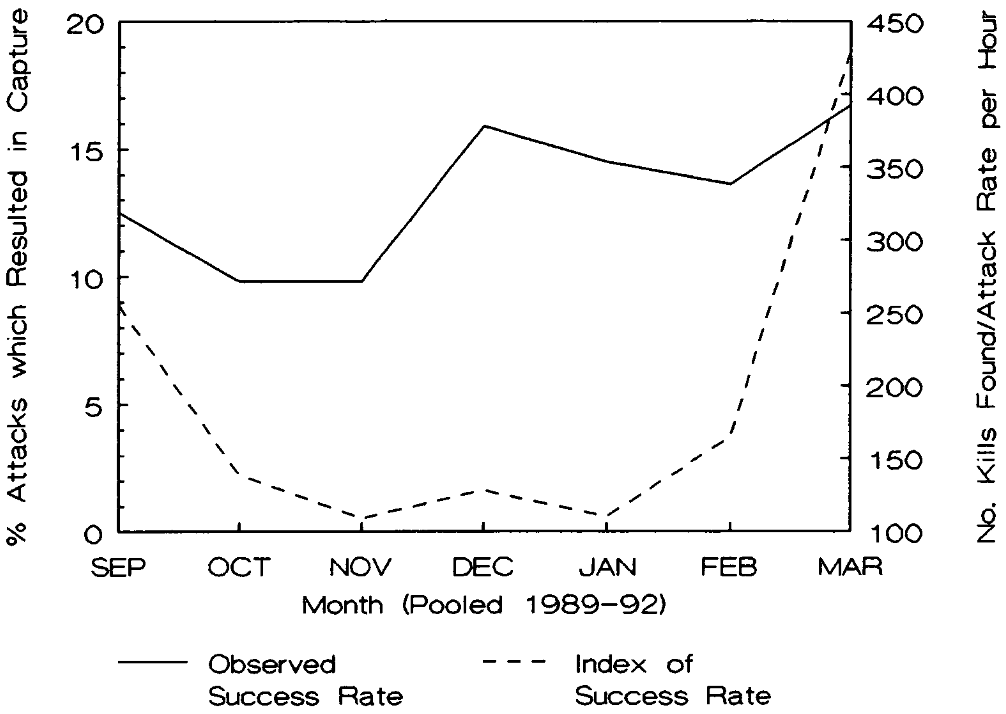
x^2 compared kills found with expected number of kills if attack rate observed was equivalent to the number of kills found, which would be the case if success rates were equal.

success rate and the indirect estimate of success rate have a similar distribution when plotted by month (Fig. 13). Success rate was initially relatively high in September and fell to its lowest value in November. It then peaked for the mid-winter period in December, and rose again at the end of the winter. The direct estimate of success rate was not found to vary significantly between month, but the indirect estimate was found to vary significantly by month (Tables 6 and 7).

Sparrowhawk success rate varied according to species attacked (Table 8). Few comparisons could be made between species due to the small number of observed captures overall. Generally capture rates were similar, 8.3% to 23.5% for 4 species, but there was a clear difference in the capture rate between most species and skylark, which were only captured in 2.7% of attacks.

Success rate of redshank captures per attack was not significantly correlated with temperature: direct estimate per month with mean monthly daily temperature, T=-1.29, Spearman's Rank Correlation, n=21 months, n=, p=0.21; indirect estimate per month with attacks in them with mean monthly temperature, T=-0.49, Spearman's Rank Correlation, n=19, p=0.63; and indirect estimate per two week period with attacks in them with mean two-weekly daily temperature, T=-1.5, Spearman's Rank Correlation, n=35, p=0.15). There was a slightly significant difference in the success rate of attacks when the attack data on redshank from two week periods was split into two classes of mean daily temperature of less than 5^{o}C and greater than 5^{o}C (5^{o}C was chosen because this temperature divided the number of kills most equally between classes). The

FIGURE 13



Success Rate of Sparrowhawk Attack on Redshanks

TABLE 8: Success Rates of Sparrowhawk Attacks (Pooled Data All Winters)

	Attacks	Kills	Captures	Kill Success Rate
Redshank	537	65	75	12.1
Dunlin	92	11	12	12.0
Turnstone	2	1	1	-
Snipe	1	1	1	-
Grey Plover	7	0	1	-
Curlew	22	0	0	0
Oystercatcher	1	0	0	-
Lapwing	1	0	1	-
All Waders	675	78	91	11.6
Great Spotted Woodpecker	1	0	0	-
Little Auk	1	1	1	-
Woodpigeon	8	0	0	-
Feral Pigeon	1	0	1	-
Skylark	110	3	3	2.7
Rock Pipit	12	1	1	8.3
Pied Wagtail	2	0	0	-
Thrush Sp.	9	0	0	-
Finch Sp.	37	0	0	0
Starling	17	3	4	17.6
Other Passerine	4	0	0	-
All Passerines	191	7	7	3.7
Bat Sp.	1	0	0	-
Rabbit	1	0	0	-
TOTAL	879	86	100	9.8

Comparing the relative frequency of attacks which resulted in captures:

Redshank vs Dunlin:	G=0.05	$p>0.05$	
Skylark vs Starling:	G=6.9	$*p<0.01$	a=0.025
Waders vs Passerines:	G=17.5	$*p<0.001$	a=0.017

a=alpha, Sequential Bonferroni, K=3

proportion of attacks which led to captures was greater at lower temperatures, 17.5% at <5°C, and 10.6% at >5°C ($G=4.8$, 1df, $n=537$ attacks and 75 captures, $p<0.05$).

Success rate did not vary significantly with time of day: for attacks which resulted in kills on all species classed by hour, $n=1011$ attacks, $n=85$ kills, $x^2=9.8$, 8df, $p=0.28$; for redshank attacks which led to kills or captures and including sparrowhawks carrying just caught prey, $n=546$ attacks, $n=78$ 'captures', $x^2=7.6$, 8df, $p=0.47$. Success rate did not vary significantly with daylength classed by hours: for attacks which resulted in kills (n as above), $x^2=4.6$, 6df, $p=0.60$; for redshank attacks which led to 'captures' (n as above), $x^2=7.4$, 6df, $p=0.28$. Success rate for the capture of waders varied significantly with tide state comparing attacks made within two hours of low water mark, 24.7% successful, with attacks not made at low tide, 9.9% successful ($G=12.7$, 1df, $n=763$ attacks, $n=85$ captures, $p<0.001$). There were no significant differences in success rate when the height of the tide was considered controlling for the tide state: e.g., comparing success rate of wader attacks within 2 hours of high water mark at low and high tide heights ($G=2.5$, 1df, $n=295$ attacks, $n=21$ captures, $p>0.05$), and comparing success rate within 2 hours of low water mark at low and high tide heights ($G=0.03$, 1df, $n=197$ attacks, $n=30$ captures, $p>0.05$).

There was no significant difference between adult and immature sparrowhawk success rate for capture of redshank controlling for sex. Adult females had a success rate of 16.0% (26/137) compared to immature female's success rate of 7.5% (3/37); $G=2.1$, 1df, $p=0.16$. Sample sizes of attacks by immature birds were small and it is likely that small sample sizes are the reason for a non-significant result.

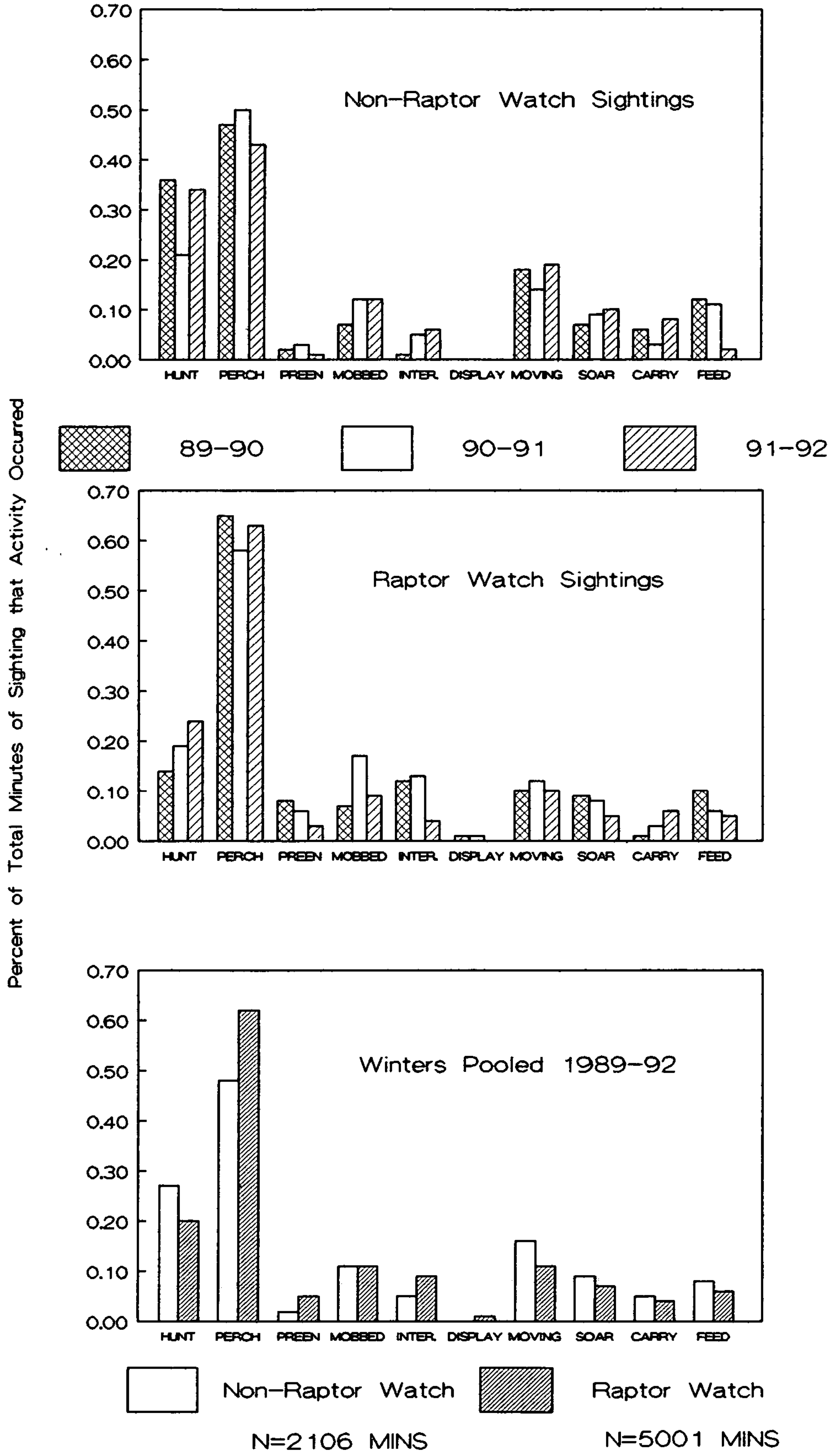
6.2.5 Time Budgets

The time budget data for sparrowhawks were very incomplete, representing only a small biased portion of their activity. Sightings ranged in length from a few seconds to 3 hours; the modal length of sighting was 1 minute (55.4%) and the mean length was 3.9 minutes. In total, out of 2557 hours in the field I recorded only 118.5 hours of sparrowhawk time budget (4.6% of the time, from 1803 sightings). For raptor watches the percentage is higher, 83.4 hours of sparrowhawk time budget in 772 RW hours (10.8% of the time).

Some time budget activities were obviously over estimated compared to others due to their relative conspicuousness. Figure 14 compares the relative frequency of the different activities between non-raptor watch and raptor watch sightings. Perching, for example, occurred in c60% of minutes of raptor watch sightings compared to c50% for non-raptor watch sightings; conversely for hunting the average occurrences were c27% for non-raptor watch and c20% for raptor watch sightings. Perched sparrowhawks were inconspicuous and without continuous telescope scanning, as in raptor watches, they were observed much less, and so under-represented in non-raptor watch sightings. The relative frequency of sparrowhawks being mobbed showed a similar percentage occurrence for both types of observation. As several carrion crows or another raptor were involved, frequently with loud mobbing or alarm calls, my attention

FIGURE 14

Sparrowhawk Time Budget Data: Comparing Raptor Watch and Non-Raptor Watch Sightings



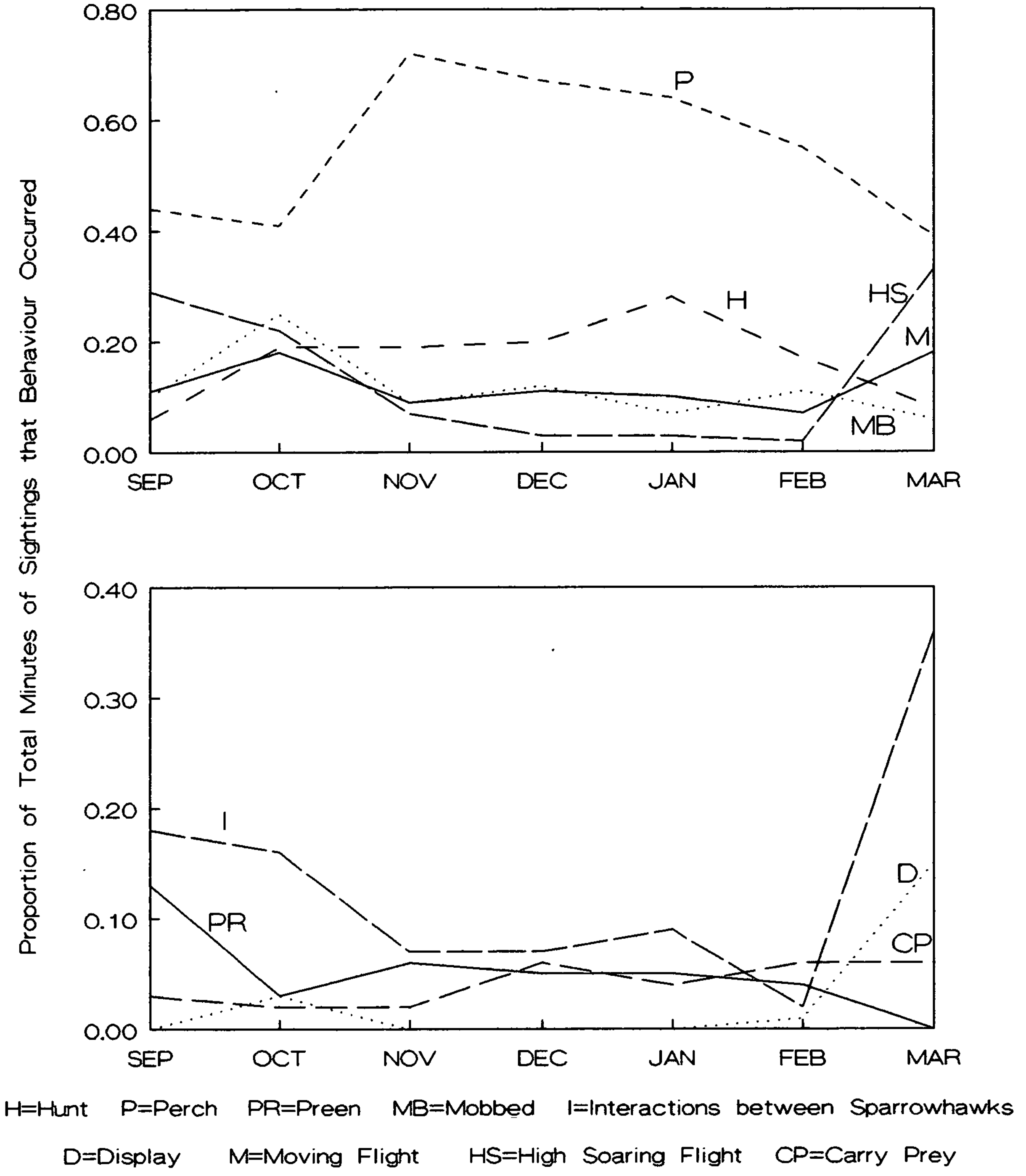
was drawn to the sparrowhawk regardless of whether I was looking for sparrowhawks at that time or not.

Raptor watch time budgets probably reflect the true time budget of sparrowhawks more than non-raptor watch periods, but they only represent sparrowhawk activity out of cover or on the edge of woodland. Some general points can probably be made. Perching, for example, was probably under-recorded overall, yet occurred in over 60% of minutes; similarly feeding and carrying prey occurred in over 15% of minutes. From these under-recorded values it can be inferred that most of the day was not spent hunting. Activities such as hunting, moving, high soaring, interactions and being mobbed were probably over recorded and it is difficult to comment on their values except in the context of a relative change with a variable such as temperature.

The proportion of total minutes of raptor watch sightings the various behaviours occurred was plotted with time of year (Fig. 15). Hunting peaked slightly in midwinter. Perching increased sharply in November; this may have been simply a consequence of leaves falling off the trees so allowing perched sparrowhawks to be seen more easily. Interactions between sparrowhawks, high soaring and display flight peaked in early autumn and in March, coincident with the finish and start of breeding. The amount of time spent in moving flight, carrying prey, being mobbed and preening remained fairly constant through the winter.

Raptor watch time budget data were analysed to determine the main factors correlating with the proportion of sighting that a behaviour occurred. The variables investigated were mean daily temperature,

FIGURE 15



Time Budgets Split by Month

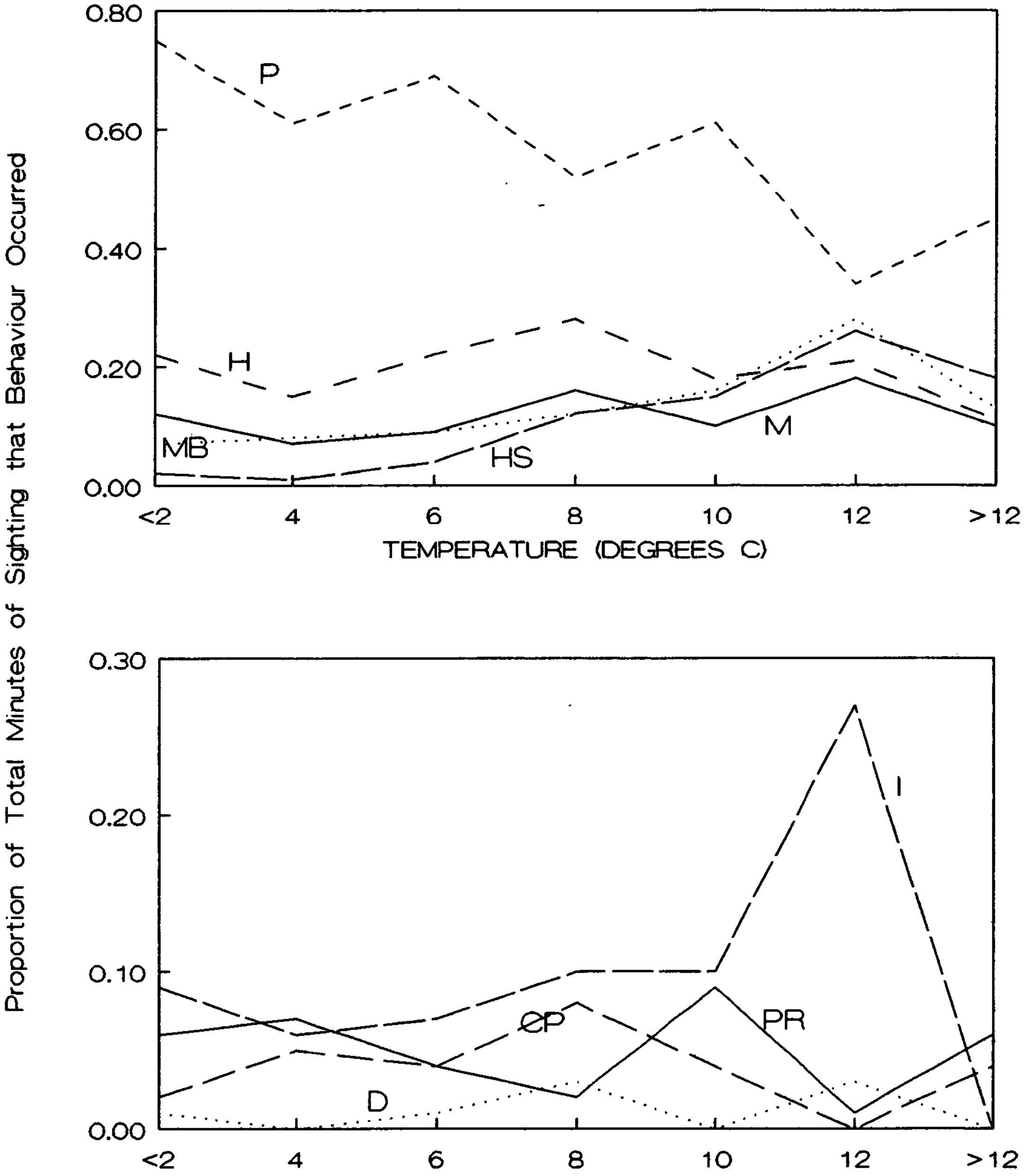
n=5001 minutes

daylength and time of day. The proportions of total sightings spent in a particular behaviour split by these variables are shown in Figures 16-18 respectively. One possible source of bias in these results is the variation in the length of the sightings: if the probability of a behaviour being recorded during a sighting depended on the length of that sighting. For example 49% (434/889) of sightings of 1-5 mins had hunting recorded in all minutes of the sighting, compared to 0% (0/207) for sightings of greater than 5 mins (x^2=22.6, Kruskall Wallis 1-way ANOVA, n=1096, p<0.0001). Similarly the proportion of a sighting in which perching was recorded was higher for longer sightings, for example 28% (243/889) of 1-5 mins length sightings had perching in them compared to 89% (184/207) for >5mins (x^2=404.3, Kruskall Wallis 1-way ANOVA, n=1096, p<0.0001). Variation in the length of sightings across the variables was investigated in order to determine the significance of the effect of sighting length on any correlations across the variables (using Kruskall Wallis 1-Way ANOVA). There was no significant variation in the length of sightings compared across different temperatures (x^2=13.3, n=1089, p=0.28), daylengths (x^2=7.6, n=1089, p=0.27), sex (x^2=0.65, n=879, p=0.42) and age (adult versus immature females; x^2=1.3, n=236, p=0.26). There was significant variation between the time of day and the length of sighting (x^2=21.8, n=1096, p<0.05). Length of sighting became significantly shorter later in the day, e.g. 4.9 mins (n=365) at 9am-12pm, and 3.1 mins (n=221) at 3-6pm (T=-4.1, Spearman's Rank Correlation, n=1096, p<0.0001, alpha=0.005, Sequential Bonferroni, K=17).

FIGURE 16

Time Budgets Split by Temperature

n=5001 minutes



H=Hunt P=Perch PR=Preen MB=Mobbed I=Interactions between Sparrowhawks

D=Display M=Moving Flight HS=High Soaring Flight CP=Carry Prey

FIGURE 17

Time Budgets Split by Daylength

n=4987 minutes

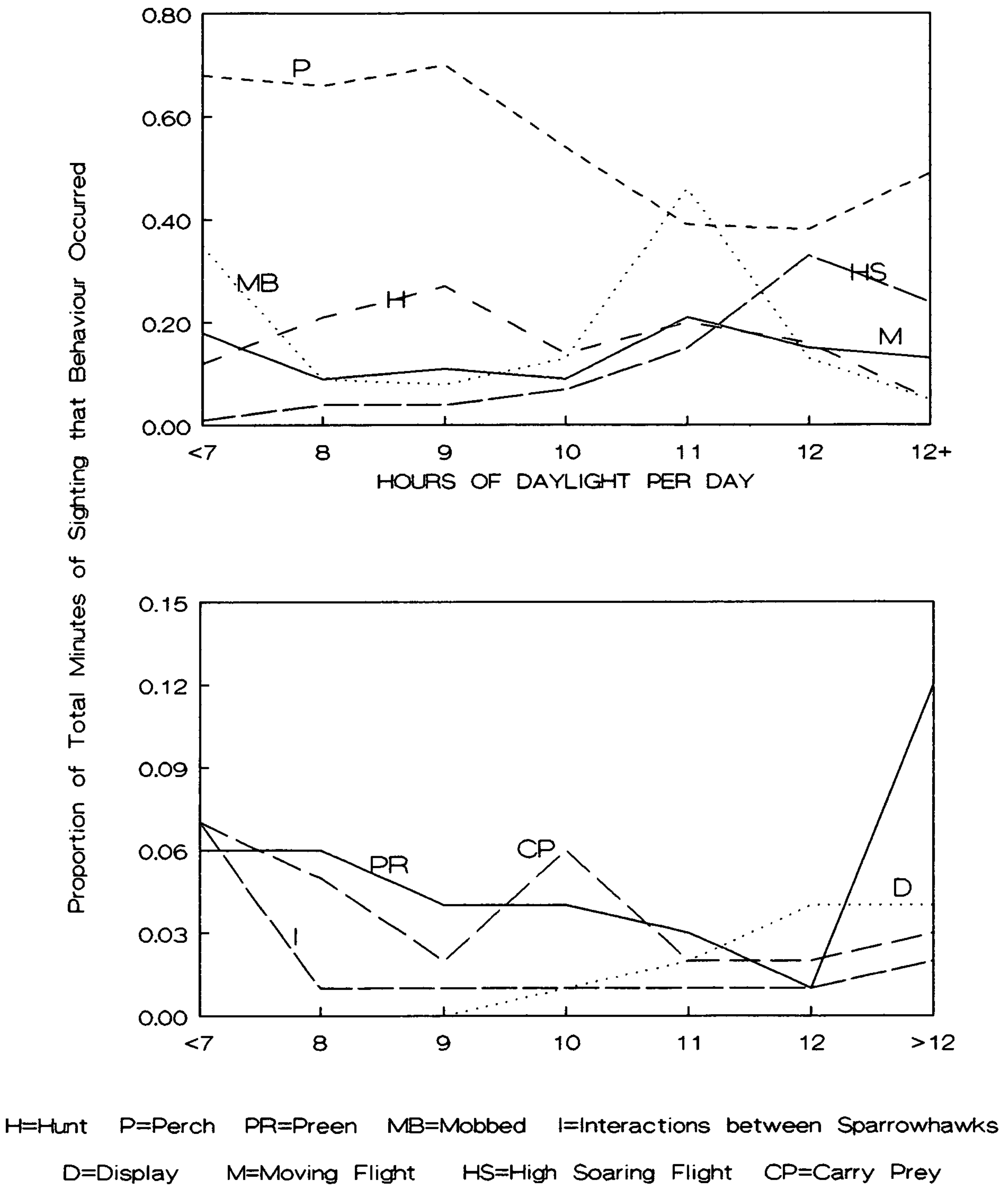
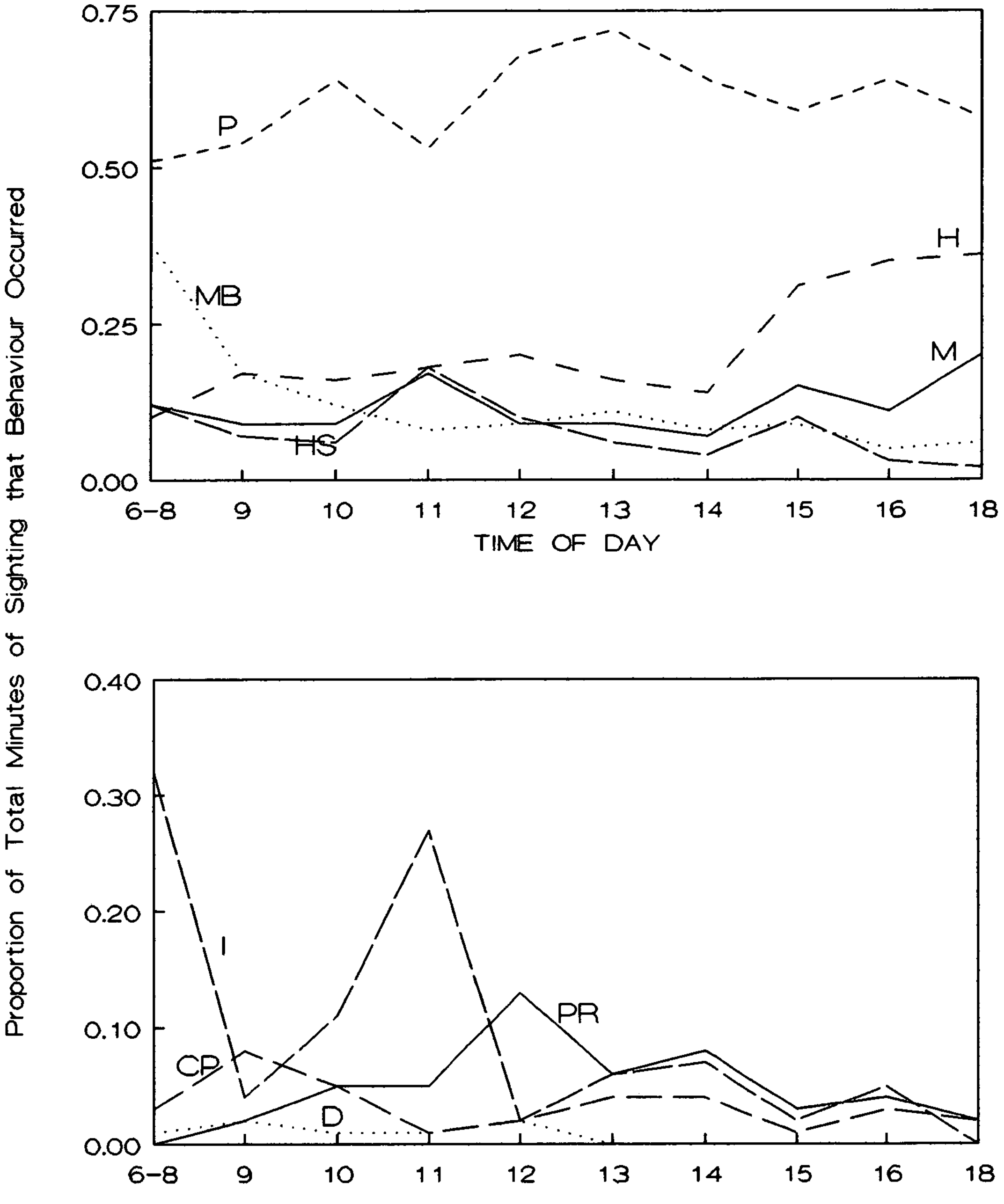


FIGURE 18

Time Budgets Split by Time of Day

n=5001 minutes



H=Hunt P=Perch PR=Preen MB=Mobbed I=Interactions between Sparrowhawks

D=Display M=Moving Flight HS=High Soaring Flight CP=Carry Prey

The proportion of each raptor watch sighting in which a particular behaviour was recorded was correlated with the three main environmental variables: mean daily temperature, daylength and time of day (Table 9). Two sets of correlations were carried out; the first with all sightings and the second with the range of sighting length which had no significant variation in the occurrence of the behaviour across that range of sighting length (to control statistically for sighting length). Overall there is good agreement between the correlations using all cases and the subset of cases used when controlling for variation across different length sightings, despite the latter's reduced sample size. The correlations were all calculated using Spearman's Rank Correlation and variation in the proportion of time a behaviour was recorded with sighting length was calculated using Kruskall-Wallis 1-Way ANOVA.

The proportion of time per sighting spent hunting for all cases correlated negatively with temperature and daylength, and positively with time of day: hunting occurred more per sighting late in the day and in mid-winter. For sightings of greater than 3 mins there was no significant variation in the proportion of time spent hunting (x^2=6.2, n=282, p=0.51). Using this subset of sightings, the correlations remained significant except for that with daylength. Perching correlated negatively with temperature for all cases. When sighting length was controlled for (sightings of 3-5 mins inclusive, x^2=1.1, n=153, p=0.59) perching was negatively correlated with temperature, daylength and time: perching was most likely to occur early in the day and midwinter. Preening was not correlated with any

TABLE 9:Correlations between RW time budget data and environmental variables using all cases and controlling for length of sighting.

		Temperature	Daylength	Time
HUNT	All cases n=1089	T=-3.7 *p<0.0005 a=0.005	T=-4.3 *p<0.0005 a=0.003	T=5.6 *p<0.0001 a=0.004
	Sightings >3 mins n=282	T=-3.5 *p<0.001 a=0.005	T=0.50 p=0.61	T=0.40 *p<0.0001 a=0.004
PERCH	All cases n=1089	T=-4.0 *p<0.0001 a=0.004	T=-1.44 p=0.15	T=-0.21 p=0.83
	Sightings 3-5 mins n=153	T=-4.4 *p<0.00005 a=0.004	T=-3.1 *p=0.002 a=0.004	T=2.1 p=0.041 a=0.006
PREEN	All cases n=1089	T=-1.7 p=0.09	T=-0.65 p=0.51	T=-0.82 p=0.41
	3-5 mins n=153	T=0.49 p=0.62	T=-0.28 p=0.78	T=-0.51 p=0.61
MOBBED	All cases n=1089	T=4.8 *p<0.00001 a=0.003	T=4.2 *p<0.00005 a=0.004	T=-4.1 *p<0.00005 a=0.005
	Sightings >1 min n=541	T=4.3 *p<0.00005 a=0.004	T=3.1 *p=0.002 a=0.005	T=-4.3 *p<0.00005 a=0.004
INTER-ACTIONS	All cases n=1089	T=0.64 p=0.52	T=1.2 p=0.22	T=-6.3 *p<0.00001 a=0.003
	Sightings >1 min n=546	T=1.4 p=0.16	T=-0.05 p=0.96	T=-4.1 *p<0.0001 a=0.006
MOVING FLIGHT	All cases n=1089	T=0.50 p=0.62	T=2.2 p=0.025 a=0.005	T=-0.14 p=0.89
	>1 min n=546	T=0.03 p=0.98	T=1.2 p=0.24	T=1.1 p=0.26
HIGH SOARING FLIGHT	All cases n=1089	T=6.9 *p<0.00001 a=0.003	T=6.2 *p<0.00001 a=0.003	T=-5.4 *p<0.00001 a=0.004
	Sighting >5 mins n=207	T=3.2 *p<0.005 a=0.006	T=3.5 *p<0.001 a=0.004	T=-1.44 p=0.15
CARRY PREY	All cases n=1089	T=-1.9 p=0.054	T=-2.0 p=0.050	T=-0.46 p=0.64
	Sighting >1 and <11 mins, n=437	T=-0.09 p=0.92	T=-2.0 p=0.043 a=0.005	T=0.83 p=0.41

Spearman's Rank Correlations, a=alpha Sequential Bonferroni, K=17 of the variables using all cases or sightings of 3-5 mins inclusive (variation in the proportion of sighting spent preening; x^2=2.7, n=153, p=0.26). Being mobbed correlated positively with temperature and daylength and negatively with time; these correlations remained with sighting of greater than 1 min (variation in the proportion of sightings spent being mobbed; x^2=11.3, n=546, p=0.25). Sparrowhawks were mobbed least midwinter and late in the day. Interactions between sparrowhawks were negatively correlated with time of day for all cases, and for sightings of greater than 1 minute (variation in the proportion of time spent interacting; x^2=9.6, n=546, p=0.39). Interactions were greatest early in the morning. There were no significant correlations for the proportion of a sighting spent in moving flight for all cases and with all sightings of greater than 1 min (variation in the proportion of a sighting spent in moving flight; x^2=9.1, n=546, p=0.42). High soaring flight was positively correlated with temperature and daylength and negatively correlated with time for all cases. For sightings of greater than 5 mins (variation in the proportion of a sighting spent high soaring; x^2=1.7, n=207, p=0.89) the correlation with time was non-significant. High soaring was most often observed at the start and end of each winter. There were no significant correlations for the proportion of a sighting spent carrying prey for all cases and for sightings of greater than 1 and less than 11 mins (variation in the proportion of a sighting carrying prey; x^2=5.7, n=442, p=0.68). This may have been due to the small relative sample sizes of observed kills rather than a lack of relationship. There is a trend for carrying prey to be seen more often at low temperatures and short daylengths, probably as a reflection of the probable increase in attack and success rate under those conditions.

Time budget data were split by age and sex, and the variation between the classes analysed using Kruskall-Wallis 1-Way ANOVA (results Table 10; data Figure 19). Overall there was little significant variation between different sex and age sparrowhawks. Female sparrowhawks hunted for a significantly greater proportion of a sighting (and were correspondingly seen carrying prey for a greater proportion of sighting) and male sparrowhawks were involved in interactions with other sparrowhawks for a greater proportion of a sighting than females. Immature female sparrowhawks perched for a significantly greater proportion of a sighting than adult female sparrowhawks.

Overall mobbing was recorded in 11.1% of minutes of raptor watching. Although this value probably over-represents the amount of time sparrowhawks were actually mobbed (as mobbed sparrowhawks were very conspicuous), it gives an indication of the relatively large amount of time during the day when a sparrowhawk will be unable to hunt effectively. In total 286 mobbing incidents were recorded in 1096 raptor watch sightings. The relative frequency of mobbing for different species of mobbing birds, for all observations of mobbing (n=457) was: carrion crow, 82.9%; Jackdaw, 0.4%; Oystercatcher, 1.1%; curlew, greenshank and lapwing all 0.2% respectively; gull species, 0.6%; rock pipit, 0.2%; blue tit, 0.4%; chaffinch, 2.6%; peregrine, 1.3%; kestrel, 0.9%; and merlin, 9.0%. Carrion crows were consistently the main species involved, frequently following a sparrowhawk noisily from perch to perch. Hunts were frequently

TABLE 10: RW time budget data comparing male with female sparrowhawks using Kruskall-Wallis 1-Way ANOVA: n=879 sightings

	x^2	p	a	direction
Hunt	16.3	p<0.0001	a=0.006	female>male
Perch	1.4	0.24		
Preen	0.6	0.43		
Mobbed	0.7	0.41		
Interactions	9.3	p<0.003	a=0.006	male>female
Display	5.0	0.026	a=0.008	
Moving	5.0	0.025	a=0.01	
High Soaring	3.8	0.051		
Carry Prey	7.2	p<0.007	a=0.007	female>male

a=alpha, Sequential Bonferroni, K=9

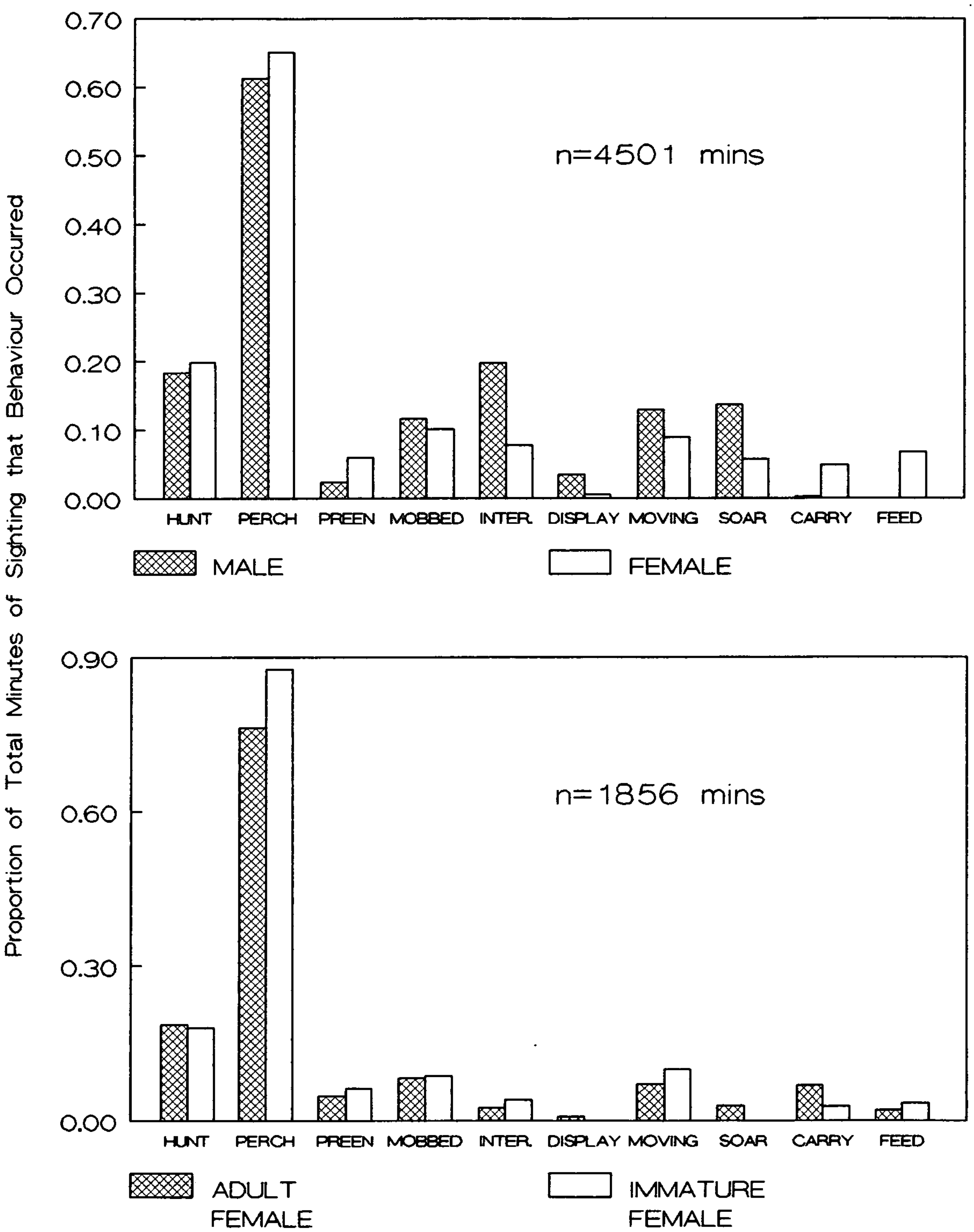
RW time budget data comparing adult female with immature female sparrowhawks using Kruskall-Wallis 1-Way ANOVA: n=236 sightings

	x^2	p	a	direction
Hunt	2.2	0.14		
Perch	10.6	p<0.002	a=0.006	Imm.>Adult
Preen	1.3	0.26		
Mobbed	0.5	0.46		
Interactions	5.1	0.024	a=0.006	
Display	1.5	0.23		
Moving	0.8	0.36		
High Soaring	4.2	0.041	a=0.007	
Carry Prey	1.0	0.33		

a=alpha, Sequential Bonferroni, K=9

FIGURE 19

Time Budgets Split by Sex and Age



terminated by the arrival of carrion crows, and subsequent chasing of the sparrowhawk back into cover. When chased by crows, sparrowhawks would frequently dive at and attack a crow. Mobbing incidents frequently involved a crow or pair of crows alternately chasing and being chased by a sparrowhawk for several minutes, until the sparrowhawk finally flew into dense cover.

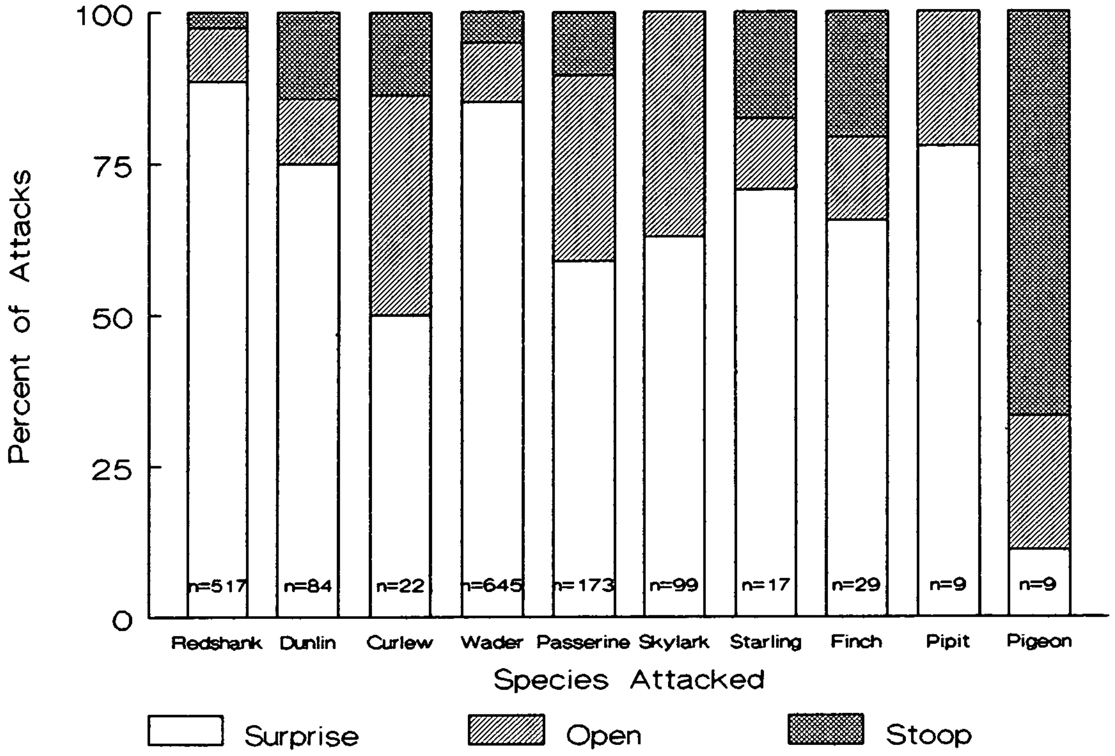
Sparrowhawks mobbed other raptor species in only 0.8% of minutes of total sightings. Peregrines were most frequently mobbed (relative to their occurrence) with 16 sightings over 37 minutes of sparrowhawks flying up to perched peregrines and perching nearby, or even stooping (on three occasions) at a perched peregrine. Merlins were observed being mobbed by sparrowhawks in 19 sightings over 19 minutes. Sparrowhawks chased merlins very vigorously in flight as if hunting, unlike peregrines, which were immediately left by the sparrowhawk when they took flight. Sparrowhawks appeared to be attempting to kleptoparasitise merlins in eight sightings, three of these being when a sparrowhawk joined a merlin already chasing a skylark. Kestrels were observed being mobbed on 4 occasions over 5 minutes. Sparrowhawks chased kestrels rapidly in flight as if hunting, as with merlins. Many sparrowhawk interactions were direct chases of one sparrowhawk by another (female after female, female after male) as if hunting.

6.2.6 Attack Behaviour During Hunts

Sparrowhawks hunt mainly by surprise (79%) with few open (14.5%) and stoop (6.2%) attacks (n=822). The type of attack used varies with species attacked (Fig. 20). For example the frequency of the three

FIGURE 20

Sparrowhawk Hunt Types
All Data Pooled 1989-92



types of attack was significantly different comparing wader and passerine attacks (G=58.3, n=822, p<0.001): waders were attacked by surprise more frequently than passerines which were frequently attacked opportunistically from the open. There were no significant differences in the relative frequencies of surprise compared to open attack split by sex or age (controlling for species attacked by using redshank attacks only). Adult females attacked by surprise in 91.4% of attacks compared to 81.6% of attacks by immature females (G=3.1, 1df, n=199, p=0.09). Known age females attacked by surprise 89.4%, compared to known age males which attacked by surprise 90.9% (G=0.02, 1df, n=210, p=0.99). Success rates of capture differed depending on the attack method and the type of prey being attacked. For waders there was a significant difference in the relative frequency of capture across type of attack (G=11.0, 2df, n=564 unsuccessful attacks, n=81 captures, p<0.01, alpha=0.025, Sequential Bonferroni, K=2); 13.7% of surprise attacks were successful, 15.2% of stoops and only 1.6% from open attacks. For 'passerines' there were no significant differences in the rate of capture (G=0.19, 2df, n=169 unsuccessful attacks, n=8 captures, p>0.05); 4.9% of surprise attacks were successful, 5.6% of stoops and 3.5% of open attacks.

Quartering hunting was used very rarely except when hunting skylarks; overall only 1.9% (n=879) of attacks were from a quartering sparrowhawk and 94.1% of these were on skylarks. Hovering was only observed in three separate sightings; each bout lasted less than 2 seconds and was in conjunction with quartering.

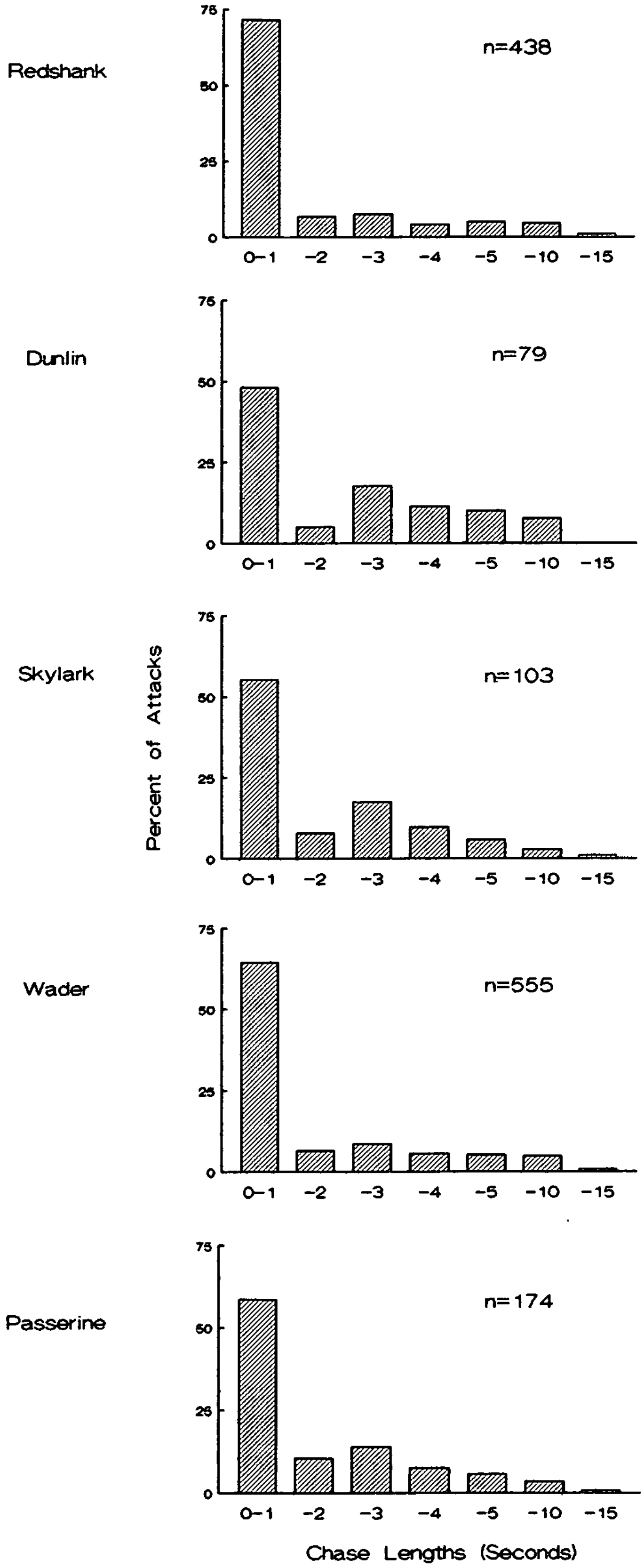
Most attacks were either launched from an elevated perch from cover or from the air; only 7.8% (n=821) of attacks were from a perch on the ground out of cover. Most prey attacked was on the ground at the start of the attack, 93.0% (n=729) although this varied significantly between passerine and wader attacks (G=37.7, n=784, p<0.001) with 17.9% of passerines being attacked while flying, compared to 3.5% for waders.

Sparrowhawks rarely made more than one attack per hunt. Of 857 attacks 88.0% were first attacks, 11.7% second attacks and 0.4% were third attacks. The success rate of second attacks within a hunt was significantly lower than the success rate of first attacks, 12.3% compared to 3.0% (G=10.0, n=758 unsuccessful attacks, n=96 captures, p<0.01). This is a robust result considering that a sparrowhawk would only be expected to make a second attack during a hunt if there was a reasonable probability of capture.

Chase lengths on attack were invariably very short (Fig. 21). The modal chase length was 0-1 second and the maximum chase length observed in 729 chases of known length was 15 seconds. There were significant differences in the chase lengths between redshank and other species, but the overall frequency distribution of the chase lengths between species was very similar and the differences may not be biologically significant. Sampling bias may account for the difference: as redshank were watched most intensively and fed close to cover it was much easier to define short attacks. With dunlin, for example, sparrowhawks would often give up tens of meters from the dunlin being attacked as they took flight and if the sparrowhawk had not been watched from the start of the attack no attack would have been recorded.

FIGURE 21

CHASE LENGTHS DURING SPARROWHAWK ATTACKS



Redshank vs Dunlin x2=25.4 p<0.0005

alpha=0.01 Sequential Bonferroni K=4

Dunlin vs Skylark x2=4.9 p=0.56

Redshank vs Skylark x2=17.8 p<0.01

alpha=0.02 Sequential Bonferroni K=4

Waders vs Passerines x2=9.6 p=0.14

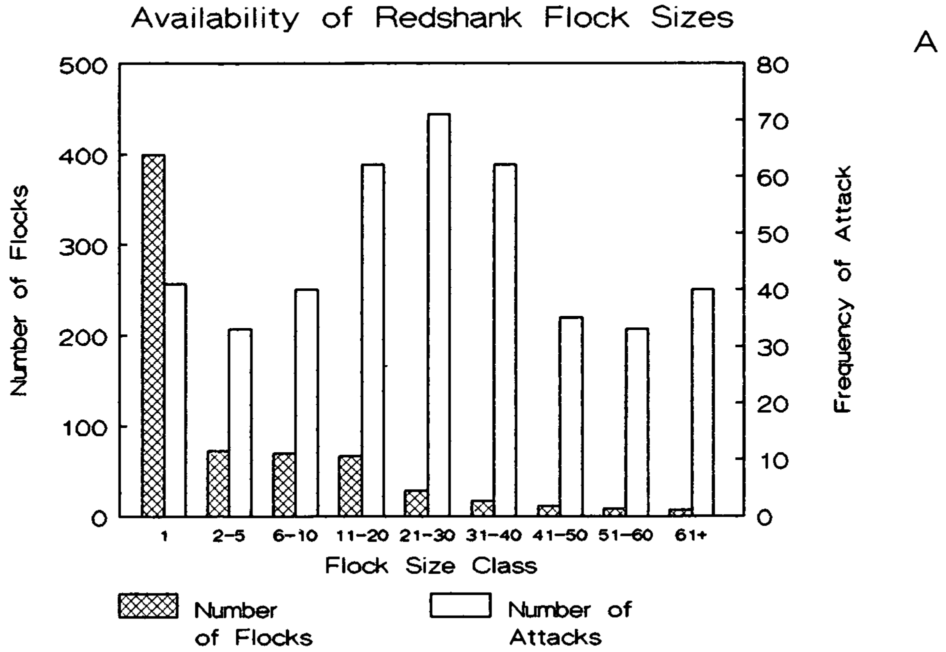
Sparrowhawks attacked prey according to flock size; larger flocks were preferentially attacked in both redshank (x^2=1175.1, 8df, p<0.0001, a=0.025, Sequential Bonferroni, K=2) and dunlin (x^2=49.1, 8df, p<0.001, a=0.05, Sequential Bonferroni, K=2; Fig. 22). The outcome of attack depended on the flock size (Chapter 4.2.4), position of the flock (Chapter 5.2.2) and the response that the attacked bird made (Chapter 4.2.6). A similar pattern occurred with dunlin attacks, although the data set was much smaller. Sparrowhawks were more successful when attacking dunlin in small flocks, 31.3% (1-10 birds) compared to large flocks, 5.5% (11-200+); G=6.2, 1df, n=63 unsuccessful attacks, n=8 captures, p<0.02). The probability of capture across all species depended on the response of the prey on attack. Rates of capture for prey on attack were: flying 5.7% (42/700), creek diving 17.5% (10/47), crouching 63.6% (28/16) and moving into cover of a bush 5.0% (1/19). The rates of capture across the different types of response were significantly different (G=91.1, 3df, p<0.0001). Overall the commonest response on attack was to fly (86.0%), with prey rarely creek diving (6.7%) or crouching (5.1%, although 27% of this response was recorded from curlews which are probably too large for sparrowhawks and so not at risk). Passerines had the escape option of moving into dense vegetation which occurred in 9.6% of passerine attacks (n=208).

6.2.7 Kleptoparasitism and Feeding Behaviour

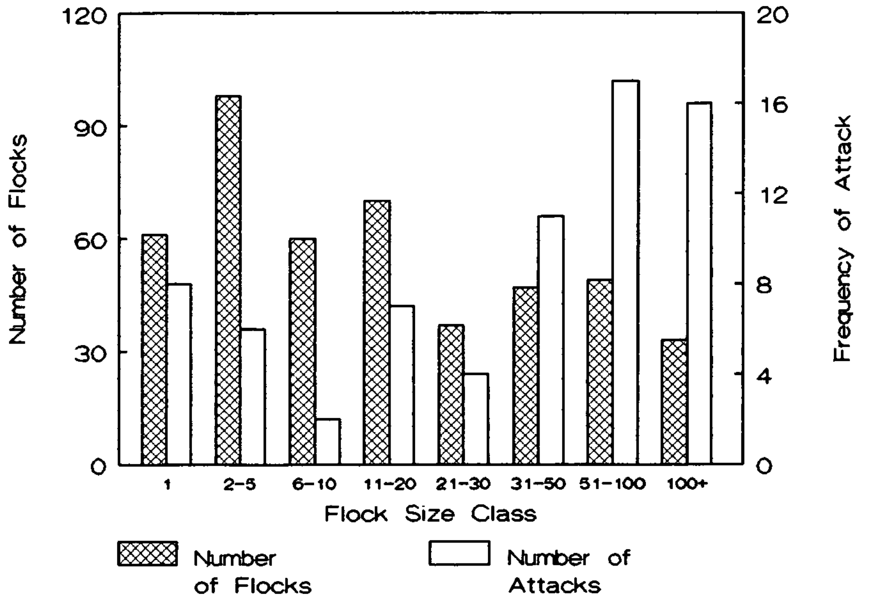
Kleptoparasitism was a major factor affecting winter hunting behaviour at Tyninghame. In 90 observations of sparrowhawks with just caught prey, 27.8% resulted in another species gaining

FIGURE 22

Frequency of Sparrowhawk Attack and Availability of Redshank Flock Sizes



Frequency of Sparrowhawk Attack and Availability of Dunlin Flock Sizes



possession of the prey. Carrion crows were the most frequent kleptoparasites, responsible for 92% of the successful kleptoparasitisms. Of 31 carrion crow attacks on sparrowhawks carrying prey 74.2% were successful. Other kleptoparasites were a kestrel (1 kleptoparasitism attempt in 3 winters which was successful) and merlins (5 attempts on sparrowhawks carrying prey, 1 successful). Some interactions between sparrowhawks were kleptoparasitism attempts. There were three sightings involving six attempts by one or two sparrowhawks attempting to grab prey from a flying or perching sparrowhawk with prey, all of which were unsuccessful.

There were many observations of raptors and carrion crows apparently mobbing hunting sparrowhawks which may have been kleptoparasitism attempts. Observations such as carrion crows repeatedly following a hunting sparrowhawk and walking up to the sparrowhawk and looking underneath it after each hunt could easily be interpreted as kleptoparasitism-based interactions. Other observations of crows persistently chasing non-hunting sparrowhawks from perch to perch were clearly mobbing behaviour. But many interactions were difficult to classify and so only a conservative estimate of the frequency of attempted kleptoparasitism (when sparrowhawks were not carrying prey) could be attempted. During winter 3, out of 140 carrion crow 'mobbing' incidents, when crows associated with sparrowhawks, 45.4% of them could clearly be judged as attempted kleptoparasitism.

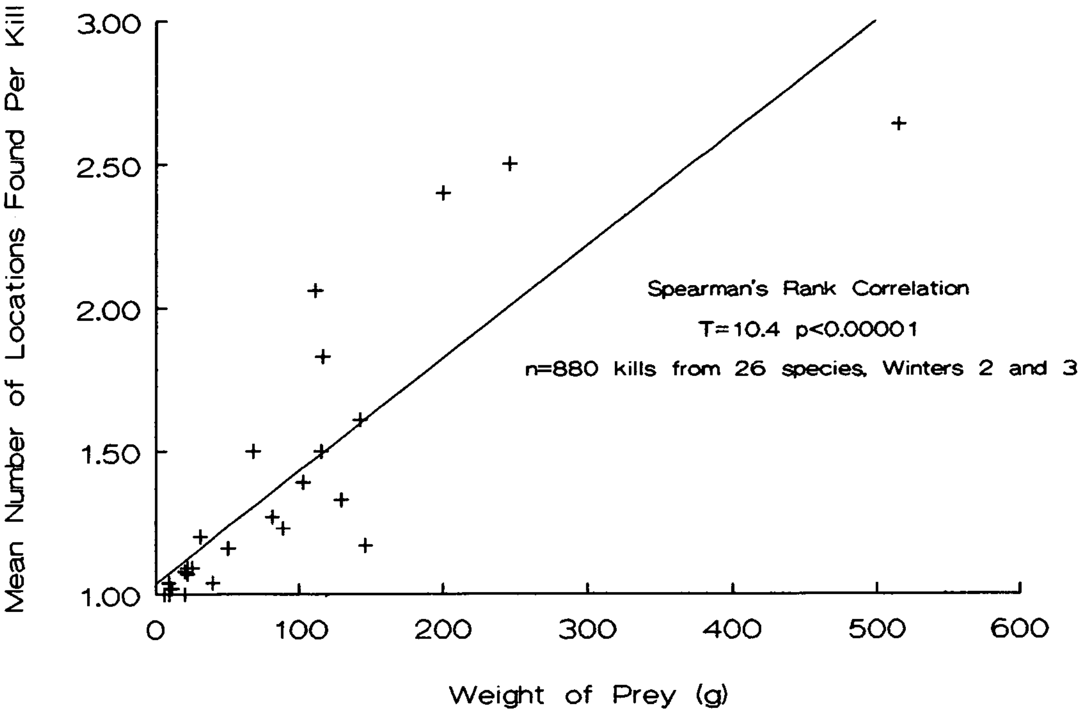
Carrion crows had a high success rate of stealing prey from sparrowhawks, unless the sparrowhawk had a sufficient head start carrying its prey so that it reached cover before the crows reached it. Carrion crows were never observed flying into cover after the sparrowhawk. On only two occasions of sparrowhawks caught up in the open carrying prey did the sparrowhawk succeed in keeping hold of the prey. On both occasions the sparrowhawk mantled the prey on the ground and lunged at the pair of carrion crows for over 30 minutes as the two crows circled separately around the sparrowhawk and attempted warily to grab the prey from underneath the sparrowhawk. The crows finally gave up and the sparrowhawk was then able to fly with the prey into cover. On one occasion where a pair of carrion crows took a redshank from a female sparrowhawk, the sparrowhawk stooped about a minute later from a tree perch above the feeding crow and displaced it. The sparrowhawk then successfully carried the prey into cover.

The limiting factor in many captures appeared to be the ability of a sparrowhawk to kill its prey. If a sparrowhawk attempted to fly into cover with a poorly gripped struggling redshank it could only fly very short distances before it over balanced and had to land again, regaining its hold by simply standing on the redshank. During these short flights it became very conspicuous, particularly if it was carrying a wader which was flapping and so flashing its white underwings. Carrion crows were soon attracted to the sparrowhawk in such cases. A sparrowhawk's ability to kill prey on capture (without interference from kleptoparasites) was related to the size of the prey. Despite a limited data set there appeared to be a higher probability of escape for larger prey on capture than smaller prey when there were no kleptoparasites present: <100g, 0% out of 12 captures escaped, 101-150g 9.8% of 39 captures escaped, and >150g 100% of 3 captures escaped. After capture a sparrowhawk would frequently spend 1-4 minutes, and on one occasion 35 minutes, standing on the prey killing it by kneading its talons into the prey (see Newton 1986). Even so, a redshank was seen to escape alive after about 4 minutes of this and after partial plucking of the neck. Its escape was due to a kleptoparasitism attempt by two carrion crows, which dislodged the sparrowhawk. The only observation I made of a male sparrowhawk catching a redshank was an example of a sparrowhawk's inability to kill larger prey. The redshank remained struggling for at least 12 minutes after capture and was alive probably for 14 minutes after capture. During this time the immature male attempted to fly into cover several times but each time it was brought down by the redshank. Eventually the redshank was killed and then carried directly although with laboured flight into cover. The sparrowhawk was not kleptoparasitised, presumably because no crows were in the saltmarsh area at the time.

Although nearly all of sparrowhawk feeding was carried out in cover, it was possible to observe some feeding sparrowhawks and make some inferences about feeding behaviour from the distribution of kills. Sparrowhawks were observed in almost all cases of kills (96.6%, n=87 sparrowhawks with just caught prey) to carry prey into the piece of cover immediately adjacent to the kill site. Prey was then plucked in several sites within cover. The order of feeding for redshank and other wader prey was head and skull eaten, bill discarded; plucking of the breast; wing and tail feathers plucked, intestines and gizzard discarded; breast eaten, upper legs eaten and then bitten off; rest of body eaten and only wing bones and frontal part of the keel discarded. Sparrowhawks frequently moved with prey while feeding, the number of moves depending on the size of the prey (Fig. 23). There was a highly significant correlation between the weight of prey and the mean number of locations per kill found (a separate location was a feeding site separated from another by over a meter, although inter-location distances were frequently tens or even hundreds of meters); T=10.4, Spearman's Rank Correlation, n=880 kills from 26 species with 5 or more kills found in winters 2 and 3, p<0.00001). This result may partly represent sampling bias, larger prey having more feathers and so being more conspicuous. Sparrowhawks certainly do eat larger prey in more locations as, for example in one month, all the feathers of small species such as wren and goldcrest could be found in one site each, where the only pigeon kill found would be spread over up to 7 locations. The trend was also present when only equally conspicuous wader and pigeon kills were considered. Legs of most prey and wing bones were very inconspicuous and rarely recovered and so the location data presented in Figure 25 is only relative: actual number of locations per weight of prey will be higher. Small passerine bones and legs were never found which suggests that they were eaten.

The ground was the preferred eating location, usually under dense conifer plantations, small sycamores or sea-buckthorn bushes, (74.3% of 226 redshank kill locations for winter 3). Logs and stumps were often used (12.4%); branches or buckthorn stems were less frequently used (6.6%) as were the flat tops of anti-tank blocks (4.9%) - these were 1.5m cubes of concrete in some areas of Tyninghame woods;

Number of Sparrowhawk Feeding Locations With Mean Weight of Prey



mounds were rarely used (1.8%). All perch types were widely available. All of the feeding perch types could be used in any order for a kill, or nearly all of a kill could be eaten on one feeding perch. Certain feeding perches were used repeatedly, month after month; these were usually first or second locations where most of the plucking was carried out.

Few eating times were recorded. A female sparrowhawk took 47 minutes to pluck a starling completely before moving to a second location carrying the intact prey. With larger prey, such as turnstone and redshank, sparrowhawks plucked for up to 90 minutes after capture. During this time they apparently fed little but sparrowhawks frequently paused for long periods during plucking: consumption of prey could potentially be much faster. Sparrowhawks did not necessarily become inactive after feeding; one female sparrowhawk hunted immediately after finishing eating a skylark it had just caught, attacking a redshank and two separate curlews within 5 minutes of finishing. Feeding, although greatly under recorded, occurred in 6.1% of raptor watch time budget minutes.

6.3 Discussion

6.3.1 Diet

Sparrowhawks at Tyninghame took a wide variety of prey; whatever was reasonably common was taken. This agrees with the only other major British study of non-breeding season diet (Newton 1986) which recorded 36 species of bird and 2 mammal species. Most of the prey from that study came from a small range of species (6 species formed 62% of the diet); at Tyninghame 6 species formed 64% of the diet by number and mammals were also rarely taken. Rabbits were not found in Newton's (1986) winter study, which was explained due to lack of availability of small enough rabbits; at Tyninghame rabbit kills were only found in early spring, coincident with the first young rabbits appearing above the ground (although sparrowhawks will also take rabbit carrion, Jones 1987). I witnessed one attack on a bat, and no kills were found; Speakman (1991) estimated from reported kills that a bat will be taken per sparrowhawk on average every 40.4 years. There were no partridge kills at Tyninghame despite it being a common species; one pheasant kill of a probably injured adult male pheasant was found. As with Newton's (1986) study, sparrowhawks were shown not to be a major predator of gamebirds. Most woodpigeons killed were probably also shot and injured birds; the only capture of a pigeon (a feral pigeon) which I observed was of an obviously weak bird, even so it escaped as the sparrowhawk tried to carry it into cover.

The total number of prey and consequent range of prey taken by sparrowhawks was variable. As temperature and daylength decreased, more sparrowhawks hunted out of cover on the estuary, and more sparrowhawks overall probably moved into the area. Directly observed attack rates were significantly higher at low tide, but attack rates per sighting were higher at high tide. This disagreement suggests that more sparrowhawks were hunting on the estuary at low tide, but hunting effort per bird was higher at high tide. Similarly the pattern of directly observed attack rate peaking in the early morning and late afternoon contrasts with the probability of attack per sighting increasing from early morning to late afternoon. Again this suggests that more sparrowhawks were hunting in the open on the estuary in early morning, and that hunting effort per sparrowhawk only increased later in the day (possibly in conjunction with an increase in the number of sparrowhawks hunting later in the day). Mueller (1973) showed that captive American kestrels had a rhythm in feeding activity, peaking in the evening, which became lost with continuing shortage of food. This parallels the situation with sparrowhawks at Tyninghame, the circadian rhythm of attack rate becoming much less defined midwinter. Numbers of sparrowhawks hunting on the estuary and attack rate per sparrowhawk was probably dependent on temperature, daylength, tide state and time of day. Most of the variables acted synergistically to produce a much greater probability of a sparrowhawk attack, for example greatest in early January, at low tide and at dusk.

The peak of attack rate midwinter, whether measured by direct observation or from time budget data, was very clear. Splitting data by month gave a good synthesis of the key variables apparently affecting attack rate, such as temperature and daylength. On hierarchical loglinear analysis temperature and daylength on their own did not have a significant effect on attack rate, but the two variables together interacted to produce a significant effect: at long daylengths temperature correlated with attack rate, but at short daylengths attack rate was always high. Daylength mid December is nearly 50% less than at the start of September, so sparrowhawks must increase attack rate to compensate for lost hunting time, while metabolic rate and consequently food consumption will have to rise in response to the decreased temperature (e.g. Koplin _et al._ 1980).

Although there were probably more sparrowhawks at Tyninghame in midwinter, the rate of prey consumption per bird increased significantly confirming the likely increase in food intake. The higher attack rate later in the day was a daily example of this increase in food intake; as it got later in the day there was less time to make a kill to maintain body weight over a possibly very cold night. Alternatively sparrowhawks may compensate by choosing larger prey species.

6.3.2 Numerical Availability and Vulnerability of Prey

Much of sparrowhawk winter hunting behaviour can probably be explained as a functional response to prey numerical availability. More sparrowhawks used the estuary as the number of prey available increased (e.g., midwinter and low tide). Kenward (1982) showed that range size in goshawk was related to food availability, with smaller range sizes occurring when food was more available. At low temperatures more prey became vulnerable as it starved and so more sparrowhawks could hunt successfully on the estuary. The fact that sparrowhawks preferentially attack large flocks, despite reduced attack success on larger flocks, may be a functional response to availability. The result of the hierarchical loglinear analysis for factors which determined the choice of attack between waders and non-waders can also probably be explained by availability of prey. At lower temperatures an attack was significantly more likely to be on a non-wader. This was probably due to the influx of hundreds of skylarks and rock pipits onto the saltmarsh during cold weather, and particularly during winters 1 and 2, which numerically swamped the redshank already there. The sparrowhawks correspondingly started to attack skylarks, presumably encountering them in a position suitable for attack much more frequently than redshank. Similarly there were relatively more non-wader attacks early in the day as the redshank that fed on the saltmarsh usually did not do so until about mid-morning (feeding on the adjacent mud area, far from cover and so mainly unavailable to sparrowhawks). Skylarks in contrast fed on the saltmarsh at all times. For most open estuary species, where sufficient data were obtained, there was a clear positive correlation of attack and kill rates with availability of prey. Significant positive correlations for several species were probably not recorded due to the small sample size of kills recovered for those species.

Relative vulnerability of prey was reasonably constant between years, despite much variation in the relative numbers of prey present. Vulnerability indices appear to be a valid measure, but their use and interpretation is difficult. The components of a species vulnerability index will be conspicuousness to the predator, attack rate and success rate. Both attack and success rate can be easily measured with sufficient time for observation, potentially allowing an inference to be made about the relative value of conspicuousness. Attack rate will have to incorporate the amount of time a sparrowhawk spends in the microhabitat of a prey species, another important component of a species' vulnerability. For example, the relative conspicuousness of a redshank to a sparrowhawk would seem to be much greater than a dunlin's, as both occur in the same area and redshank have a higher vulnerability index. Attack rate is much greater on redshank, but this may be simply a consequence of the greater food value of the redshank. In order to remove the effects of profitability similar size prey should be used for interpretation of vulnerability indices. Within passerines for example, despite my limited data set, there was significant variation in success rate; rock pipits were captured far more per attack than skylarks, but were attacked far less frequently. Without the attack and success rate data, the vulnerability indices alone would appear to show rock pipits (VI=1.5) as twice as conspicuous as skylark (VI=0.8), when the reverse appeared to be the case.

The unprofitable prey hypothesis (Baker & Parker 1979) has been frequently supported by the use of vulnerability index data to draw conclusions about whether conspicuous species are preferentially taken (e.g., Baker & Hounsome 1983, Baker & Bibby 1987). In these papers no account was taken of the relative amount of time a predator spent within a species' habitat or attack rate or success rate on each species. Similarly, interpretations of vulnerability indices in terms of species' different habits (e.g. Tinbergen 1938, in Newton 1986) without reference to attack and success rate data are meaningless. Tinbergen, for example, interpreted swallows (Hirundo rustica) low vulnerability index, despite their conspicuousness, as a function of their flying ability and consequent ease of escape on attack by a sparrowhawk, while spotted flycatchers (Muscicapa striata) were relatively invulnerable because of their inconspicuousness. It can be argued equally that swallows were never attacked as sparrowhawks ignored flying prey, and that spotted flycatchers which inhabit the same canopy and woodland edge habitat as sparrowhawks were very conspicuous because of their flycatching behaviour, and were frequently attacked but not captured because of their superior flying ability and continual vigilance for flying prey. Conspicuousness to sparrowhawks is best understood within a species, where such interspecific habitat and behavioural differences are controlled for. My data, although limited, shows that more brightly coloured males are preferentially taken, but not significantly so. Interspecific behavioural differences which lead to different attack and capture rates rather than any plumage conspicuousness, were probably far more important to a hunting sparrowhawk when it chose prey to attack.

Success rate was not very variable and overall similar to other reported rates (Rudebeck 1950, Whitfield 1985a, Lindstrom 1989, Wilson & Weir 1989). The different success rates of capture for different species was expected: curlews and treecreepers present completely different problems (size versus concealment) to an attacking sparrowhawk. The slightly significant increase in success rate with low temperature was also expected as waders respond to severe weather by metabolising their pectoral muscles (Davidson & Evans 1982) and so correspondingly decrease their ability to escape from a sparrowhawk. For example, at the end of a very cold period in winter 2, I was able to catch a flightless redshank, and some complete kills recovered at that time had almost no pectoral muscle indicating that the redshank were also flightless on capture. The significant decrease in success rate at high tide is probably explained by flocking effects, such as vigilance (Pulliam 1973) and the 'confusion' effect (Neill & Cullen 1974): most open estuary waders and passerines were congregated in dense flocks at high tide. The change in the success rate of capture of redshank over the winter was due to a number of factors. In September there were many inexperienced juvenile redshank which may be easier to capture (see Chapter 4.2.7); these were killed or learned to avoid sparrowhawks and so the success rate declined. Success rate rose again in midwinter due to temperature effects. The steep rise again in March is probably a sample size effect as very few attacks and only one kill were seen.

The difference in capture rate of redshank by adult versus immature female sparrowhawks that I recorded was not significant, but this was probably a sample size effect. Adult raptors have rarely been found to be much more successful at capturing prey even in intensive studies (e.g. Dekker 1988). Immature female sparrowhawks attacked redshank (non-significantly) less by surprise than adult females presumably as a consequence of inexperience, which may account partly for the difference in success rate. However differences are probably very slight, and will become less as the winter progresses and so it will be difficult to get sufficient data to demonstrate a significant difference.

Prey behaviour such as flocking was a major determinant of attack success (as discussed in Chapter 4) and therefore prey vulnerability. Lindstrom (1989) reported a higher success rate of capture for sparrowhawk attacks on larger flocks of finches, in contrast to my redshank flock result. Lindstrom suggests that by attacking very large flocks, a sparrowhawk increased its probability of encountering a sub-standard individual, which could then be easily caught. Madsen (1988) observed a goshawk gradually splitting up large flocks of brent geese (Branta bernicla) by repeatedly stooping at them, until eventually one bird was left; this method of hunting would rapidly identify sub-standard individuals. Murton *et al.* (1971) showed that sub-standard woodpigeons were usually solitary, and this may have been the case for waders: injured dunlin and redshank were usually seen on their own at Tyninghame (n=3/4 observations of injured birds). Encounter of sub-standard individuals however, may explain the high attack rate for sparrowhawk on very large flocks which have a low rate of success overall. These attacks were rarely pressed home, with very short chase lengths, and probably represent very little effort to the sparrowhawk, for the possible gain of identifying a weakened bird.

The response of prey on attack by a sparrowhawk was almost invariably to fly, and initially flying prey was rarely attacked (Kenward 1982 found that only 3% of goshawk attacks were launched at prey already in flight). When an attacking sparrowhawk was seen very late by a wader, it usually creek dived if it was near water. Crouching was only recorded by very large species such as curlew which were little at risk, or by those birds that were caught. Passerines which flew into dense cover such as sea-buckthorn were rarely followed; instead the sparrowhawk often perched by the bush and watched the passerine within cover for a minute or so. Escape responses on attack by avian predators have been rarely quantified (e.g., Whitfield 1985, Lindstrom 1989) but all studies, including anecdotal data tend to show that flight is the best escape response on attack by a sparrowhawk, followed by seeking a refuge in cover or water. Vulnerability of a prey individual may in most cases be determined by behavioural responses (see Lima & Dill 1990).

Some sparrowhawks at Tyninghame appeared to be specialising on redshank and not responding directly to the abundance of prey. The number of kills found in each month only correlated significantly with the previous month's census count, implying that the sparrowhawks gained experience in capturing redshank so that redshank were attacked preferentially, even as their numbers declined. Ruggerio et al. (1979) showed that captive American kestrels were most likely to attack familiar prey and that learning of specific prey characteristics was rapid. As so many redshank were killed by sparrowhawks during the study, it was likely that 2 or even 3 sparrowhawks were feeding almost entirely on redshank. Success rate of capture of redshank was not significantly different to dunlin for example, but redshank represented the most profitable prey. Success rate of capture per gram of prey was nearly 3 times as great for redshank compared to dunlin. Sparrowhawks clearly preferred larger prey (up to c150g) whether attacking waders or non-waders, as would be expected from optimal foraging theory if attack success was equal across the prey size range. Above about 150g, success rate fell to about zero and so it is not very profitable for sparrowhawks to hunt larger prey. The occasional attacks observed on species such as woodpigeons and curlew were almost always very opportunistic on single prey that approached very close. With very large prey, even a very low probability of success (and then probably only potentially with injured or ill prey) will be compensated for by the large potential gain in food. The significant decrease in the mean size of prey taken by sparrowhawks later in the winter probably reflects the decline in redshank numbers (through sparrowhawk predation). As available redshank became relatively rarer (as the redshank which fed habitually in small flocks close to cover were removed from the population) sparrowhawks were forced to switch to alternative prey. The apparent specialisation of sparrowhawks on redshank was probably due to the coincidence of redshank being the largest, fairly common, and most vulnerable prey available at Tyninghame throughout most of the winter.

Selection of prey was probably dependent on a number of factors as well as abundance, success rate of capture and profitability. Certain species were more vulnerable to sparrowhawk predation probably due to their association with other species. Turnstone, for example, were not caught by sparrowhawks in relation to their abundance but were one of the most vulnerable species. Turnstone fed frequently in the same upper rocky shore areas to redshank, and were probably caught as a consequence of sparrowhawks hunting redshank in the area. Turnstones on the upper rocky shore were usually solitary and would possibly normally have a reduced rate of attack due their inconspicuousness, but with sparrowhawks entering the area in response to redshank, the turnstone then became very vulnerable. A similar situation probably occurred with snipe and ruff on the saltmarsh.

6.3.3 Raptor Interactions, Mobbing and Non-hunting Constraints

Time budgeting of sparrowhawks by direct observation has not been attempted previously due to the difficulty of observing sparrowhawks for long enough periods, and radio-tracking studies such as Marquiss & Newton (1981) could only give data on the time spent moving relative to perching. Marquiss & Newton found that sparrowhawks in winter remained inactive for considerable parts of the day-time, which agrees with my estimate of 60-70% of time spent perching. Moving activity was recorded as peaking in early morning, which agrees generally with my observations of most mobile behaviours peaking in the morning with the exception of hunting, which I observed peaking in late afternoon. In a similar radio-tracking study on goshawk, Kenward (1982) could distinguish soaring flight, and found high soaring to peak in August to October with little recorded mid-winter, which is identical to my observations.

Hunting, despite probably being over-recorded, still did not form much more than a quarter of the daily time budget while sparrowhawks were out of cover. Despite a low attack success (on average 5-10%) each attack would rarely last for more than 10-20 seconds. Even when moving time between different areas of prey is included, and during the shortest days, there was still much time in the day for a sparrowhawk to make the one or two successful attacks necessary to maintain body weight. One problem of repeated attacks is the disturbance of prey, creating an area of very vigilant prey, which become uncatchable after the first attack (Ian Taylor pers. comm.). Other raptors in the same area will contribute to this problem. The success rates of attack observed at Tyninghame will take this into account; if there had been fewer raptors at Tyninghame then success rates might have been higher. Conversely many hunting raptors within one area may benefit each other, particularly if a prey species such as a wader cannot conceal itself or leave the estuary, and which flocks anyway. Multiple attacks and chases will eventually weaken all the waders in a flock, as there will be little time to feed, and so make them all easier to catch.

The potential for, or the risk of kleptoparasitism appeared to be the main reason for the interactions between other raptor species and sparrowhawks, as according to Temeles' (1990) hypothesis. Merlins were most often ignored by sparrowhawks except when carrying prey and peregrines were mobbed warily when perched in the area. These types of interactions were confused by the fact that raptors hunt and kill other raptors (Klem et al. 1985), for example peregrines take sparrowhawks (Baker 1967) and sparrowhawk females will eat conspecific males (Newton 1986). All of my observations of peregrines 'mobbing' sparrowhawks and merlins were in the context of peregrine hunts and of a similar attack type to those on non-raptor species before and afterwards. Despite mobbing and kleptoparasitism taking large proportions of hunting time out of a sparrowhawk's daily time budget, even in mid-winter a sparrowhawk was unlikely to be constrained in terms of time left available to hunt successfully.

Newton (1986) hypothesised that raptor-raptor interactions and kleptoparasitism had shaped much of sparrowhawk feeding behaviour, but in the raptor-depleted fauna of Britain few interactions would now be observed. My observations at relatively raptor-rich Tyninghame seem to confirm the idea: in areas where raptors are common, kleptoparasitism will be common. There was probably a strong selective pressure operating on sparrowhawks at Tyninghame to carry prey immediately into cover to avoid losing prey, either to another raptor or crows. Selection of large prey according to profitability may be balanced by selection of smaller prey which, although less profitable, are easier to kill and carry quickly into cover so reducing losses to kleptoparasitism. In areas of few kleptoparasites sparrowhawks would be expected to take larger prey. The unusual observation of Broadley (1985) of a male sparrowhawk drowning a struggling blackbird in a puddle in order to kill it conforms with the idea that sparrowhawks are limited in their ability to handle and kill large prey effectively.

The eating of large prey in several locations is also probably an adaptation to kleptoparasitism. If the probability of encountering a kleptoparasite is a function of time, then the observed pattern of multiple locations for larger prey (which would take longer to eat) would be observed. Raptors have food- processing constraints (e.g. Temeles 1989), and so are unable to eat all of a large prey at one time. Changes in location may represent movement with prey to a favoured roosting area and then to an adjacent feeding perch after the first full crop has been digested. Sparrowhawks will leave large prey and return repeatedly over several days to feed (e.g. Ashmole 1987) but this may be associated with prey that is too large to carry easily. No obvious cached prey items or sparrowhawks caching prey were seen at Tyninghame but it is likely that this was missed.

6.3.4 Hunting Strategies

The main sparrowhawk hunting strategy was surprise; it was the most successful method of attack and no attacks succeeded unless the sparrowhawk got within about 25m or so of the prey before the prey took flight. My frequencies of hunting types were obviously biased towards hunts out of cover. Newton (1986) recorded the commonest hunt type, short stay perch hunting, only when he radio-tagged the sparrowhawks. Otherwise his account of hunting techniques used by sparrowhawks is very similar to mine. Generally the results of previous studies agree with mine: contour hugging, cover using, surprise attacks were most frequent, with stoop attacks from high soaring sparrowhawks being recorded less frequently. Still hunting (Newton 1986), ambush type attacks from the open ground and quartering were observed rarely. The rare occurrence of more than one attack per hunt and very short chase lengths confirms surprise as the most important hunting strategy.

Despite the frequently very stereotyped attack behaviour of sparrowhawks (see Wilson & Weir 1989 for an extreme example) they are to some extent opportunistic hunters. Passerines were attacked more opportunistically than waders, and this may reflect problems of detection of the prey, and of the predator by the prey. Low hunting sparrowhawks would frequently surprise species such as a solitary rock pipit very close to them, and suddenly deviate to attempt to grab it. Despite the low success rate for open attacks, the effort per attack was probably so low that it was worth the low probability of reward.

6.3.5 Conclusion

Overall, sparrowhawks at Tyninghame appeared to be generalist predators, responding to prey availability (which was predominantly determined by vulnerability), and with some individuals specialising on very abundant or available species. The methods of capture and surprise attack behaviour used are effective across almost every available species of bird prey and so prey choice can be rapidly switched. The sparrowhawk's very mobile, cover-using behaviour combined with long periods of immobile perching probably prevent any bird species from effectively hiding from or avoiding a sparrowhawk. Behavioural anti-predator responses, such as flocking, which reduce the risk of individual predation under any circumstances are probably the only effective response, by the prey, to a predator such as the sparrowhawk. Much of the behaviour shown by passerines and some waders in winter is probably directly attributable to the sparrowhawk, both now and in the evolutionary past.

CHAPTER 7: PEREGRINE AND MERLIN WINTER HUNTING BEHAVIOUR

7.1 Introduction

Merlins and peregrines are both widespread wintering raptors in Britain and both occur frequently in coastal habitats (Lack 1986). Although the weight and wing loading of the smallest peregrine are more than twice as great as those of the largest merlin, the range in the size of the prey taken by the two species overlaps widely (Brown & Amadon 1968). Both species are generalist hunters of other birds, within the same habitats. Merlins and peregrines, unlike sparrowhawks, almost invariably perch and hunt in the open allowing for consistently comparable data to be collected for the two species. Predatory habits and efficiencies of raptors should not be compared unless the locality, time of year and prey species are the same (Dekker 1988); the degree of observational sampling bias should also be the same, precluding a direct comparison between sparrowhawks, and merlins and peregrines. At Tyninghame, merlins and peregrines occurred commonly in three winters so that a comparison could be made of the winter hunting behaviour of two closely related and, except in size, morphologically similar predator species. This chapter attempts to unify the various components of merlin and peregrine winter behaviour by using optimal foraging theory. Specific factors which were compared between the two species were:

7.1.1 Diet

a) To what extent do they overlap in diet?

b) To what extent does intraspecific sexual size dimorphism reduce overlap in diet?

7.1.2 Attack and Hunt Strategies

a) Do the two raptor species attack similar species in the same way?

b) In what ways do hunting differences reflect age and morphological differences between and within the two species?

c) How successful are the two species in hunting?

7.1.3 Interference and Mobbing

a) Does the presence of other raptors interfere with successful hunting?

b) How important is kleptoparasitism?

c) How important is mobbing?

7.1.1 Diet

Merlins and peregrines take a wide variety of prey, and as a general rule, almost every bird species available, within certain different size limits for the two raptor species, has been recorded as prey. Merlin diet has been summarised as 80% birds, 15% insects and 5% mammals (Brown & Amadon 1968), although feeding on insects is seasonally restricted and mammalian prey appears to be more widely recorded in non-British studies. Most studies of merlin diet come from the breeding season (e.g. Watson 1979, Newton et al. 1984), and refer primarily to birds caught by the smaller male (due to incubation and nest provision scheduling). Winter foods of merlins have not been systematically studied in Britain (Lack 1986), although Dickson (1988) showed that diet of merlins wintering inland in Galloway, Scotland, was similar to breeding season diet (skylark > starling > finches > pipits). Other European studies have shown merlin prey in winter to be locally abundant small bird species

(Cramp & Simmons 1980). Canadian studies of wintering, predominantly urban merlins, showed that 94% of prey was birds, and 89% of the total prey in numbers and 92% of the total prey biomass came from the two most locally abundant bird species (Warkentin & Oliphant 1990). Despite concentrating on a limited range of species, a wide variety of other prey is taken, varying in size from a goldcrest (Regulus regulus: 6g) to young woodcock (Scolopax rusticola: Cramp & Simmons 1980) and regularly up to rock doves (>300g; Warkentin 1988). Non-breeding merlins in North America have been recorded attacking and capturing most species of available wader prey within the weight class specified above (Page & Whitacre 1975, Dekker 1988). In general, the primary prey of merlins is the most locally abundant bird species of less than 50g (Cade 1982).

Peregrine diet is almost exclusively living birds, with choice of prey varying with availability and type of habitat; Ratcliffe (1963) reported at least 117 species as prey, and at least 145 species have been reported for European peregrines (Brown 1976). Most diet data were collected in the breeding season (see Cramp & Simmons 1980, and Ratcliffe 1980 for a review). During the non-breeding season choice of prey and consequently diet is probably even more varied (Cramp & Simmons 1980), due to the wide ranging behaviour of peregrines, and the ability to hunt over any habitat. Mearns (1982) found that Scottish coastal wintering peregrines took 48% passerines (17% redwings and fieldfares), 30% pigeons and 14% waders, although there were clear biases in finding certain types of prey more frequently than others. The most authoritative study of peregrine winter diet was of predominantly coastal peregrines in Essex. Baker (1967) methodically followed hunting peregrines to observe kills, rather than just searching for kills (which leads to biases in finding the more conspicuous and unambiguous kills). Out of 691 identified kills, Baker found that 17% were gulls, 16% waders, duck 8%, pigeons 39%, gamebirds 5%, corvids 5% and small to medium-sized passerines 5%. Of the pigeon prey, woodpigeons were almost exclusively taken, and domestic and feral pigeons (Columba livia) were ignored - the main breeding season prey in many areas. Prey was generally taken in accordance to its abundance, with seasonal peaks in prey species being taken reflected in the seasonal peaks in abundance of the prey. Specialisation on the most abundant prey species, as in merlins, did not occur: the maximum single species percentage, in any one winter, was 54% woodpigeon. Peregrines can potentially take prey in a size range from goldcrests to geese (6-1800g; Cramp & Simmons 1980), and appear regularly to do so, although the average weight of prey taken in Britain was 289g (Ratcliffe 1963).

Merlins are the smallest commonly occurring British raptor species (25-30cm in length, and 162-212g in weight), while peregrines are the largest commonly occurring British falcon species (36-48cm in length, and c600-1300g in weight), (Cramp & Simmons 1980). Both species show marked, reversed sexual size dimorphism, with the male being considerably smaller than the female. The main explanation for sexual size dimorphism in raptors is that specialising on avian prey leads to severe competition for resources. Dimorphism is therefore adaptive because, for example, a small male individual will only be in competition with other males, compared to a large male which will then have to compete with smaller females. This leads to partitioning of food within a species, or a greater range of prey available to the species (Newton 1979). Sex-related differences in diet have been documented for several species of dimorphic raptors (e.g. Storer 1966, Newton & Marquiss 1982, Bertochi et al. 1984, Newton et al. 1984, Newton 1986, Dickson 1988). Some nesting populations showed no significant intersexual dietary differences (see Kennedy & Johnson 1986), but differences may only be apparent in times of food shortage, or energetic stress, such as during the winter. Temeles (1985) suggested that as raptor success rates are so low, availability of avian prey is further reduced, so increasing the selective pressure for dimorphism, to reduce intraspecific competition. If this is the case, the two sexes of merlin and peregrine at Tyninghame should attack and kill different sizes of prey.

Quantification of winter diet for peregrines and merlins is important because data are limited. Both of the raptor species are listed red data species (Batten et al. 1990) and availability of prey determines raptor density (Newton 1979, Kenward 1982). Factors which affect the main prey species will be the most important factors affecting wintering raptors. Data on which prey are the most important will allow more effective winter habitat management for the raptor species.

7.1.2 Attack and Hunt Strategies

There is much anecdotal data on merlin and peregrine hunting behaviour, but there has been little rigo rous quantitative recording of attack and success rates, the relative frequency of use of different hunting methods, and the factors affecting this. Detailed anecdotal accounts of merlin hunting methods are found in Rudebeck 1951, Brown 1976, Cramp & Simmons 1983, and Dickson 1984. Quantitative data on the relative use of different hunting methods were presented in Page & Whitacre 1975, Kus 1985, Toland 1986, Buchanan et al. 1988, Dekker 1988, and Warkentin & Oliphant 1990. Merlins hunted mostly in low flights (<1m above the ground), and prey were caught after a short distance surprise attack, although prolonged, persistent chasing, with many stoops, occurred frequently. Prey was usually struck in the air close to the ground, or actually on the ground.

Detailed anecdotal accounts of peregrine hunting methods are found in Rudebeck 1951, Baker 1967, Campbell 1975, Brown 1976 Ratcliffe 1980, Cramp & Simmons 1983, and Bertochi et al. 1984. Quantitative data on the relative use of the different hunting methods were presented in Dekker 1980, Treleaven 1980, Thiollay 1982 cited in Dekker 1988, Roalkvan 1985, Toland 1986, and Dekker 1988. Peregrines hunted mostly from elevated perches or from high soaring, using pursuit flight, with the peregrine finally rising above the prey preparatory to a rapid stoop. Prey were usually killed by being struck in the air, and occasionally on the ground.

Merlin and peregrine hunting success rates have been documented in a few studies (see Temeles 1985 for a review). Merlin hunting success has been determined as 5-25%, and usually around 10% (Rudebeck 1951, Page & Whitacre 1975, Toland 1986, Buchanan et al. 1988, Dekker 1988, Dickson 1988, Warkentin & Oliphant 1990). Analysis of peregrine hunting success in the past has resulted in two conflicting hypotheses being put forward. The 'high efficiency' hypothesis (>50%), as expressed by Brown (1976), Ratcliffe (1980), and Treleaven (1980), describes most unsuccessful attacks by peregrines as 'mock' or 'playful' and ones in which the peregrine did not 'press home its attack in earnest' or was 'half-heartedly hunting'. This hypothesis is characterised by limited quantitative data, from very few breeding birds (which may have been watched because of their high hunting success), and the use of a few convincing, but anecdotal examples of peregrines apparently giving up a chase for no apparent reason. There is also no rigo rous definition of what a 'mock' or 'half-hearted' attack is, except in the context of the outcome of the attack. The high success rate of falconry peregrines is frequently used to support the hypothesis, despite the fact that falconry birds are rarely flown at prey unless there is a high chance of success already (e.g. a flushed grouse). The 'low efficiency' hypothesis (<10%) as expressed by Rudebeck 1951, and shown by Roalkvan 1985, Toland 1986, and Dekker 1988, includes all directed attacks at potential prey in calculating success rate. The hypothesis is characterised by extensive quantitative data, sampling from a large population of peregrines and non-subjective definitions of what constitutes an attack. Even so, Temeles (1985) speculated that even in studies that concluded low efficiencies, it was likely that hunts that were aborted early (through the prey reacting very early) were not recorded. Consequently, even low efficiency studies may have over-recorded success rates: this problem will be particularly pronounced with peregrines compared to merlins, due to their extensive use of large areas, and frequent attacks at prey several hundreds of metres away. Ignoring all studies which looked at hunting success for a pair, or single bird on the breeding site, peregrine hunting success has been determined as 7.3%-18.8% (Rudebeck 1951, Dekker 1988, Roalkvan 1985, Toland 1986); those studies with the largest sample sizes found success rate to be around 7%.

Differences in hunting ability shown by different aged raptors, that reflect gained experience are likely to be subtle. It will be difficult to collect enough data to demonstrate experience-related differences, as location, species attacked and time of year will have to be constant. Most studies of age-related differential hunting success in raptors show a trend, rather than a significant difference probably for this reason (e.g. Mueller & Berger 1970, Toland 1986, Dekker 1988, Warkentin & Oliphant 1990). There was much variation in success rates found in studies which sampled a small number of raptors, which may be accounted for by variation in degree of experience by individual raptors. For example, some raptors may become very good, very quickly through chance early experience of a rare prey type which becomes more common later. Alternatively, an individual raptor with an apparently low success rate of attack may be specialising on harder to catch, but larger and more profitable prey, and so actually be highly successful in terms of energy obtained per unit of time or hunting effort.

Data on hunting strategies and success rate of avian predators is necessary to understand the anti-predator responses of birds. Much of bird behaviour in winter, particularly that of waders, appears to be a specific response to the risk of predation. As the data in

Chapters 3 and 5 demonstrated, small differences in the hunting behaviour of wader predators were responsible for quite large scale effects on population dynamics, at least on a local scale. Data on hunting success is also needed to interpret raptor choice of prey and consequently wintering areas: prey may be common in an area but unavailable as capture success rate is too low.

7.1.3 Non-hunting Behaviour, Interference and Mobbing

There have been few quantitative studies of non-breeding merlin and peregrine behaviour, other than hunting. In general, most wintering raptors have been found to spend most of their time perching, apparently doing nothing (e.g. Koplin et al. 1980, Widen 1984, Masman et al. 1988). The most complete study of wintering merlin behaviour was by Warkentin & Oliphant (1990), who radio-tracked and observed several urban, Canadian merlins. They were able to quantify territoriality, home ranges, and diurnal levels of activity. Merlins spent most of the day inactive and had defined home ranges, although several birds' home ranges overlapped extensively, and there were few territorial interactions. European merlins frequently show territorial behaviour, although merlins frequently use communal roosts non-aggressively (Cramp & Simmons 1980). There have been no British over-winter studies of general merlin behaviour, although Dickson (1988) gave a general account based on several winters of observations of non-coastal merlins. Over-winter, non-hunting peregrine behaviour was extensively studied by Baker (1967), although much of the data was anecdotal. Peregrines move widely over large areas during the winter, and are usually solitary; extensive and comparable observations, even anecdotal observations, are difficult to obtain.

Quantification of non-hunting behaviour is necessary to determine the relative importance of these other activities, and the consequent flexibility a raptor species has in adjusting its time available to hunt. Success rates of attacks are mostly usefully interpreted in terms of prey caught per unit time. Constraints such as time spent processing or handling prey, and travel time between patches must be quantified if raptor behaviour is to be interpreted in terms of optimal foraging theory.

Interactions between raptor species are probably very important. Raptors may interfere with each other during hunting particularly if hunting predominantly by surprise. Conversely, raptors may benefit each other when hunting, particularly if escape responses by the prey are different to the two raptor species (e.g. sparrowhawks and peregrines hunting redshank in Chapter 4, and merlins and hen harriers (Circus cyaneus) hunting passerines in Dickson 1984). Kleptoparasitism (reviewed in Brockmann and Barnard 1979) occurs particularly between raptors because they feed at low success rates on large prey (for examples see Beebe 1960, Fishcher 1985), and kleptoparasitism may be very important in shaping the capture and feeding behaviour of raptors (Newton 1986). Raptors also prey frequently on other raptors (see Klem et al. 1985 for a review). The degree of interference competition between raptors using the same areas has been rarely quantified, despite its potential for being a major determinant of raptor density, to some extent independent of prey density. For example, Temeles (1990) demonstrated that, in northern harriers, inter-specific territoriality was entirely governed by the ability of an intruding raptor to kleptoparasitise the resident harrier, or the ability of the resident harrier to kleptoparasitise the intruding raptor: larger potential kleptoparasites were excluded.

Interactions between raptors and potential prey species, where the prey species actively mobs the raptor can also have significant effects on the distribution and hunting efficiency of raptors (e.g. Pettifor 1990). A raptor being mobbed cannot hunt by surprise ('perception advertisement') and may attract the attention of larger, potential predators of the raptor being mobbed, both causing the raptor to 'move on', out of the area (Curio 1978). The frequency of mobbing to hunting raptors and its effect on hunting patterns has rarely been quantified, despite its importance to both predator and prey.

Profitability of an area to a raptor and consequently raptor density may be dependant on the density of mobbing species such as crows. Again quantitative data on the frequency of mobbing is needed to interpret optimal choice of hunting areas by raptors. As merlin and peregrine differ markedly in size the relative effects of potential kleptoparasitism and mobbing are likely to differ, and this may influence differences in hunting behaviour and choice of prey.

7.1.4 Optimal Foraging

The different components of winter hunting behaviour outlined above can best be synthesised within the context of optimal foraging theory. Using this approach raptors are assumed to maximise a currency, such as energy intake, relative to energy expenditure. For example a raptor will be expected to take the most profitable prey, which can be caught most easily.

Warkentin & West (1990) showed that wintering merlins in Canada perched for 94% of the day. There are several reasons for long periods of raptor perching. Raptors have a processing constraint and any food caught immediately after feeding cannot be eaten until the crop has emptied (e.g. Temeles 1989, Warkentin & West 1990). Inactivity is more likely to be a strategy to minimise energy expenditure during the winter (Masman et al. 1988, Warkentin & West 1990). European kestrels were shown to maximise energy gain in the summer, as this maximised reproductive output; in the winter energy use was minimised by reducing activity (Masman et al. 1988). Kenward et al. (1981) estimated that male and female goshawks, which were for example, 20% above mean weight, could survive at 0°C for 6 and 8 days respectively without feeding. This suggests that, at least for moderately large birds of prey, there is not a need to hunt very often during the winter. A single relatively large prey every day will provide an excess of daily energy needs. Even in extreme conditions such as a merlin (the smallest raptor at Tyninghame, and so less able to cope with prolonged food shortage) hunting at between -17.3°C and -30.7°C, only 4 house sparrows or 106.4g of food (the equivalent of two dunlin) were taken daily (Warkentin & West 1990).

Assuming that raptors in winter are energy use minimisers, and correspondingly energy intake minimisers, peregrines and merlins would be expected to:

1) Spend most of their time perched and inactive if time available for hunting is not limiting.

2) To increase hunting effort and maximise food intake as time available to feed decreases.

3) To hunt in ways that minimise energy expenditure (e.g. by surprise and from perches) wherever possible and to give up readily if prey is not captured immediately.

4) To attack the largest prey available which minimises attack time and success rate, while minimising the risk of kleptoparasitism, injury and handling time.

The aim of this chapter is to interpret peregrine and merlin winter hunting behaviour as optimal by testing the broad hypotheses outlined above. Optimality models are only as good as the assumptions upon which they are based, and basic ecological data are needed to make sound assumptions. Therefore all aspects of the winter behaviour of the two raptor species are considered.

There have been few comparative studies of hunting behaviour of different raptor species, in which raptors in the same area, hunting the same species, at the same time were compared (e.g. Dekker 1988, Thiollay & Clobert 1990). The comparative approach (e.g. Clutton-Brock & Harvey 1979) provides a powerful method of determining the influence of ecology on the evolution of behaviour of closely related species. Similarities in the behavioural responses of peregrines and merlins to the same problem of catching a range of avian prey should provide insights into the evolutionary constraints operating on the two species.

7.2 Results

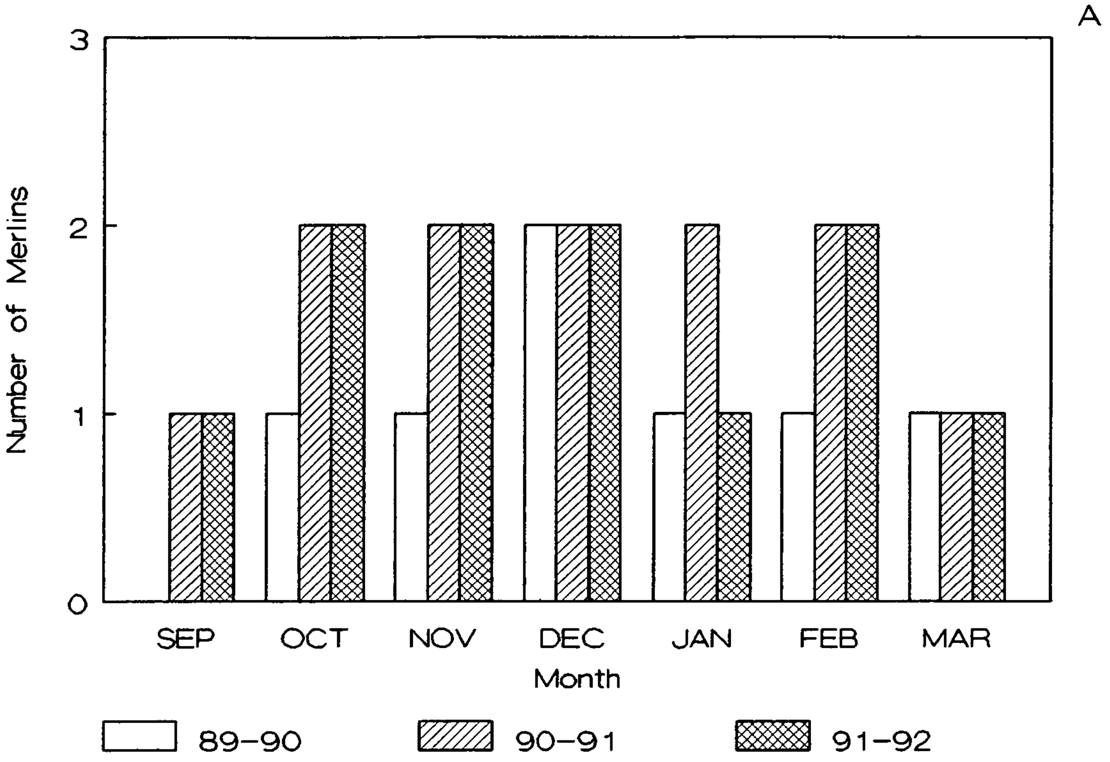
7.2.1 Numbers of Merlins

Only a small number of merlins were present at Tyninghame. Merlins, although relatively inconspicuous, rarely used cover and had habitual perches so it was easy to determine the presence or absence of them in the study area at all times. The maximum number of merlins seen together in any one month was two (Fig. 1A). In winter 1 the monthly mean total number of different merlins seen in each month (Fig. 1B) peaked midwinter, averaging one sighting per day with very few sightings except in November to January inclusive. In winters 2 and 3 midwinter peaks were less obvious. Most sightings were between October and February inclusive with only very infrequent, brief sightings in September and March.

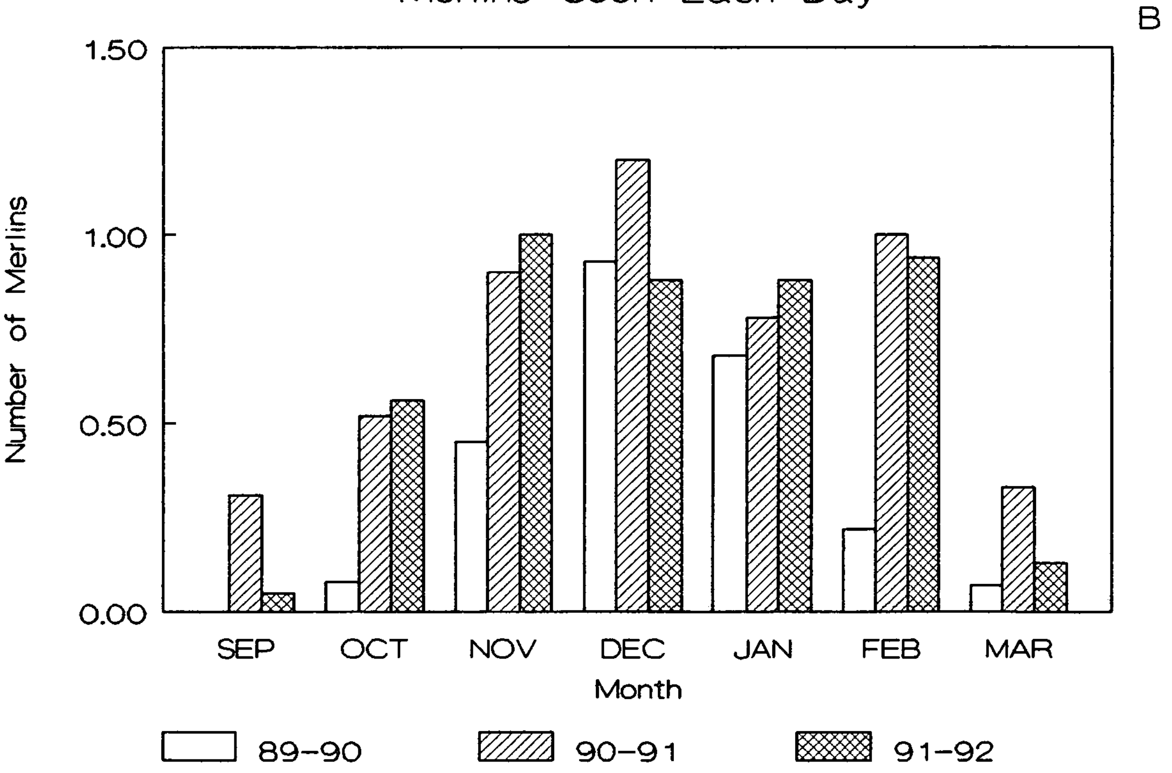
The pattern of sightings between the winters was significantly different; mean length of sighting winter 1 x=6.7 mins (n=72), winter 2 x=16.9 mins (n=289) and winter 3, x=28.7 mins (n=292); x^2=74.4, Kruskall-Wallis 1-way ANOVA, p<0.0001. In winter 1 the distribution of merlin sightings was similar to the distribution of sighting lengths of sparrowhawks with 72.2% of sightings being of 5 minutes or less, and 43.1% being of one minute or less. In winters 2 and 3 sightings were much longer: 37.9% of sightings were 5 minutes or less and 37.0% of sightings were 20 minutes or longer. In winter 1 merlins were therefore only occasional visitors to the estuary; at least 4 different merlins were seen (males n=32 and females n=32

FIGURE 1

Maximum Number of Merlins Seen Together in Any Month



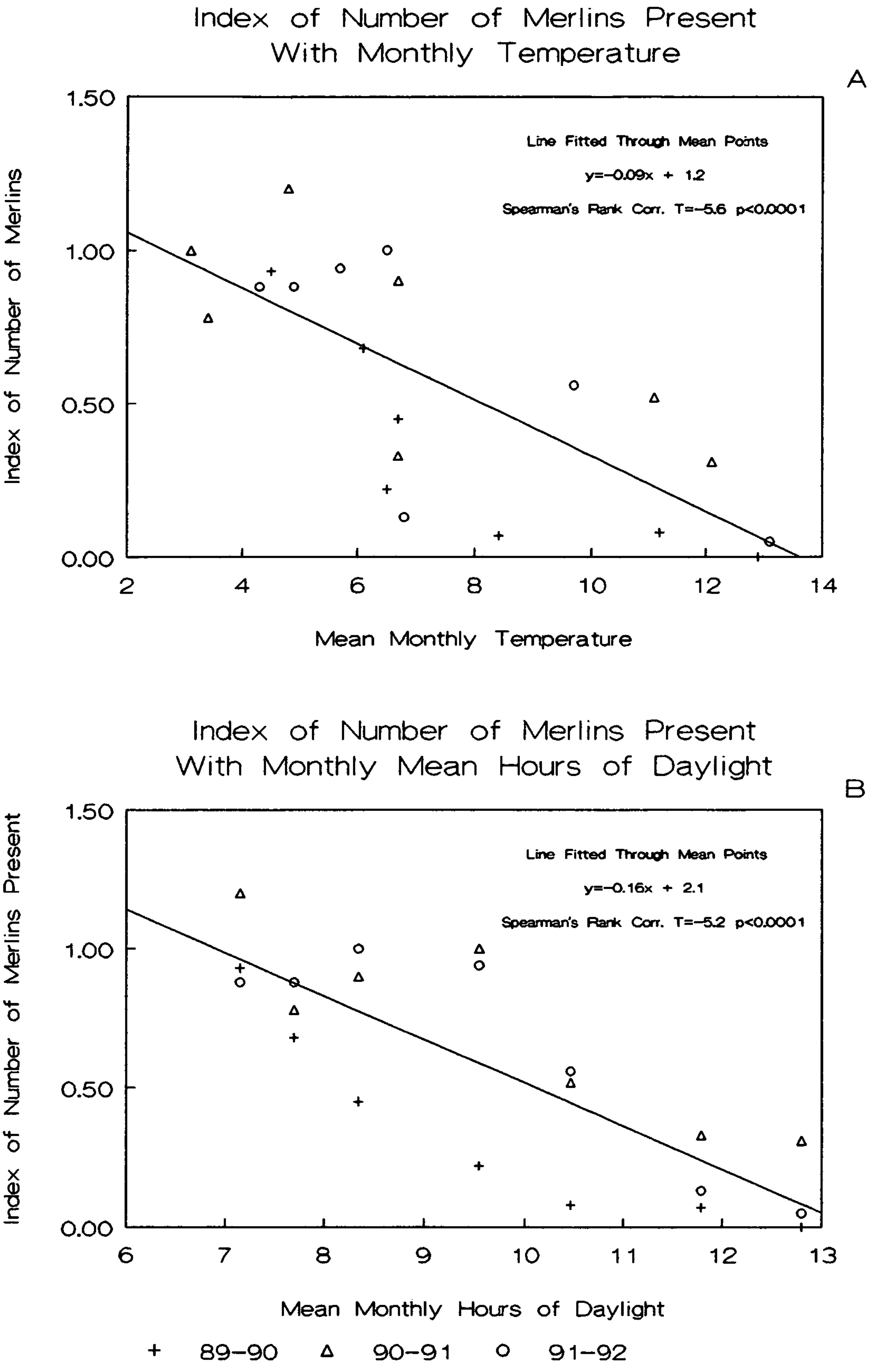
Monthly Mean Total Number of Different Merlins Seen Each Day



sightings). In winters 2 and 3 there was one resident female merlin on the study area, which was occasionally joined by a second female merlin which was resident (and not normally visible) on the south side of the estuary. In addition merlins of either sex were occasional visitors. Most of the merlin data collected came from a minimum of one female merlin, although plumage and behavioural differences between the two resident females in the study area in winters 2 and 3 suggested that two different birds were probably involved. The degree to which the second resident female (outside of the study area) hunted within the study area was impossible to assess as both females were apparently identically plumaged. A conservative estimate of the number of merlins from which most of the data were recorded was 2-3 female birds, with another 9 different individual merlins (of both sexes) providing small amounts of additional data.

The monthly mean of daily estimates of the number of different merlins in the study area was used in subsequent analysis as an index of the actual number of merlins present. The index of number of merlins present correlated (Spearman's Rank Correlation) negatively with mean monthly temperature ($T=-5.6$, $n=20$, $p<0.0001$; Fig. 2A), and mean monthly daylength ($T=-5.2$, $n=20$, $p<0.0001$; Fig. 2B); there were more birds present in the study area at low temperatures and during short daylengths. The index also correlated (Spearman's Rank Correlation) positively with number of prey taken ($T=3.9$, $n=18$ excluding September as no prey was found, $p<0.005$) and total weight of prey taken ($T=3.7$, $n=18$, $p<0.005$).

FIGURE 2



Index of Number of Merlins Present With Monthly Temperature

Index of Number of Merlins Present With Monthly Mean Hours of Daylight

7.2.2 Numbers of Peregrines

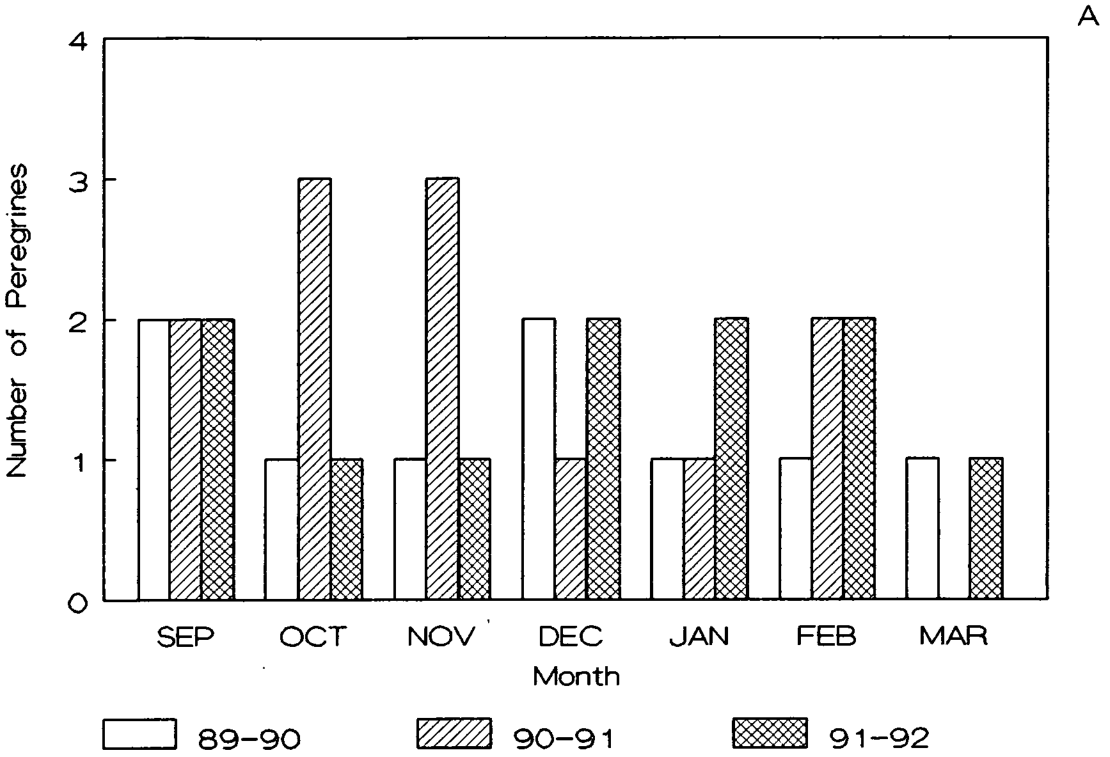
Peregrines were regular but brief visitors to the study area, except in August and September when individuals would remain for several hours each day at Tyninghame. The maximum number of peregrines seen together in any month was usually between 1 and 2, and rarely 3 (Fig. 3A). The monthly mean total of different peregrines seen each day peaked at the start of each winter, but apart from March, there were on average usually between 0.5 and 1 peregrines present on the study site per day (Fig 3B).

The pattern of sightings across all winters was significantly different; mean length of sighting winter 1, $x=9.4$ minutes ($n=83$), winter 2, $x=18.7$ ($n=117$) and winter 3, $x=14.8$ ($n=123$); $x^2=8.4$, Kruskall-Wallis 1-way ANOVA, $p<0.05$. Winters 2 and 3 had a similar distribution of lengths of sightings ($x^2=8.4$, Kruskall-Wallis 1-way ANOVA, $p=0.36$). Overall, 56.1% of sightings were of 5 minutes or less, and 24.2% of sightings were of 20 minutes or more.

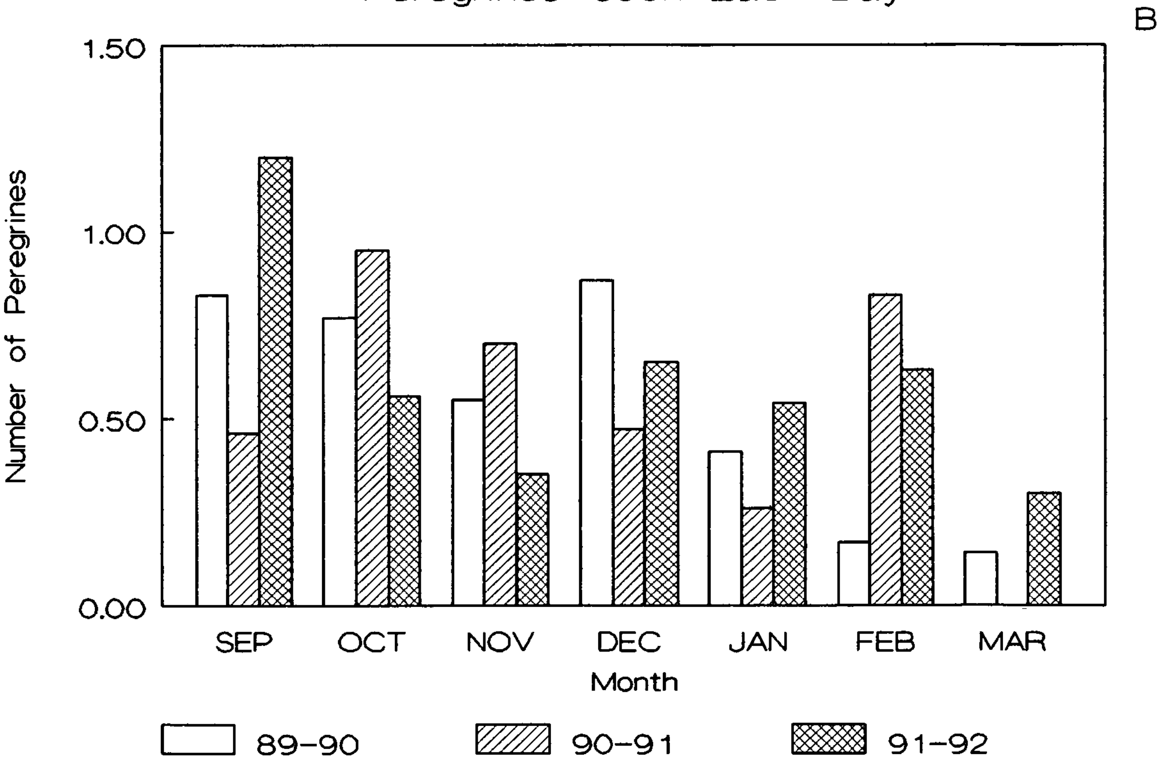
The number of different peregrines visiting the study area was difficult to estimate. The overall probability of seeing a peregrine in any minute was low ($p=0.03$ for total minutes, and $p=0.07$ for raptor watch minutes) so that the likelihood of simultaneous sightings was very low. Peregrines from a wide area could potentially have visited the study area. Peregrines were occasionally watched flying into the study area from up to 5km to the south and then continuing north for another 6km along the coast. During winter 2, between November and February inclusive, an immature female lacking an outer primary visited the estuary. The peregrine consequently had a unique flight silhouette allowing for

FIGURE 3

Maximum Number of Peregrines Seen Together in Any Month



Monthly Mean Total Number of Different Peregrines Seen Each Day



individual recognition even at distance of c1000m. The ratio of sightings of the recognisable peregrine to unknown birds was n=14/46, and the ratio remained constant from November to February inclusive (G=1.2, 3df, p=0.76). Assuming that the probability of any peregrine visiting the estuary was similar then there were probably between 4 and 5 different individual peregrines visiting the estuary during this period. This estimate agrees with the numbers of differently plumaged and sexed peregrines recorded over the same period: an adult male and two females, an immature male (also individually recognisable) and the individually recognisable immature female. In each winter an immature female and male were recorded, and as immatures acquire adult plumage over their second summer (Ferguson-Lees _et al._ 1983) at least 2 different peregrines were regularly visiting the study site each winter. A conservative estimate of the number of peregrines from which most data were collected was therefore 8 different individuals (assuming the same adult male and female pair over 3 years). Observations were spread evenly between age and sex classes (adult/immature n=211/243); male/female n=127/148).

The monthly mean of daily estimates of the number of different peregrines in the study area was used as an index of the actual number of peregrines present. The index of peregrines present did not correlate (Spearman's Rank Correlation) significantly with mean monthly temperature (T=0.75, n=21, p=0.46) or mean monthly daylength (T=0.08, n=21, p=0.94).

7.2.3 Diet

7.2.3.1 Merlin Diet

Merlins at Tyninghame took a wide variety of prey overall, but in any one month only a limited number of species were taken. In total 18 species of prey were taken; each month on average 3.3+/-1.8 species were found killed (n=16 months in which merlin kills were found). Merlins preyed mostly on dunlin and skylarks (Table 1); the two species accounted for 82.5% of kills by number and 75.0% by weight (Fig. 4A). The relative proportion of the different prey species by number and weight varied by month (Fig. 5A and 5B respectively; winter 1 data was excluded as only 8 definite merlin kills were found). Skylarks were relatively more important in winter 2, but in both winters Dunlin were the most important prey. Redshank were found killed by merlins in winter 3, although 2 redshank kills in winter 2, classified only as falcon/owl kills were probably merlin kills as they were associated with probable merlin pellets.

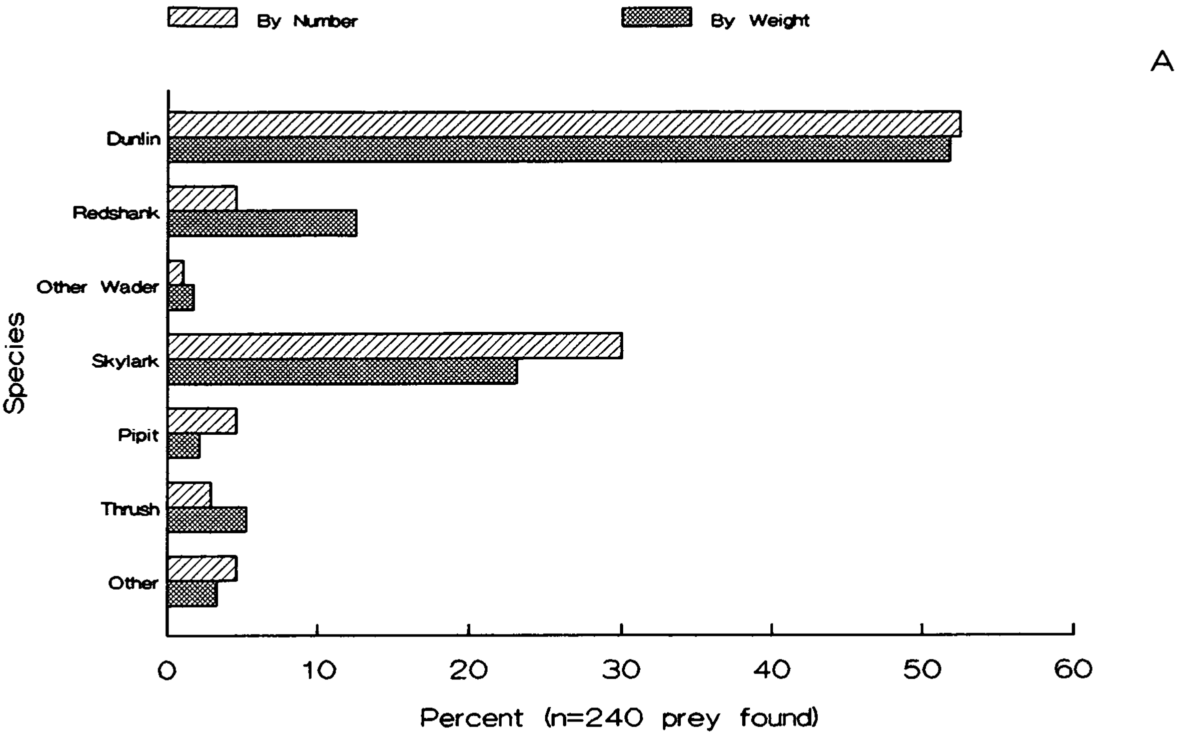
The total number of prey taken increased through the winter, peaking in winter 2 in February, and in winter 3 in December. The total number of prey found correlated (Spearman's Rank Correlation) negatively with both mean monthly temperature (T=-3.8, n=20 months that merlins were recorded at Tyninghame, $p<0.005$) and mean monthly daylength (T=-2.7, n=20, $p<0.05$). The correlation with daylength disappeared when the total number of prey was divided by the daily index of the number of merlins present (T=-2.3, n=20, p=0.07). There was still a significant negative correlation between the number of prey/index of number of merlins and temperature (T=-3.0, n=20,

Table 1: Prey Found Killed By Merlins

	Kills Found	Percent by Number	Weight	Percent by Weight
Knot	1	0.4%	146	1.2%
Dunlin	126	52.5%	51	51.8%
Jack Snipe	1	0.4%	60	0.5%
Redshank	11	4.6%	142	12.6%
Skylark	72	30.0%	40	23.2%
Meadow Pipit	2	0.8%	19	0.3%
Rock Pipit	9	3.8%	25	1.8%
Wren	1	0.4%	9	0.1%
Dunnock	1	0.4%	22	0.2%
Blackbird	1	0.4%	103	0.8%
Song Thrush	3	1.3%	81	2.0%
Mistle Thrush	1	0.4%	129	1.0%
Redwing	1	0.4%	68	0.5%
Fieldfare	1	0.4%	116	0.9%
Blue Tit	1	0.4%	11	0.1%
Starling	3	1.3%	89	2.2%
Chaffinch	1	0.4%	22	0.2%
Linnet	4	1.7%	20	0.6%
Total	240			

FIGURE 4

Prey Found Killed by Merlins



Prey Found Killed by Peregrines

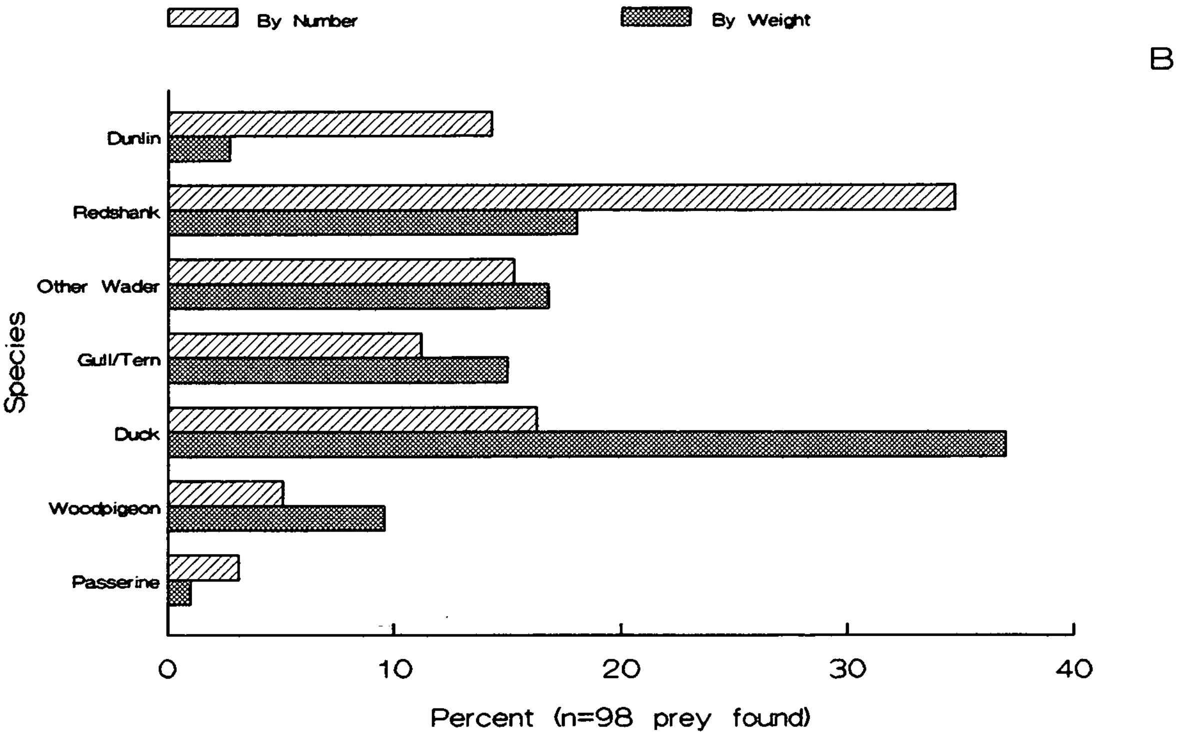
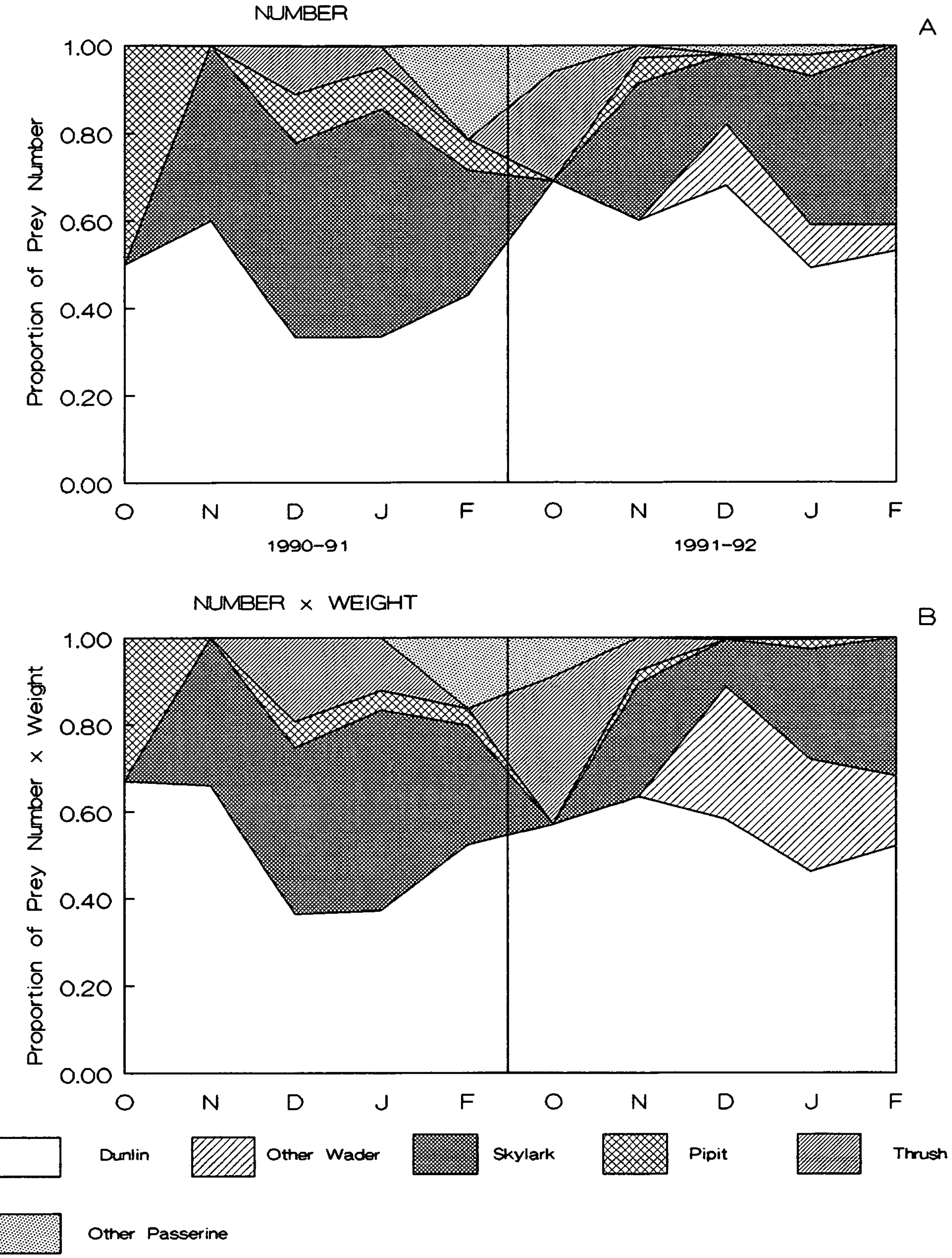


FIGURE 5

Variation in Merlin Prey By Month

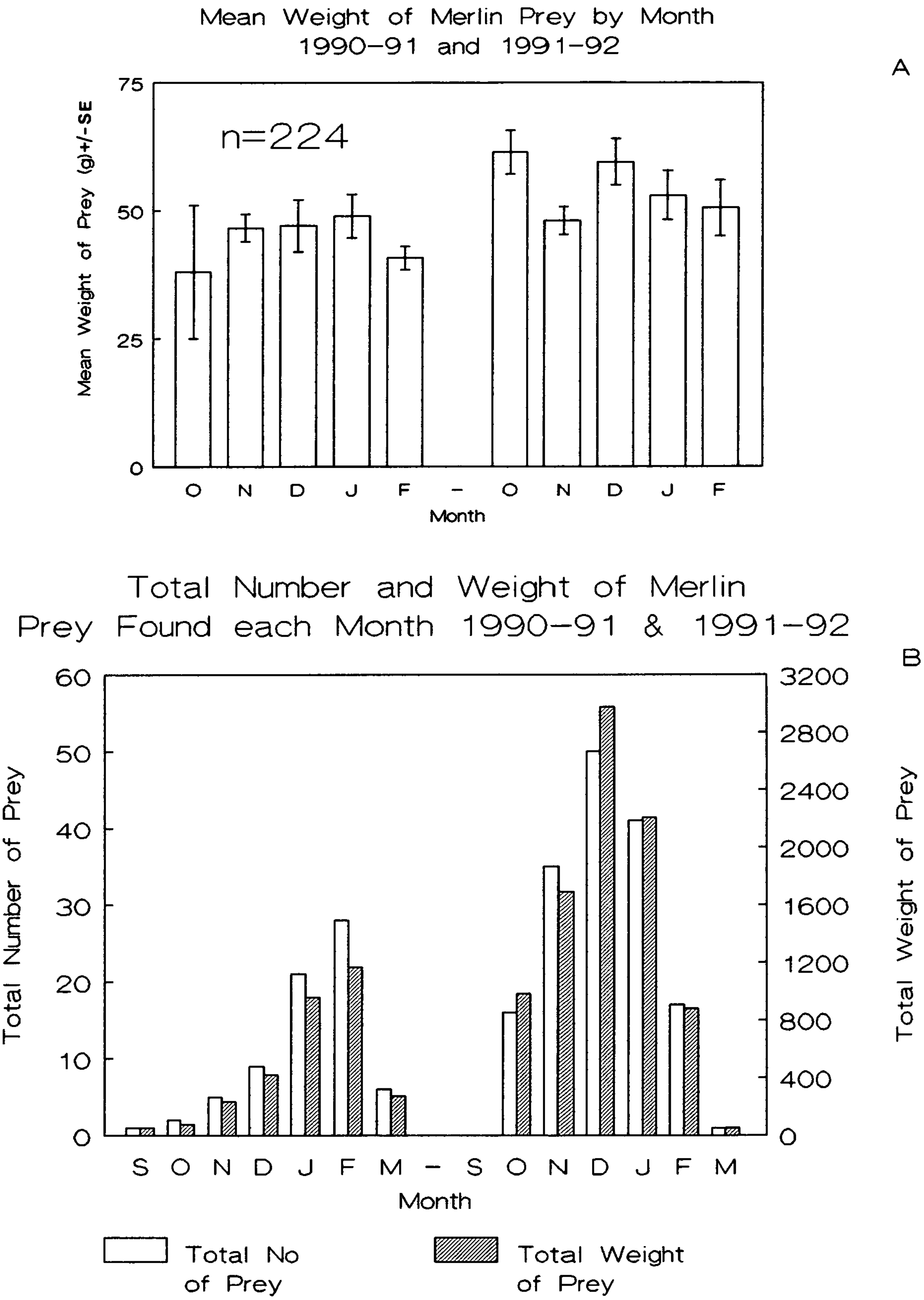


$p<0.01$). At low temperatures merlins probably ate significantly more prey.

The total weight of prey taken increased approximately in accordance with the total number of prey taken (Fig. 6B). Total weight of prey found was significantly correlated (Spearman's Rank Correlation) negatively with mean monthly temperature ($T=-3.4$, $n=20$, $p<0.005$) and mean monthly daylength ($T=-2.6$, $n=20$, $p<0.05$). The correlation with daylength disappeared when the total weight of prey was adjusted by the index of number of merlins ($T=-1.8$, $n=20$, $p=0.09$) but was still significant for mean monthly temperature ($T=-2.7$, $n=20$, $p<0.05$). Merlins probably ate a greater weight of prey in cold weather.

There was significant variation in the mean weight of prey taken between and within the two winters (2 and 3) in which sufficiently large sample sizes of kills were found. The variances of the mean weight of prey between winters 2 and 3 were significantly different ($F=28.8$, Bartletts-Box test, $p<0.001$). The mean weight of prey was significantly different between winter 2 ($x=44.8$g+/-1.7, $n=70$) and winter 3 ($x=54.5$g+/-2.1, $n=162$); $z=-3.6$, Mann Whitney-u-Wilcoxon Rank Sum W test, $p<0.001$). During winter 2 there was no significant variation by month; $x^2=2.4$, Kruskall-Wallis 1-way ANOVA, $p=0.88$. During winter 3 there was significant variation by month, probably attributable to the taking of redshank later in the winter; $x^2=17.5$, Kruskall-Wallis 1-way ANOVA, $p<0.005$ (Fig. 6A). Overall the mean weight of prey taken by merlins at Tyninghame (almost all by females) was $x=51.6$g+/-1.6, ($n=232$).

FIGURE 6



Mean Weight of Merlin Prey by Month 1990-91 and 1991-92

Total Number and Weight of Merlin Prey Found each Month 1990-91 & 1991-92

7.2.3.2 Peregrine Diet

Sample sizes of definite peregrine kills found were small and there was an obvious bias towards larger prey in my method of classification of peregrine kills. For example, large sharp notches in the sternum, characteristic of peregrine kills, would tend to be found more on larger prey. On small prey such as dunlin the whole sternum would be destroyed by one or two female peregrine sized notches. Sample sizes of observed peregrine kills were too small to determine the extent of the bias towards larger prey.

Considering the unknown degree to which I recorded larger peregrine prey more frequently, the data set does not merit intensive analysis. Overall 18 species of prey were recorded (Table 1), with potentially 25 species being taken if all falcon/owl kills were peregrine kills. Only 3.3+/-1.9 species (n=20 months in which peregrine kills were found) were found killed in each month. The most frequent prey item found was redshank, but this species was only second in importance by weight, with ducks being the most important prey items (Fig. 4B). Peregrine kills from all three winters were pooled due to small sample sizes to analyse variation by month (Fig. 7A and 7B). Redshank became more important by number and by weight later in the winter, with ducks more important early in the winter. Gulls and waders were relatively a greater part of the peregrine's diet by weight later in the winter.

7.2.3.3 Selection of Prey by Merlins and Peregrines

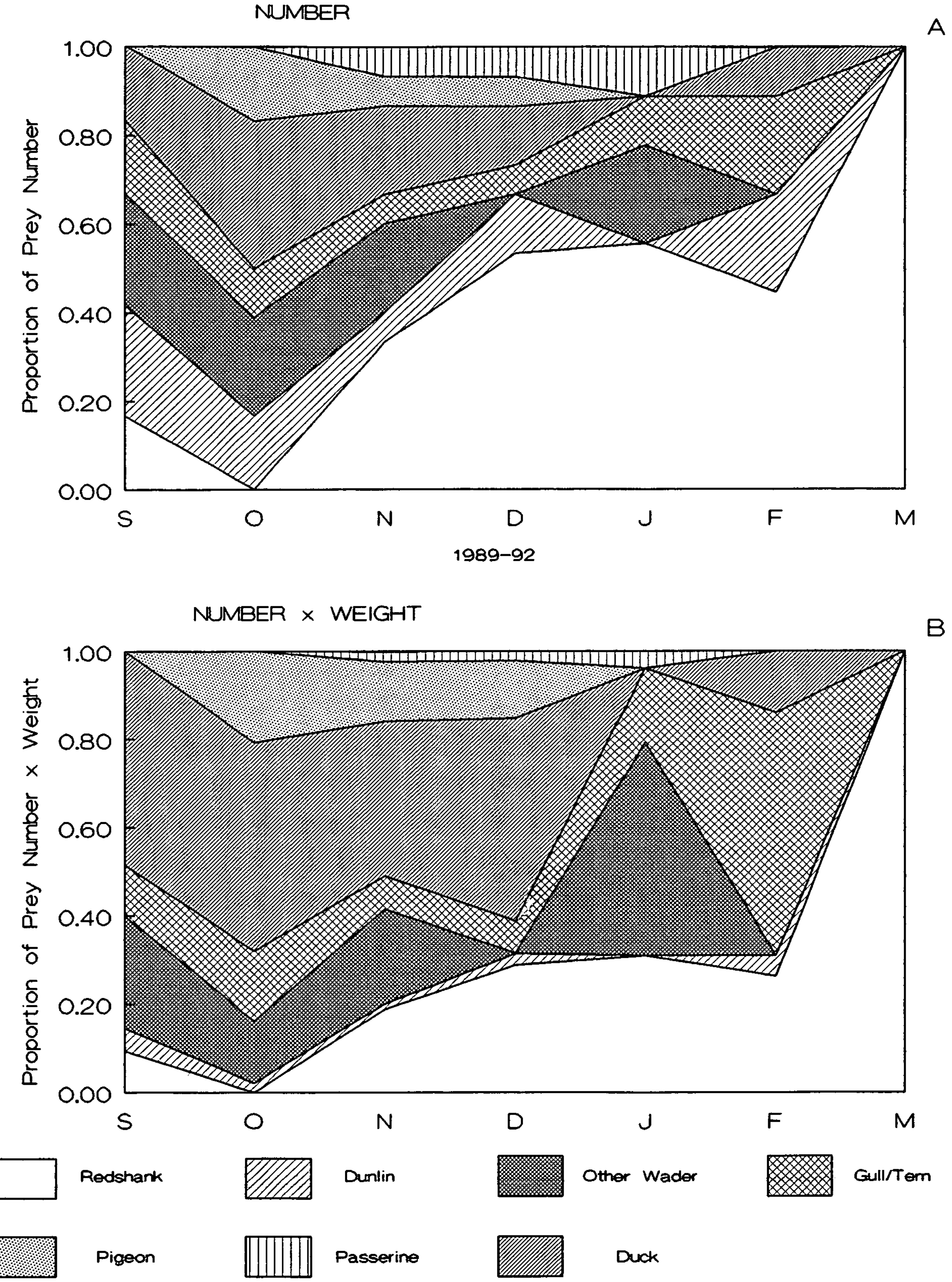
The weight of wader prey preferentially selected by merlins was between 51-100g; no wader prey over 150g was found to be taken (Fig.

Table 2: Prey Found Killed By Peregrines and Falcon/Owls

	Peregrine Kills Found	Falcon/Owl Kills Found
Mallard	1	
Teal	7	
Wigeon	8	
Pintail	1	
Ringed Plover		2
Grey Plover	10	2
Knot	1	6
Dunlin	14	81
Snipe		2
Redshank	34	47
Curlew	1	
Whimbrel	1	
Bar-tailed Godwit	1	
Turnstone		3
Black-headed Gull	6	
Herring Gull	2	
Common Gull	1	
Common Tern	1	
Woodpigeon	5	
Blackbird		1
Fieldfare		6
Blue Tit		1
Starling	3	2
Total	98	153

FIGURE 7

Variation in Peregrine Prey By Month

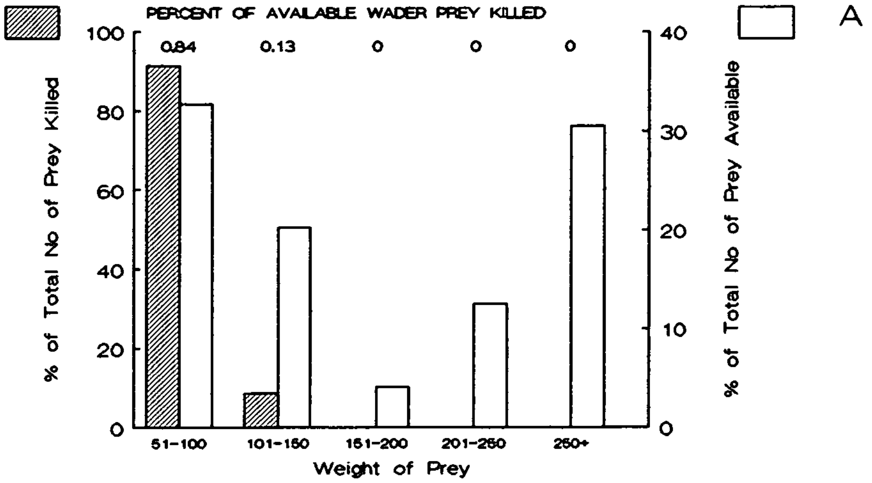


8A). Peregrines preferentially selected waders of between 101-150g, although waders were taken from all available weight classes (Fig. 8B). When passerine prey was considered, merlins were found to preferentially take prey of less than 50g (Fig. 8C); as most of the passerine prey were skylarks, the modal weight of prey selected was c40g. Passerines of weights of between 51-100g and 101-150g were selected approximately one half and a third as often respectively, compared to prey of weight of less than 50g. As with waders no prey of greater than 150g was recorded as taken by merlin. Weight of prey attacked by the different sexes of merlin and peregrine was found to be significantly different. Male merlins attacked significantly smaller prey than females (Table 3). Male peregrines attacked significantly smaller prey, controlling for age (Table 5), but immatures attacked the same size of prey compared to adults when controlling for sex (Table 4).

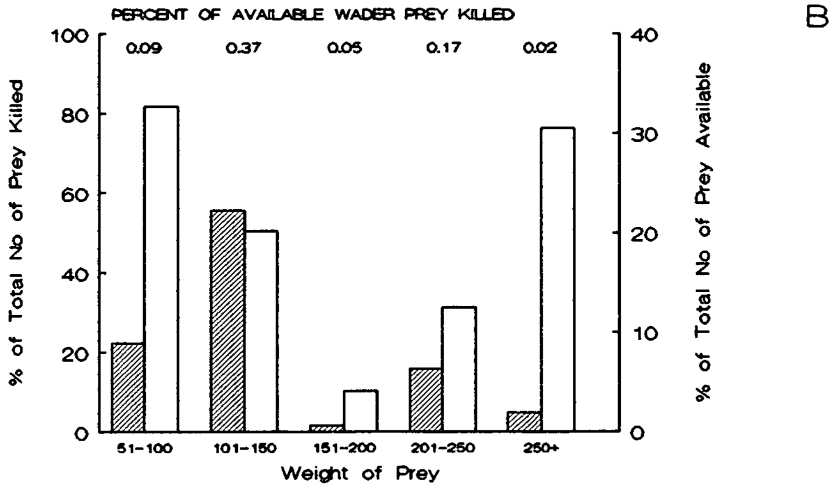
Different species of waders were more vulnerable to predation by merlins than peregrines and vice-versa. Sufficient redshank and dunlin kills were found for both peregrines and merlins to enable vulnerability indices (occurrence in the diet relative to occurrence in the population) to be calculated by pooling data from all three winters. For merlin vulnerability indices for redshank were 0.25 (n=11 kills) and for dunlin 1.4 (n=126 kills); for peregrine vulnerability indices for redshank were 2.2 (n=34 kills) and for dunlin 0.43 (n=14 kills). Relatively more redshank compared to dunlin were killed by peregrines than by merlins (G=69.6, 1df, $p<0.0001$).

FIGURE 8

WEIGHT OF WADERS SELECTED BY MERLINS



WEIGHT OF WADERS SELECTED BY PEREGRINES



WEIGHT OF PASSERINES SELECTED BY MERLINS

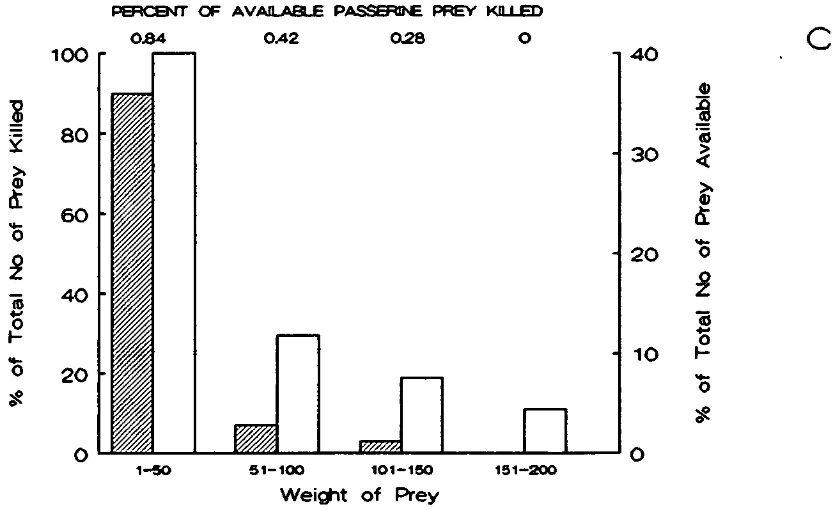


Table 3: Weight of prey attacked by male and female merlins.

	Weight in Grammes			
	<50	51-100	101+	
MALE	37	6	2	
FEMALE	240	148	56	G=14.0 p<0.001

Table 4: Weight of prey attacked by adult and immature peregrines controlling for sex.

	Weight in Grammes			
	<100	100-200	200+	
ADULT MALE	15	19	8	
IMM. MALE	14	9	5	G=1.5, p>0.05
ADULT FEMALE	2	11	12	
IMM. FEMALE	7	23	53	G=2.2, p>0.05

Table 5: Weight of prey attacked by male and female peregrines controlling for age.

	Weight in Grammes			
	<100	100-200	200+	
ADULT MALE	15	19	8	
ADULT FEMALE	2	11	12	G=9.5, p<0.01 alpha=0.05
IMM. MALE	14	9	5	
IMM. FEMALE	7	23	53	G=25.4, p<0.001 alpha=0.025

Sequential Bonferroni K=2

Vulnerability indices were calculated for passerine prey taken by merlins (Table 6). Most passerines had low vulnerability indices apart from the species which shared the same open habitat as merlins such as skylarks and pipits. Song thrushes were surprisingly vulnerable but this was probably an anomaly of sample size (n=3 kills only). Skylarks were attacked approximately 15 times more frequently than rock pipits, but overall were only approximately 3 times more common. Skylarks were either more conspicuous or were being preferentially attacked (success rates of attacks being similar for the two species - Table 9). There was no significant correlation between the weight of a prey species and its vulnerability index (T=1.0, Spearman's Rank Correlation, n=14 cases from Table 6, p=0.32).

The number of prey species killed by merlins and peregrines did not correlate significantly with the availability of prey, although sample sizes of kills were small in most cases. For merlins there were no significant correlations between availability and number of kills found for dunlin, redshank and skylark (Fig. 9). There was a slightly significant correlation for pipits (combining meadow and rock pipit data to obtain larger sample sizes of kills - as they associated freely in the main merlin hunting areas the pooling was probably valid; Fig. 9). Sample sizes of peregrine kills for three wader species were sufficiently large enough for analysis; there were no significant correlations between availability and number of kills found for grey plover, redshank and dunlin (Fig. 10).

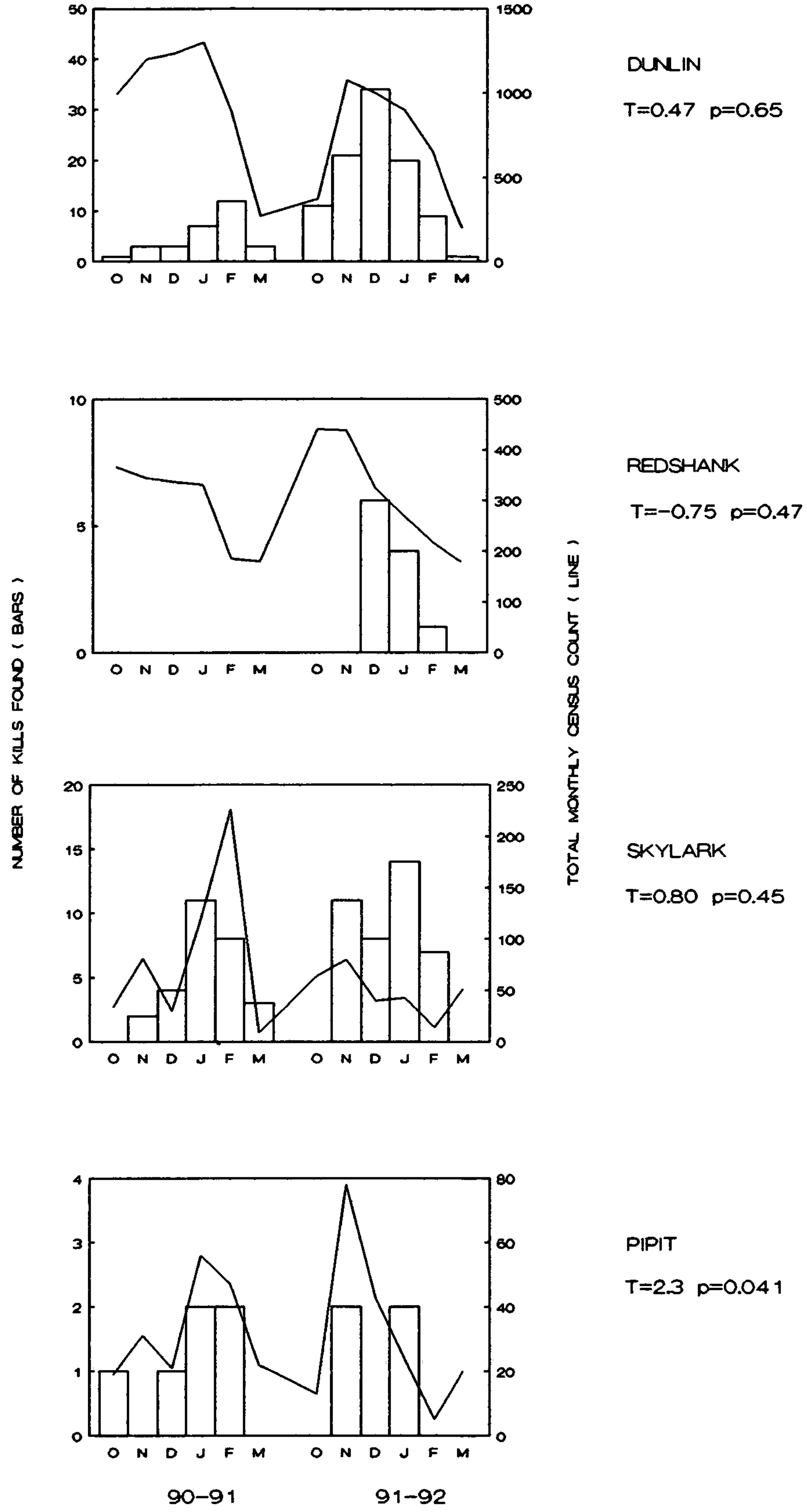
Sufficient merlin attacks necessary to calculate a meaningful attack rate were seen on only a few species. There was no

Table 6: Vulnerability Indices of Passerines to Merlins 1989-92.

Skylark	4.2
Rock Pipit	1.6
Meadow Pipit	1.0
Wren	0.1
Dunnock	0.2
Blackbird	0.2
Mistle Thrush	0.6
Song Thrush	2.1
Redwing	0.9
Fieldfare	0.2
Blue Tit	0.1
Starling	0.2
Chaffinch	0.1
Linnet	0.5

FIGURE 9

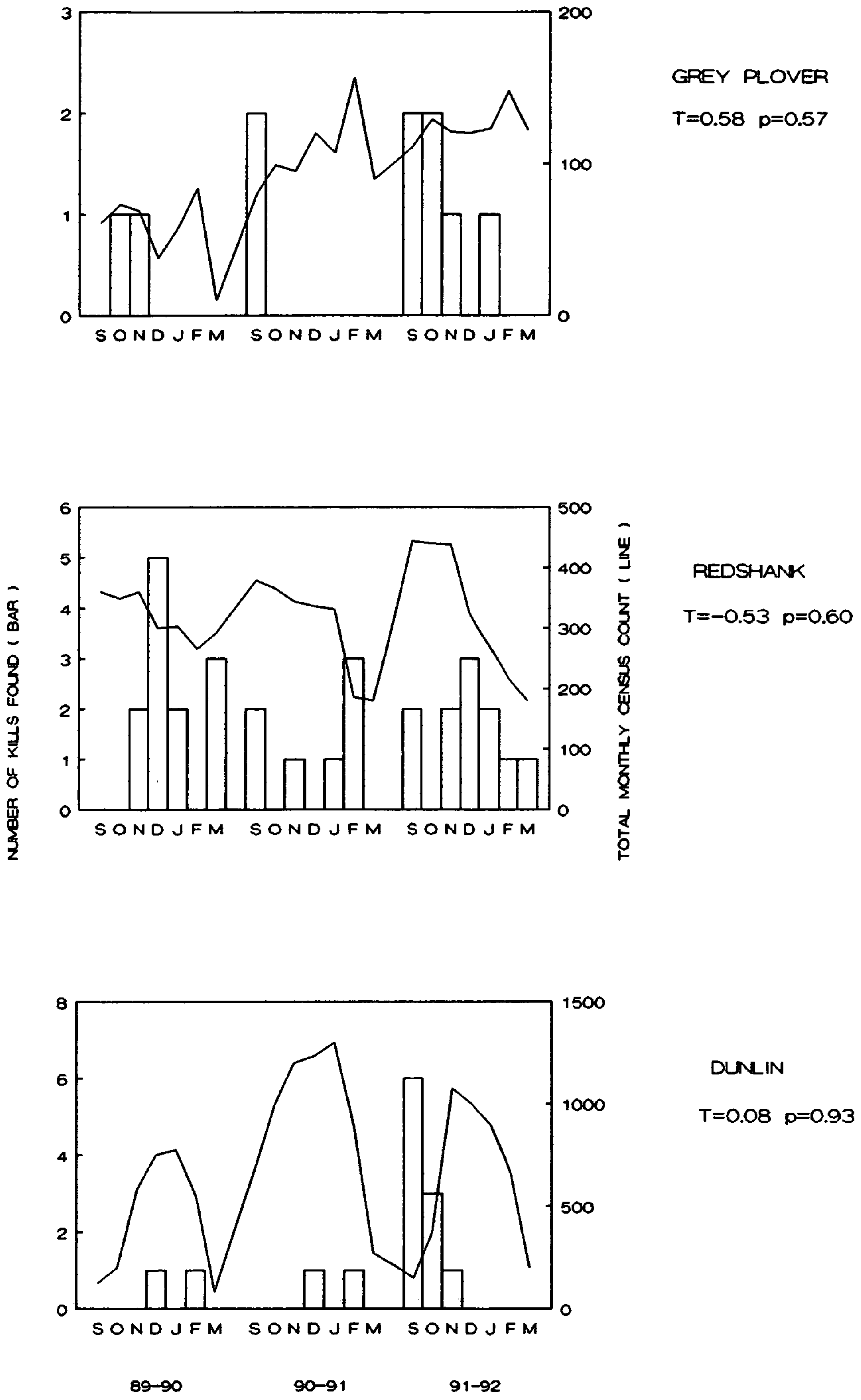
NUMBER OF PREY SPECIES CENSUSED AND FOUND KILLED BY MERLINS IN EACH MONTH



Spearman's Rank Correlation no. of kills with current month's census count

FIGURE 10

NUMBER OF PREY SPECIES CENSUSED AND FOUND KILLED BY PEREGRINES IN EACH MONTH



Spearman's Rank Correlation no. of kills with current month's census figure significant correlation between merlin attack rate (as measured by attacks per minute of sighting) and availability of dunlin or skylark prey (Fig. 11A and 11B). In winters 2 and 3 (nearly all attack data came from these winters) there was a seasonal pattern of attack apparently not related to availability of prey: skylark attack rate remained fairly constant through the winter while dunlin attack rate started high and fell to a very low rate midwinter, rising again slightly in February (Fig. 11C). The ratio of dunlin to skylark attacks was significantly different by month (October to February inclusive): winter 2, G=40.3, 4df, n=102 skylark attacks, n=41 dunlin attacks, $p<0.001$, alpha=0.025; winter 3, G=20.2, 4df, n=139 skylark attacks, n=108 dunlin attacks, $p<0.001$, alpha=0.05; sequential Bonferroni K=2. Only data from female merlins were used for the analysis due to sex differences in prey choice. Sample sizes of attacks on single species by peregrines of known sex were too small to correlate a meaningful attack rate by month.

7.2.4 Attack Rate

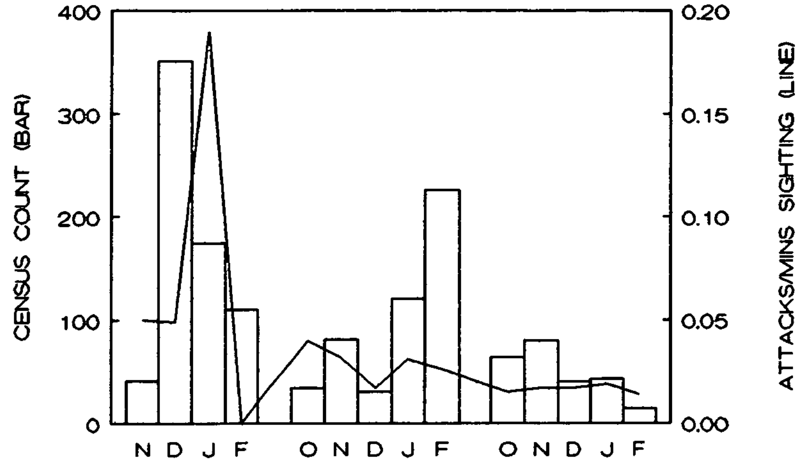
Attack rate for both merlin and peregrine was calculated as the number of attacks per minutes of sighting. As most sightings of merlins and peregrines were longer than 1 minute, attack rate per raptor watch hour (used as a measure of attack rate for sparrowhawks) did not correspond to attack rate per minute of sighting (Fig. 12). There were no significant correlations between attack rate per minute and attack rate per raptor watch hour for merlin and peregrine, except in winter 1 for merlin, when the frequency distribution of sighting lengths was similar to

MERLIN ATTACK RATES AND AVAILABILITY OF PREY

FIGURE 11

SKYLARK

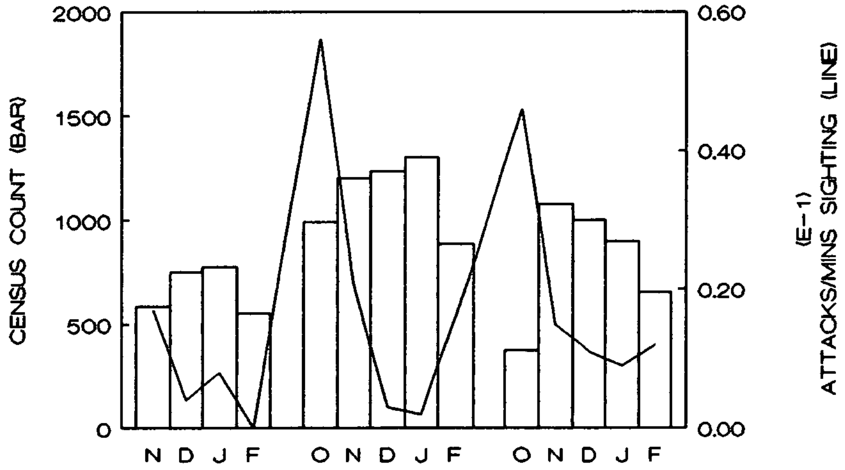
A



T=1.4 p=0.19

DUNLIN

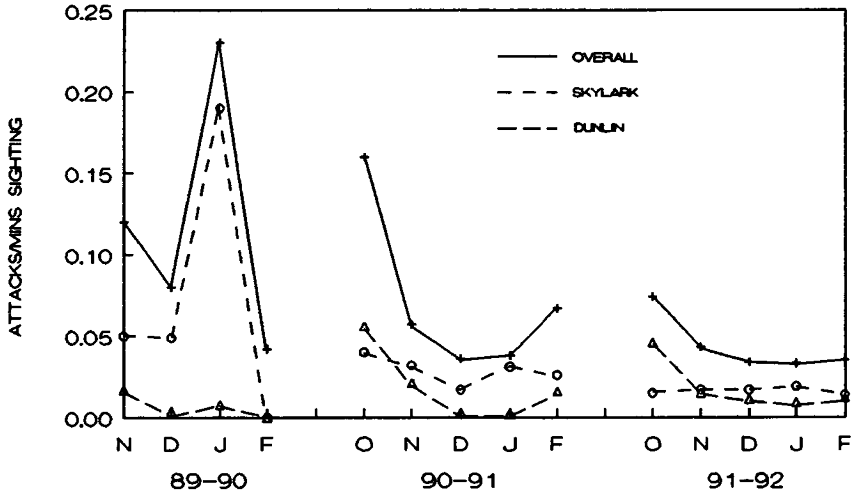
B



T=-0.52 p=0.62

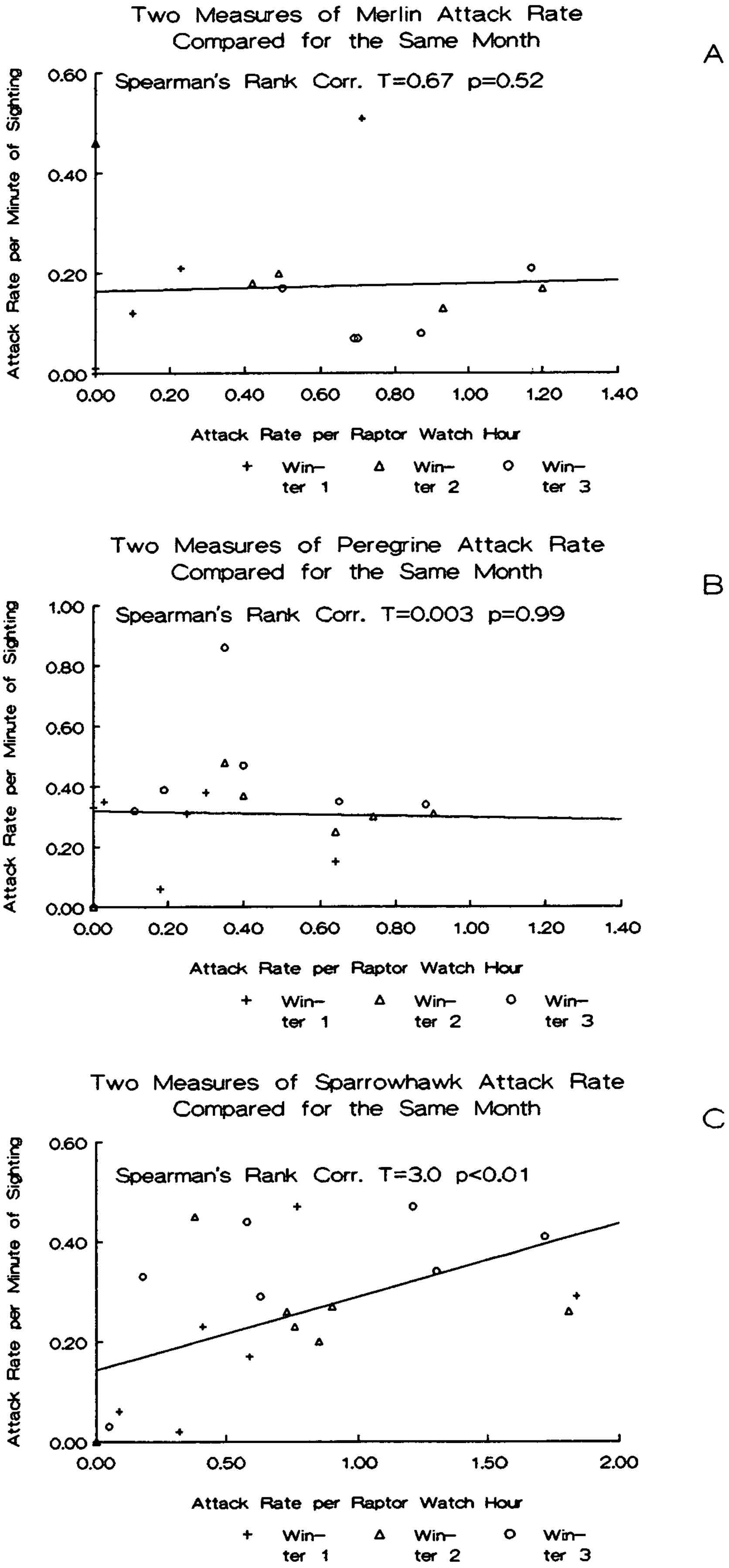
ATTACK RATES

C



Spearman's Rank Correlation attack rate with census count

FIGURE 12



Two Measures of Merlin Attack Rate Compared for the Same Month

Two Measures of Peregrine Attack Rate Compared for the Same Month

Two Measures of Sparrowhawk Attack Rate Compared for the Same Month sparrowhawks'. Attack rate, calculated as attacks per minute of sighting, was independent of the number of raptors present, but one potential source of bias was variation in the probability of seeing attacks with different lengths of sighting. Although attack rate decreased as sighting length increased, the decrease was not significant for merlins or peregrines: merlins, $x^2=3.8$, using all cases (n=653), sighting lengths split into 4 classes (1-2, 3-5, 6-10, 11+), p=0.28; peregrine, $x^2=9.3$, using all cases n=320, in 6 classes (1, 2-5, 6-10, 11-20, 21-50, 51+), p=0.10; Kruskall-Wallis 1-way ANOVA. A potential source of variation was the difference in observation method during raptor watch and non-raptor watch periods. There was no significant variation in attack rate comparing raptor watch and non-raptor watch periods in either merlins or peregrines; merlin, $x^2=0.03$, n=364 non-RW cases, n=289 RW cases, p=0.86; peregrine, $x^2=0.46$, n=197 non-RW cases, n=123 RW cases, p=0.50; Kruskall-Wallis 1-way ANOVA.

For merlin there was no significant variation in the overall attack rate on all species between winters: winters 1 and 2, $x^2=3.0$, p=0.08; winters 1 and 3, $x^2=4.7$, p=0.09, and winters 2 and 3 $x^2=0.17$, p=0.68; Kruskall-Wallis 1-way ANOVA.

Attack rate did not vary significantly with time of day, controlling for month (Table 7). Attack rate varied significantly with month, controlling for time of day, except early in the morning (6-9am) when attack rate was uniformly low (Table 7). Attack rate was highest in October, falling to a mid-winter low and then rising again slightly in February. Only data from winters 2 and 3, from October-February inclusive were pooled for the analysis in Table 7,

Table 7: Merlin attack rate with time of day and month, winters 2 and 3 pooled (n=822 with sightings of greater than 30 minutes split up into 30 minutes segments). A=number of attacks, M=minutes of sighting, and AR=attack rate.

		OCT	NOV	DEC	JAN	FEB	
6-9am	A	2	12	11	9	12	$x^2=1.6$
	M	84	381	450	263	304	
	AR	0.02	0.03	0.02	0.03	0.04	
9-12	A	25	44	51	59	32	$x^2=20.7$
	M	293	959	1371	1863	611	*$p<0.001$
	AR	0.09	0.05	0.01	0.03	0.05	a=0.006
12-3pm	A	17	50	33	49	62	$x^2=19.5$
	M	160	1234	987	1229	1170	*$p<0.001$
	AR	0.11	0.04	0.03	0.04	0.05	a=0.006
3-6pm	A	10	26	12	21	26	$x^2=18.1$
	M	104	359	300	782	589	*$p<0.005$
	AR	0.10	0.07	0.04	0.03	0.04	a=0.007
		$x^2=4.7$	$x^2=8.1$ p=0.03 a=0.008	$x^2=1.9$	$x^2=2.7$	$x^2=1.4$	

a=alpha, Sequential Bonferroni K=9

because nearly all data came from resident birds and there were relatively very few 'attack only' sightings (sparrowhawk-like sightings). Sightings from winter 1 and from September and March in all winters were usually of merlins passing very quickly through the study site. It was likely that those birds which attacked while in transit, would be noticed more often, giving a biased high attack rate. This may be the explanation for the higher attack rate in October as well.

For peregrine attack rate varied significantly between some winters: winters 1 and 2, x^2=0.76, p=0.38; winters 1 and 3, x^2=5.8, p=0.016, alpha=0.017, and winters 2 and 3, x^2=3.0, p=0.09; Kruskall-Wallis 1-way ANOVA, sequential Bonferonni K=3. Attack rate did not vary significantly by month in any of the winters: winter 1, September to March inclusive, x^2=7.6, p=0.27; winter 2, August to February inclusive, x^2=7.4, p=0.29; winter 3, August to March inclusive, x^2=10.6, p=0.16; Kruskall-Wallis 1-way ANOVA. Attack rate did not vary significantly by time of day: winter 1, x^2=6.3, p=0.51; winter 2, x^2=6.9, p=0.55; winter 3, x^2=16.8, p=0.03, alpha=0.017; Kruskall-Wallis 1-way ANOVA, sequential Bonferroni, K=3.

A multiple regression analysis was carried out using merlin (M) and peregrine (P) attack data separately in order to determine which environmental variables were significantly correlated with attack rate on all species. It was possible to transform the distribution of attack rates into an approximately normal distribution (transformed attack rate=log10[(number of attacks + 0.1)/minutes of sighting]), when only sightings of greater than 2 minutes were used (Mz=0.98 and Pz=1.3, Kolmogorov-Smirnov comparison to a normal distribution, Mp=0.29 and Pp=0.07). The subset of cases (greater than 2 mins sighting length) was then analysed for sampling variation which might have affected the recorded attack rate. Attack rate was not significantly different comparing raptor watch and non-raptor watch periods; $Mx^2=1.6$ and $Px^2=1.4$, Kruskall-Wallis 1-way ANOVA, Mp=0.79 and Pp=0.24. There were significant differences however in the distribution of merlin sighting lengths between some winters; winters 1 and 2, $x^2=12.0$, $p<0.001$, alpha=0.025, winters 1 and 3, $x^2=16.4$, $p<0.001$, alpha=0.017, but not in winters 2 and 3 $x^2=0.07$, $p=0.80$; Kruskall-Wallis 1-way ANOVA, sequential Bonferroni K=3. The multiple regression analysis for merlin was therefore carried out on sightings of greater than 2 minutes in length, pooling winters 2 and 3 only (n=438 sightings). Relatively few merlin data were lost by removing sightings of less than 3 minutes; in winters 2 and 3 pooled, only 1.4% of minutes of time budget and 12.2% of attacks were lost. For peregrines there were no significant differences in the distribution of sighting lengths comparing across the three winters ($x^2=0.15$, Kruskall-Wallis 1-way ANOVA, $p=0.93$); data were therefore pooled for the analysis. Relatively few peregrine data were lost by removing sightings of less than 3 minutes; 3.9% of minutes of time budget and 17.3% of attacks.

Environmental variables put into the regression analysis with transformed attack rate were daylength, mean daily temperature, time to the nearest high tide (tide difference), month and time. For merlin, after backwards deletion of variables, the only significant variable remaining in the equation was daylength. There was a significant slight increase in attack rate with increasing daylength ($y=0.09x - 2.3$, $T=2.7$, $p<0.01$). Variables not in the equation were: tide difference, $T=-0.57$, $p=0.57$; mean daily temperature, $T=0.45$, $p=0.65$; month, $T=1.0$, $p=0.31$ and time, $T=0.70$, $p=0.48$. For peregrine, after backwards deletion of variables, all variables were removed from the equation: tide difference, $T=0.84$, $p=0.40$; temperature, $T=-0.20$, $p=0.84$; month, $T=-0.64$, $p=0.52$, daylength, $T=0.72$, $p=0.47$, and time, $T=1.2$, $p=0.25$.

For peregrine, pooling all data and not controlling for age or sex respectively, there was no significant difference in attack rate by sex ($x^2=0.13$, $n=43$ male and $n=76$ female cases, $p=0.72$), but there was a significantly higher attack rate for immatures (0.47 attacks per minute of sighting) compared to adults (0.28 attacks per minute of sighting); $x^2=4.0$, $n=102$ adult and $n=129$ immature cases, $p<0.05$).

7.2.5 Merlin Success Rate

Overall 544 merlin attacks (excluding all corvid attacks, $n=6$, non-avian attacks, $n=1$ and attacks of unknown outcome, $n=52$), 55 kills and 60 captures were seen (Table 8). Most attacks were on skylarks and dunlin, allowing for single species analysis of success rate (in calculating single species success rates, attacks where more than one raptor was involved were excluded). There was no significant variation in success rate of attack on dunlin or skylark between winters: skylark, winters 1 to 3, $G=5.8$, 2df, $p=0.06$; dunlin, winter 2 and 3 (no kills were seen in winter 1), $G=0.025$, 1df, $p=0.9$. Overall there was no significant variation in success rate of attacks pooling all species over the three winters ($G=4.1$, 2df,

TABLE 8: Success Rates of Merlin Attacks (Pooled Data All Winters)

	Attacks	Kills	Captures	Kill Success Rate
Redshank	48	0	2	-
Dunlin	134	17	19	12.7
Knot	1	0	0	-
Snipe	1	0	0	-
Jack Snipe	1	1	1	-
Curlew	2	0	0	-
Unknown Wader	18	0	0	-
All Waders	205	18	22	8.8
Skylark	257	30	31	11.7
Rock Pipit	20	4	4	20.0
Dunnock	3	0	0	-
Mistle Thrush	2	0	0	-
Starling	7	0	0	-
Chaffinch	12	1	1	-
Linnet	14	2	2	14.3
Greenfinch	1	0	0	-
Brambling	1	0	0	-
Unknown Passerine	22	0	0	-
All Passerines	339	37	38	10.9
Red Admiral Butterfly	1	0	0	-
TOTAL	545	55	60	10.1

Comparing the relative frequency of attacks which resulted in kills:

Redshank vs Dunlin: Fisher's Exact Test *p=0.007 a=0.017

Skylark vs Rock Pipit: G=0.73 p>0.05

Dunlin vs Skylark: G=0.06 p>0.05

a=alpha, Sequential Bonferroni, K=3

p=0.13). Within one winter (using winter 3 as sample sizes were largest in that winter) and pooling all winters there was no significant variation in success rate by month: skylark, November to February inclusive, winter 3, G=0.42, 3df, p=0.9, and winters 1-3, G=1.5, 3df, p=0.69; dunlin, October to February inclusive, winter 3, G=0.58, 4df, p=0.9, and winters 1-3, G=1.4, 4df, p=0.9. Success rate between species did not vary significantly except between redshank and dunlin (Table 8). Between prey species with more than one kill seen (dunlin, skylark, rock pipit and linnet) there was no significant difference in success rate (overall success rate 12.5%); G=0.96, 3df, p=0.9.

To analyse possible correlations of environmental variables with success rate, attack rates on all species were pooled to maintain sample sizes. Attacks were split into classes so that approximately equal numbers of kills occurred in each class. There were no significant differences in attack success rate with mean daily temperature (G=0.60, 2df, p=0.75, comparing <3, 3.1-6, >6^{o}C), daylength (G=0.24, 1df, p=0.7, comparing <8 and >8 hours), tide difference (G=0.15, 1df, p=0.7, comparing low and high tide +/-3 hours), and time of day (G=0.87, 3df, p=0.3, comparing 6-9am, 9.01am-12pm, 12.01-3pm, 3.01-6pm, and splitting all sightings of greater than 30 minutes into 30 minute or less cases).

There was no significant difference in the success rate for attacks on all species comparing male and female merlins (G=0.01, 1df, p=0.9, using data from winters 1 and 2 only, as no attacks by males were seen in winter 3).

7.2.6 Peregrine Success Rate

Overall 488 peregrine attacks (excluding all corvid attacks, n=47, non-avian attacks, n=1, and attacks of unknown outcome, n=5), 28 kills and 33 captures were seen (Table 9). Data were pooled due to small sample sizes of observed kills. There was no significant variation in success rate by winter (G=0.03, 2df, p=0.9) or by month (G=4.0, 5df, p=0.55, September to February inclusive, pooling winters). There was no significant difference in success rate according to species (Table 10), for example redshank (7.6%) compared to dunlin (13.2%), but this was probably a consequence of sample size.

There were no significant differences in capture success rate with mean daily temperature (G=2.0, 2df, p=0.37, comparing <3, 3.1-6, >6^{o}C), daylength (G=3.7, 2df, p=0.16, comparing <8, 8.1-10 and >10 hours), tide difference (G=0.10, 1df, p=0.9, comparing low and high tide +/-3 hours), and time of day (G=1.7, 3df, p=0.64, comparing 6-9am, 9.01am-12pm, 12.01-3pm, 3.01-6pm, and splitting all sightings of greater than 30 minutes into 30 minute or less cases). There were no significant differences in success rate according to sex (G=1.6, 1df, male n=3/124 captures/unsuccessful attacks, female n=8/140, p=0.21) or age (G=2.1, 1df, adult n=13/198, immature n=8/235, p=0.15).

Peregrines had a significantly higher success rate of capture in the first minute of arrival on the estuary (16.4%), when no peregrines had been flying on the study site for the preceding hour or more, compared to subsequent minutes, or when a peregrine had been flying in the study area in the preceding hour (2.1%); G=17.5,

TABLE 9: Success Rates of Peregrine Attacks (Pooled Data All Winters)

	Attacks	Kills	Captures	Kill Success Rate
Shelduck	3	0	0	-
Wigeon	26	1	1	3.8
Teal	5	2	2	40.0
Mallard	1	0	0	-
Eider	1	0	0	-
All Ducks	36	3	3	8.3
Pheasant	1	0	0	-
Oystercatcher	14	0	0	-
Redshank	157	12	15	7.6
Knot	1	0	0	-
Dunlin	76	10	10	13.2
Snipe	1	0	0	-
Lapwing	12	0	0	-
Grey Plover	13	1	2	7.7
Bar-tailed Godwit	4	0	0	-
Curlew	46	0	0	-
Whimbrel	1	0	0	-
Turnstone	7	0	0	-
Unknown Wader	36	2	2	-
All Waders	368	25	29	6.8
Sandwich Tern	2	0	0	-
Herring Gull	3	0	0	-
Common Gull	1	0	0	-
Black-headed Gull	13	0	0	-
Unknown Gull	5	0	0	-
All Gull/Terns	24	0	0	-
Woodpigeon	29	0	1	-
Feral Pigeon	6	0	0	-
All Pigeons	35	0	1	-
Skylark	21	0	0	-
Fieldfare	1	0	0	-
Starling	2	0	0	-
All Passerines	24	0	0	-
Rabbit	1	0	0	-
TOTAL	489	28	33	5.7

Comparing the relative frequency of attacks which resulted in kills:

Redshank vs Dunlin: $G=1.4$ $p>0.05$

Waders vs Ducks: $G=0.09$ $p>0.05$

1df, p<0.001, winters 1 and 2 data, 12/61 captures/unsuccessful attacks in the first minute, and 5/241 for all other minutes). Peregrines made significantly more attacks than expected in the first minute of arrival on the estuary (with no peregrine flight sightings in the preceding hour or more) than in all other minutes (x^2=31.8, 1df, p<0.001, winters 1 and 2 data, n=85 attacks in the first minute, n=246 attacks in subsequent and all other minutes). Data from all three winters was classified into three classes of minutes since the last peregrine flight sighting over the whole estuary, 1-10, 11-20 and 21+ minutes, capture rate was 3.0%, 8.1% and 10.0% respectively (G=9.0, 2df, n=31 captures, n=441 unsuccessful attacks, p<0.02).

7.2.7 Time Budget Data

In total 13,762 minutes of merlin time budget data from 653 cases and 4,785 minutes of peregrine time budget data from 323 cases were recorded representing 8.9% and 3.1% respectively of the total time spent in the field (2557 hours). For raptor watches (n=772 hours) merlin time budget data were collected 19.8% of the time, and peregrine time budget data were collected 6.6% of the time. Merlin sightings had a mean length of 21.1 minutes and ranged from one minute to 279 minutes in length. Peregrine sightings had a mean length of 14.8 minutes and ranged from one minute to 394 minutes in length. Both raptor species had a modal sighting length of one minute. Comparing raptor watch with non-raptor watch periods (Table 10) there were few significant differences in the proportion of minutes in which an activity was recorded. For merlin preening was

Table 10: Variation in the proportion of minutes of sightings in which a behaviour was recorded comparing raptor watch and non-raptor watch observations.

	Merlin:			Peregrine:		
	x^2	p value	alpha	x^2	p value	alpha
Hunt	0.18	0.67		0.21	0.65	
Perch	2.3	0.13		5.2	0.023	0.006
Preen	19.6	*0.0001	0.005	0.004	0.95	
Mobbed	1.4	0.24		0.28	0.60	
Mobbing	2.8	0.10		2.2	0.14	
Interactions	0.15	0.70		8.4	*0.004	0.005
Moving	0.92	0.34		1.0	0.31	
Hunt/Move	6.1	0.013	0.005	-	-	
High Soar	0.14	0.71		1.3	0.26	
Carry Prey	0.01	0.93		3.4	0.07	
Feed	0.44	0.51		1.1	0.30	

Sequential Bonferroni: K=11 K=10

Kruskall-Wallis 1-way ANOVA

the only behaviour which was recorded at a different frequency with the different sampling methods; preening was recorded 2% of minutes more in raptor watch periods. For peregrine, interactions were the only behaviour which were recorded at different frequency with the different sampling methods; interactions were recorded c2% more in raptor watch periods.

There was significant variation in the proportion of minutes in which an activity was recorded over each winter for some behaviours (Table 11). For merlin, perching, preening and feeding were recorded less frequently in winter 1 as no resident merlins were present, for example, in winters 1 and 2 perching was recorded in 85% of minutes, compared to 76% for winter 1. For peregrines, hunting was recorded with significantly different frequencies in each winter: winter 1, 14.4%, winter 2, 11.4% and winter 3, 16.3%. Despite significant variation for a behaviour between winters, the variation was relatively small compared to the major differences between different classes of behaviour (Fig. 13A and 13B).

There was significant variation in the proportion of minutes in which an activity was recorded by month (pooling winters) for some behaviours (Table 12). For merlin there were more interactions between merlins in October (2.1% of all time budget minutes) compared to all other months (0.4%). Hunting/moving flight and perching were recorded less frequently in October (2.2% and 79% respectively) compared to all other months (5.6% and c83% respectively). Prey was observed being carried more in January and February (2.2%) compared to all other months (0.8%). Merlins were observed being mobbed in relatively more minutes in October (4.5%)

Table 11: Variation in the proportion of minutes of sightings in which a behaviour was recorded comparing winters 1 to 3.

	Merlin:			Peregrine:		
	x^2	p value	alpha	x^2	p value	alpha
Hunt	7.6	0.023	0.01	19.3	*0.0001	0.005
Perch	45.3	*0.0001	0.005	1.7	0.43	
Preen	52.7	*0.0001	0.005	5.3	0.07	
Mobbed	8.5	0.015	0.007	2.6	0.27	
Mobbing	4.4	0.11		5.8	0.06	
Interactions	1.5	0.46		5.8	0.06	
Moving	5.7	0.06		1.7	0.43	
Hunt/Move	9.1	0.011	0.006	-	-	
High Soar	5.0	0.08		0.19	0.91	
Carry Prey	8.4	0.015	0.008	0.15	0.93	
Feed	11.7	*0.0003	0.006	0.48	0.79	

Sequential Bonferroni: K=11 K=10

Kruskall-Wallis 1-way ANOVA

Peregrine and Merlin Time Budget Data

FIGURE 13

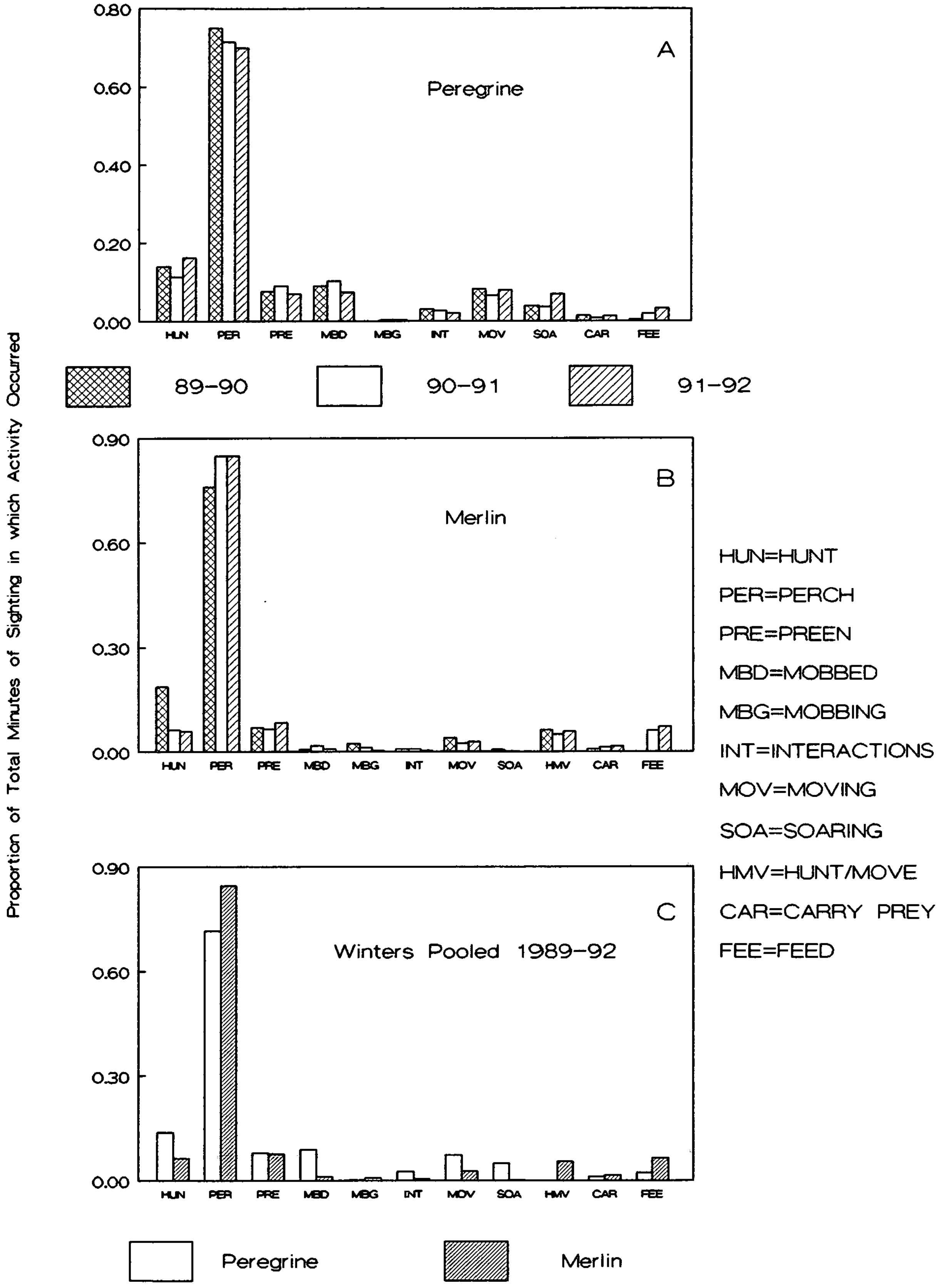


Table 12: Variation in the proportion of minutes of sightings in which a behaviour was recorded by month: October - February inclusive for merlin, and September to February Inclusive for peregrine.

	Merlin:			Peregrine:		
	x^2	p value	alpha	x^2	p value	alpha
Hunt	4.4	0.35		3.3	0.65	
Perch	14.0	*0.007	0.007	10.1	0.07	
Preen	6.0	0.20		6.8	0.23	
Mobbed	15.9	*0.003	0.005	12.3	0.03	0.006
Mobbing	5.3	0.26		1.6	0.90	
Interactions	25.0	*0.0001	0.005	2.9	0.72	
Moving	3.1	0.55		19.0	*0.002	0.005
Hunt/Move	14.8	*0.005	0.006	-	-	
High Soar	5.3	0.26		7.5	0.19	
Carry Prey	15.1	*0.004	0.006	10.2	0.07	
Feed	11.4	0.02	0.008	2.7	0.75	
Sequential Bonferroni:			K=11			K=10

Kruskall-Wallis 1-way ANOVA

compared to mid-winter months such as January (0.5%). For peregrine only the proportion of minutes in which moving flight was recorded varied significantly with month, but with no consistent pattern.

Visibility of peregrines and merlins was not activity-dependent as with sparrowhawks. Peregrines and merlins use conspicuous perches and rarely entered cover. Merlins were generally less conspicuous than peregrines, for example, flying low over the ground between perches and often perching on the ground. As most time budget data came from resident merlins, which could be followed continuously for several hours, inconspicuous behaviours were unlikely to be under-recorded relative to those of peregrines: time budget data for the two species were probably comparable. Figure 13C compares time budget data for merlins and peregrines. There were significant differences in the proportion of minutes in which a particular behaviour occurred comparing merlins (M) and peregrines (P): hunt, $x^2=47.5$ (P>M); perch, $x^2=130.1$ (M>P); preen, $x^2=14.9$ (M>P); mobbed, $x^2=15.7$ (P>M); mobbing, $x^2=16.2$ (M>P); interactions, $x^2=29.9$ (P>M); high soar, $x^2=127.0$ (P>M) and feed, $x^2=13.3$ (M>P); Kruskall-Wallis 1-way ANOVA; smallest value of $p=0.0001$; smallest value of alpha=0.005, Sequential Bonferroni, K=10. The proportion of minutes of a sighting spent carrying prey was not significantly different between the two raptors ($x^2=0.23$, Kruskall-Wallis 1-way ANOVA, $p=0.63$). Despite the significant interspecific differences, the frequency distribution of the different behaviours was similar. Most of the raptors' time was spent perched, c75%, with hunting as the next most significant behaviour, c6-13%; behaviours associated with hunting/moving occurred in c8-11% of minutes of total sightings.

Peregrines tended to move between attack areas by high soaring while merlins used low ground-hugging flights.

Raptor time budget data were analysed to determine the main factors correlating with the proportion of minutes of a sighting in which a behaviour occurred. The variables investigated were mean daily temperature, daylength and time of day. One potential source of bias in the analysis was the probability of a behaviour occurring more or less frequently with different lengths of sightings. For example, preening would be unlikely to be seen in very short sightings as these would inevitably be of moving birds. For merlin, length of sighting was significantly correlated with mean daily temperature ($T=-3.3$, Spearman's Rank Correlation, $p<0.001$) but not with daylength ($T=-1.7$, Spearman's Rank Correlation, $p=0.08$) and varied significantly with time of day ($x^2=19.1$, Kruskall-Wallis 1-way ANOVA, $p<0.05$). For peregrine length of sighting was not significantly correlated with mean daily temperature or daylength ($T=0.48$, $p=0.63$ and $T=-0.00$, $p=0.99$ respectively) but was significantly correlated with time of day ($T=-3.6$, $p<0.0005$); Spearman's Rank Correlation all tests. Behaviours which were more likely to occur in long sightings would therefore be recorded more frequently at low temperatures for merlins, and less frequently later in the day for peregrines. There was significant variation in the proportion of minutes of sightings in which a behaviour was recorded over different length sightings for many behaviours, for both merlin and peregrine (Table 13).

Correlations between a merlin time budget activity and the environmental variables were carried out controlling for variation

Table 13: Variation in the proportion of minutes of sightings in which a behaviour was recorded comparing sighting lengths, and the range of sighting lengths over which there was no significant variation in the occurrence of a behaviour. Sighting lengths were classified into the following categories: 1, 2, 3, 4, 5, 6-10, 11-20, 21-40, 41+ and analysed with Kruskall-Wallis 1-way ANOVA.

MERLIN:

	ALL SIGHTINGS		RANGE OF SIGHTINGS		
	x^2	p	Range	x^2	p
HUNT	18.6	p=0.02	>5 and <40	3.2	p=0.20
PERCH	208.3	p<0.0001	>20	0.41	p=0.52
PREEN	265.0	p<0.0001	>10 and <41	0.93	p=0.33
MOBBED	12.4	p=0.13			
MOBBING	15.6	p=0.048			
INTERACTIONS	8.0	p=0.43			
MOVING	30.4	p<0.001	<21	2.8	p=0.83
HIGH SOAR	13.0	p=0.11			
HUNT/MOVE	61.4	p<0.0001	>4	3.6	p=0.46
CARRY PREY	38.9	p<0.0001	>4 and <41	2.5	p=0.47
FEED	81.7	p<0.0001	-	-	-

PEREGRINE:

	ALL SIGHTINGS		RANGE OF SIGHTINGS		
	x^2	p	Range	x^2	p
HUNT	21.5	p=0.006	>4 and <41	4.9	p=0.30
PERCH	241.3	p<0.0001	>20	2.0	p=0.16
PREEN	181.5	p<0.0001	-	-	-
MOBBED	80.3	p<0.0001	>10	4.7	p=0.10
MOBBING	7.8	p=0.45			
INTERACTIONS	5.0	p=0.75			
MOVING	12.3	p=0.14			
HIGH SOAR	24.4	p=0.0019	>5	4.0	p=0.27
CARRY PREY	7.1	p=0.52			
FEED	35.7	p<0.0001	-	-	-

according to observation method (Table 10), winter (Table 11) and sighting length (Table 13). Where significant variation occurred a subset of cases was chosen which minimised this variation and maximised the sample size of sightings. Where significant variation occurred according to winter, each winter was analysed separately (in two cases for merlin, hunt and mobbed, winters 2 and 3 were pooled as there was no significant variation in the behaviours between the two winters (x^2=0.004 and x^2=0.42, respectively, Kruskall-Wallis 1-way ANOVA, p=0.95 and p=0.52 respectively). Where significant variation occurred with observation method, raptor watch sightings only were analysed. For some behaviours it was impossible to control for the length of sighting: for merlin and peregrine, the proportion of time spent feeding, and for peregrine, the proportion of time spent preening was too closely associated with sighting length to separate out a large enough subset of cases for analysis.

For merlin there were few significant correlations between mean daily temperature, daylength or time of day and the proportion of a sighting in which a behaviour occurred (Table 14). Perching was highly significantly negatively correlated with temperature in winters 2 and 3, but this was a consequence of sighting length. The only significant table-wide correlation was a positive correlation between daylength and the proportion of a sighting in which the merlin was mobbed: merlins were mobbed more, early and late in the winter. As merlins were mobbed in total in only 1.1% of minutes of sightings, merlins were unlikely to be affected in any major way by the differing rates of mobbing over the winter. Overall there were no highly significant changes in the amount of time a merlin spent

Table 14: Correlations between merlin time budget data and environmental variables, controlling for variation by winter (W), raptor watch(RW)/non-raptor watch (NRW) observation method and length of sighting (LOS) where necessary. Significant results are underlined.

		Temperature	Daylength	Time
HUNT	W1 (n=72)	T=-2.0 p=0.047 a=0.003	T=-2.3 p=0.022 a=0.003	x^2=11.0 p=0.14
	W2+3 (n=581)	T=1.0 p=0.30	T=2.0 p=0.046 a=0.003	x^2=8.5 p=0.49
	LOS >5,<41 (n=269)	T=-0.18 p=0.86	T=1.5 p=0.14	x^2=13.2 p=0.14
PERCH	W1 (n=72)	T=0.92 p=0.36	T=0.92 p=0.36	x^2=6.8 p=0.45
	W2 (n=289)	T=-3.3 *p=0.001 a=0.002	T=-1.2 p=0.22	x^2=16.7 p=0.033 a=0.003
	W3 (n=292)	T=-4.5 *p<0.001 a=0.002	T=-2.8 p=0.006 a=0.003	x^2=9.0 p=0.35
	LOS >20 (n=213)	T=-1.1 p=0.28	T=-0.87 p=0.39	x^2=12.5 p=0.13
PREEN	RW+W1 (n=53)	T=-0.40 p=0.69	T=-2.4 p=0.022 a=0.003	x^2=15.5 p=0.030 a=0.003
	RW+W2 (n=127)	T=1.8 p=0.08	T=-0.54 p=0.59	x^2=5.0 p=0.76
	RW+W3 (n=184)	T-1.2 p=0.22	T=-2.7 p=0.007 a=0.002	x^2=19.2 p=0.014 a=0.002
	LOS >10,<41	T=1.3 p=0.20	T=-1.4 p=0.17	x^2=14.6 p=0.07
MOB-BED	W1 (n=79)	T=-2.4 p=0.021 a=0.003	T=-2.6 p=0.012 a=0.003	x^2=8.1 p=0.32
	W2+3 (n=581)	T=2.7 p=0.008 a=0.003	T=3.1 *p=0.002 a=0.002	x^2=15.6 p=0.049 a=0.003
MOB-BING	(n=653)	T=0.73 p=0.46	T=-0.46 p=0.65	x^2=12.3 p=0.14
MOV-ING	(n=653)	T=1.6 p=0.12	T=-0.30 p=0.77	x^2=13.5 p=0.10
	LOS <21 (n=440)	T=0.75 p=0.46	T=-0.49 p=0.62	x^2=10.1 p=0.26
INTER-ACTIONS	(n=653)	T=2.1 p=0.039 a=0.003	T=1.1 p=0.29	x^2=6.7 p=0.57

T values Spearman's Rank Correlation, x^2 values Kruskall-Wallis 1-way ANOVA.

a=alpha, Sequential Bonferroni K=23

Table 14 (Continued): Correlations between merlin time budget data and environmental variables, controlling for variation by winter (W), raptor watch(RW)/non-raptor watch (NRW) observation method and length of sighting (LOS) where necessary. Significant results are underlined.

		Temperature	Daylength	Time
HUNT/	RW+W3	T=-3.0	T=-2.4	$x^2=8.8$
MOVE	(n=184)	p=0.003 a=0.002	p=0.019 a=0.002	p=0.36
	RW+LOS >4	T=-1.5	T=-1.5	$x^2=20.5$
	(n=248)	p=0.13	p=0.13	p=0.009 a=0.002
	RW+LOS>4+W3	T=-1.7	T=-2.2	$x^2=17.6$
	(n=151)	p=0.08	p=0.027 a=0.003	p=0.024 a=0.002
CARRY	W3 (n=292)	T=-0.68	T=-0.25	$x^2=5.3$
PREY		p=0.50	p=0.80	p=0.72
	LOS >4, <41	T=-2.7	T=1.2	$x^2=6.6$
		p=0.008 a=0.003	p=0.24	p=0.58
FEED	(n=653)	T=-1.4	T=0.05	$x^2=1.7$
		p=0.17	p=0.96	p=0.99

T values Spearman's Rank Correlation, x^2 values Kruskall-Wallis 1-way ANOVA.

a=alpha, Sequential Bonferroni K=23

performing the behaviours with changes in the environmental variables examined. The relative proportions of behaviours shown in Figures 13B and 13C were therefore representative of merlin behaviour at any time over the winter at Tyninghame.

For peregrine there were few significant correlations between mean daily temperature, daylength and time of day (Table 15). The proportion of a sighting that was spent high soaring was significantly positively correlated with daylength and the correlation became more significant when sighting length was controlled for. Peregrines spent more time high soaring early and late in the winter: using raptor watch data only, pooled for all winters the proportion of time spent high soaring was September, 10.1%, October 6.0%, November 2.5%, December 1.1%, January 2.2% and February 6.7%. There was significant variation in the proportion of time spent in moving flight with time of day; peregrines spent more time in moving flight later in the day ($T=2.0$, Spearman's Rank Correlation, $p<0.05$). The proportion of time spent in moving flight for 6-9am was 9.0% compared to 16.2%, for 3-6pm. Overall, apart from moving and high soaring flight, the relative proportions of behaviours shown in Figures 13A and 13C were fairly representative of peregrine behaviour at any time over the winter at Tyninghame.

As long sightings of merlins and peregrines were common, time at the start of the time budget, as used in all analyses, will have been inaccurate in many cases. To obtain more accurate measures of the time of day at which behaviours occurred, correlations were carried out using only cases of 30 minutes or more, split into 30 minute cases. Time was taken at the start of each case (Table 16).

Table 15: Correlations between peregrine time budget data and environmental variables, controlling for variation by winter (W), raptor watch(RW)/non-raptor watch (NRW) observation method and length of sighting (LOS) where necessary. Significant results are underlined.

		Temperature	Daylength	Time
HUNT	W1 (n=83)	T=-0.29 p=0.77	T=-0.41 p=0.69	$x^2=14.7$ p=0.04
	W2 (n=115)	T=-2.6 p=0.011 a=0.003	T=-1.4 p=0.16	$x^2=7.9$ p=0.44
	W3 (n=123)	T=-0.19 p=0.85	T=-1.2 p=0.21	$x^2=12.3$ p=0.14
	LOS 4-40 (n=132)	T=-0.27 p=0.78	T=-0.16 p=0.88	$x^2=7.3$ p=0.51
PERCH	RW (n=200)	T=-0.55 p=0.58	T=-1.4 p=0.15	$x^2=11.2$ p=0.19
	LOS >20 (n=44)	T=0.39 p=0.70	T=0.74 p=0.46	$x^2=9.0$ p=0.34
PREEN	(n=321)	T=0.05 p=0.96	T=-1.1 p=0.27	$x^2=11.8$ p=0.16
MOB-BED	(n=321)	T=1.0 p=0.30	T=-0.00 p=0.99	$x^2=16.9$ p=0.03 a=0.003
	LOS >10 (n=96)	T=0.75 p=0.45	T=0.008 p=0.93	$x^2=6.3$ p=0.61
MOB-BING	(n=321)	T=-0.52 p=0.60	T=-0.67 p=0.51	$x^2=4.5$ p=0.81
MOV-ING	(n=321)	T=-3.3 *p=0.001 a=0.003	T=-1.3 p=0.20	$x^2=23.3$ *p=0.003 a=0.003
INTER-ACTIONS	RW(n=200)	T=1.6 p=0.11	T=1.7 p=0.09	$x^2=8.9$ p=0.35
HIGH SOAR	(n=321)	T=2.1 p=0.037 a=0.004	T=2.9 *p=0.003 a=0.003	$x^2=8.8$ p=0.37
	LOS >5	T=2.5 p=0.012 a=0.004	T=3.9 *p<0.001 a=0.003	$x^2=8.7$ p=0.37
CARRY PREY	(n=321)	T=2.0 p=0.05	T=1.8 p=0.07	$x^2=4.3$ p=0.83
FEED	(n=321)	T=-1.1 p=0.26	T=-0.05 p=0.96	$x^2=8.1$ p=0.42

T values Spearman's Rank Correlation, x^2 values Kruskall-Wallis 1-way ANOVA.

a=alpha, Sequential Bonferroni K=16

Table 16: Correlations of the proportion of minutes in which a behaviour was recorded with time of day, using only sightings of 30 minutes or more split into 30 minute cases. Merlin: Winter 3 data only, n=178, 30 minute cases. Peregrine: all winters to maintain sample sizes, n=83, 30 minute cases.

Spearman's Rank Correlation

	Merlin			Peregrine		
	T	p	alpha	T	p	alpha
HUNT	0.89	0.37		-0.98	0.33	
PREEN	-2.4	0.018	0.006	-1.9	0.07	
PERCH	0.82	0.41		0.28	0.78	
MOBBED	-0.34	0.73		-1.1	0.27	
MOBBING	-2.7	0.009	0.006	1.0	0.30	
MOVING	0.22	0.82		-0.83	0.41	
HUNT/MOVE	0.85	0.39		-	-	
CARRY PREY	1.2	0.24		0.88	0.38	
FEED	1.1	0.29		0.96	0.33	

There were no significant correlations with time of day for merlin and peregrine.

Raptor watch time budget data were analysed for significant variation by sex or age for peregrines. The data set for male merlins was too small, and from mostly very short sighting lengths compared to females, to allow a meaningful comparison to be made. For peregrines there was no significant variation in the proportion of a sighting in which a behaviour occurred for any of the behaviour types (Table 17). There was a trend for immature peregrines to spend more of a sighting hunting than adults (17.2%, n=138/804 minutes for immature compared to 11.7%, 160/1362 for adults).

Peregrines and merlins were affected by mobbing and mobbed other raptors very differently. Merlins were recorded as being mobbed in 1.1% of 9187 RW minutes (n=78 mobbing incidents, in 364 RW sightings). Peregrines were mobbed in 8.8% of 3049 RW minutes (n=112 mobbing incidents in 200 RW sightings). Merlins were observed being mobbed in total 119 times by: carrion crow 65.5%, jackdaw 0.8%, chaffinch 3.4%, rock pipit 1.7%, unknown passerine species 1.7%, gull species 5.0%, sparrowhawk 16.0% (8/19 occasions were attempted kleptoparasitisms of merlins carrying prey), kestrel 3.4% (3/4 were attempted kleptoparasitisms of merlins carrying prey) and peregrines 2.5% (3/4 were attempted kleptoparasitisms in which a peregrine joined a merlin hunting a skylark). Peregrines were observed being mobbed in total 168 times by: carrion crow 69.6%, swallow 4.2%, chaffinch 3.0%, starling and unknown passerine each 1.8%, gull species 1.2%, lapwing and redwing each 0.6%, sparrowhawk 8.3%, merlin 7.1% and kestrel 1.8%.

Table 17: Raptor Watch time budget data comparing male with female peregrines using Kruskall-Wallis 1-way ANOVA: n=85 sightings.

	x^2	p
HUNT	0.33	0.57
PERCH	0.04	0.84
PREEN	1.0	0.32
MOBBED	0.11	0.74
MOBBING	0.05	0.83
MOVING	0.06	0.81
HIGH SOAR	0.03	0.61
CARRY PREY	0.61	0.43
FEED	0.13	0.72

Raptor Watch time budget data comparing adult with immature peregrines using Kruskall-Wallis 1-way ANOVA: n=127 sightings.

	x^2	p	alpha
HUNT	6.5	0.011	0.005
PERCH	2.4	0.12	
PREEN	1.3	0.25	
MOBBED	3.6	0.06	
MOBBING	0.01	0.93	
MOVING	0.11	0.74	
HIGH SOAR	0.52	0.47	
CARRY PREY	0.72	0.40	
FEED	0.06	0.80	

Sequential Bonferroni K=10

Both merlins and peregrines were predominantly mobbed by carrion crows. Merlins invariably outflew mobbing crows and all incidents of crow mobbing were less than c30 seconds. Merlins were only seen to attack carrion crows on 4 occasions (0.6% of 602 attacks) and magpies on 2 occasions (0.3%); of these 6 incidents only 2 were at mobbing carrion crows. Peregrines usually remained perched when mobbed by carrion crows and would only move perches or attack the crows after several minutes of mobbing. Peregrines attacked carrion crows on 43 occasions (8.0% of 536 attacks) and 88.4% of these were on mobbing birds. A peregrine was observed to attack carrion crows on 5 occasions unrelated to an initial mobbing incident (one attack on a flock of c50 crows involved 30+ stoops over 5 minutes), jackdaws twice and a magpie once; these incidents were probably hunts.

Merlins mobbed other raptor species in 0.6% of 13,672 total minutes of observations (n=57 incidents lasting 85 minutes). Peregrines mobbed in 0.2% of minutes (n=9 incidents lasting 11 minutes). Mobbing incidents by merlins and peregrines were qualitatively different. Merlin mobbing appeared to be 'territorial' exclusion chases in most cases, while peregrine mobbing incidents appeared to be brief hunt-like attacks. Merlins were observed mobbing sparrowhawks on 42 occasions, in 43 minutes of sightings; 9 of these were kleptoparasitism attempts on sparrowhawks carrying prey, 1 of which was successful. Merlins were observed mobbing peregrines on 12 occasions, in 39 minutes of sightings, with no obvious kleptoparasitism attempts. Merlins were observed mobbing kestrels on 3 occasions, in 3 minutes of sightings, one of which was an unsuccessful kleptoparasitism attempt on a kestrel carrying prey. A peregrine was observed to mob a buzzard (Buteo buteo) on one occasion, over 3 minutes; kestrels on 2 occasions, both of which appeared to be hunts, one of which involved the kestrel being struck and forced onto the ground; sparrowhawks on 3 occasions, 2 of which appeared to be hunts where the sparrowhawk was stooped at and chased until it reached cover; and a merlin on 3 occasions, 1 of which was a rapid hunting-like chase, and 2 of which when a peregrine joined a hunting merlin, attacking the prey already being chased by the merlin.

Conspecific interactions between merlins and peregrines were relatively rare. Two merlins were observed together on 30 occasions (lasting 0.4% of total minutes of sightings): 93.3% of minutes were simply one merlin chasing the other out of the study area, 3.3% of minutes was one attempted kleptoparasitism on another merlin carrying prey, and a final 3.3% of minutes was one case of two merlins attacking the same skylark, before the female of the pair chased the male out of the study area. Two or more peregrines were observed together on 23 occasions (1.2% of total minutes of sightings): 56.5% of minutes were one peregrine chasing the other out of the estuary area, 8.7% of minutes were attempted kleptoparasitisms on a second peregrine carrying prey, 13.0% of minutes were of an adult male and female pair hunting together, and 21.7% were of two peregrines associating but with no antagonistic interaction, for example, two birds high soaring together.

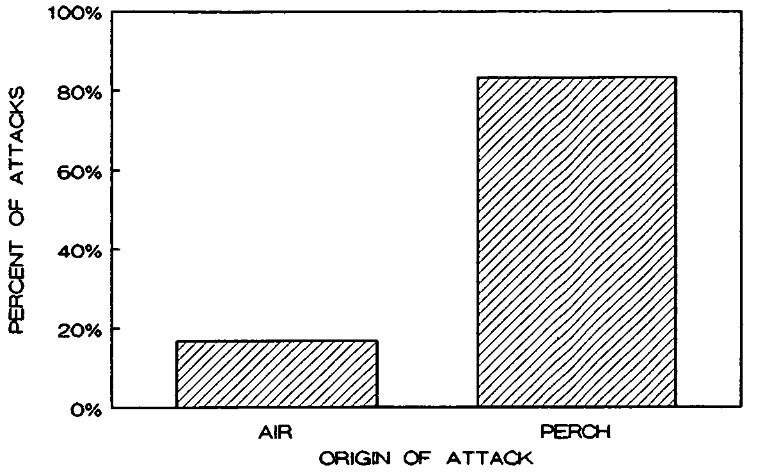
7.2.8 Attack Behaviour During Hunts

Merlin initiated most attacks from perches (Fig. 14A) at prey which was usually less than 100m away (Fig 14B) and on the ground (Fig.14C). Merlins were flexible in their hunting method and regularly hunted from the air, at prey which was flying and occasionally at distances of over 900 meters. The attack type used depended on the species attacked (Fig. 15A) but the commonest attack strategy was surprise for all species (a ringing attack usually started with a surprise attack). Open attacks and stoops were rare; ringing was only used frequently when attacking skylarks. During an attack, chase lengths were highly variable (Fig. 15B). Most chase lengths were short (61.3% $\leq$ 5 seconds) but merlins frequently chased prey for more than 2 minutes (8.8% of attacks), these were invariably skylarks, and the maximum chase length recorded before the merlin was lost was over 9 minutes. Most attacks had no stoops in them, but long skylark chases had very many, regularly over 30 for chases longer than 2 minutes (Fig. 15c). The maximum number of stoops by a merlin at a skylark, before the merlin was lost still attacking, was 52.

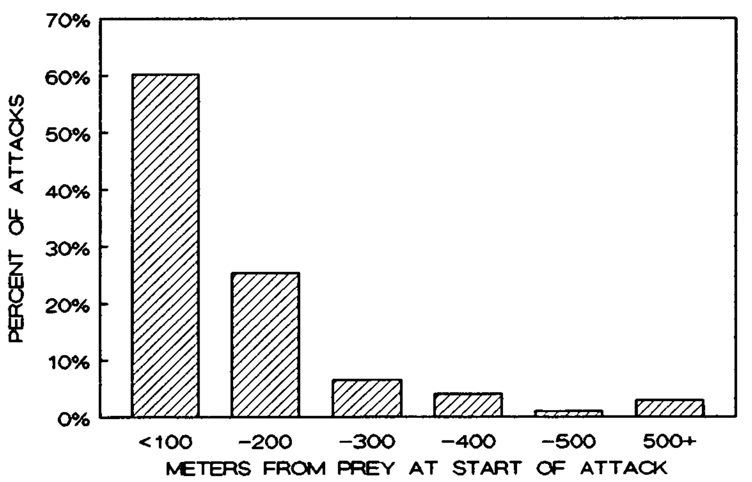
Peregrines initiated most attacks from the air (Fig. 16A) at prey that was usually less than 100m away (Fig. 16B) at prey either on the ground or in flight (Fig. 16C). First attacks of a hunt were usually at prey at greater than 300m away (58.1% of 93 first attacks of a hunt) and 33.3% of first attacks were at prey at greater than 500m away (this compares to 25.9% for >300m and 17.7% for >500m for second and subsequent attacks during a hunt): G=58.3, 5df, p<0.0001, comparing attack dash distances split into 100m classes, and all

MERLIN HUNTING BEHAVIOUR I. FIGURE 14

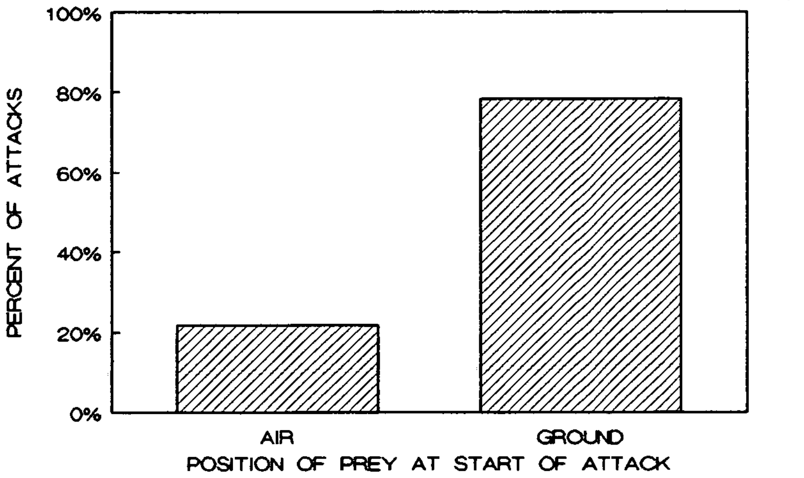
ATTACK ORIGINS
n=436



ATTACK DASH LENGTHS
n=387



POSITION OF PREY AT START OF ATTACK
n=484

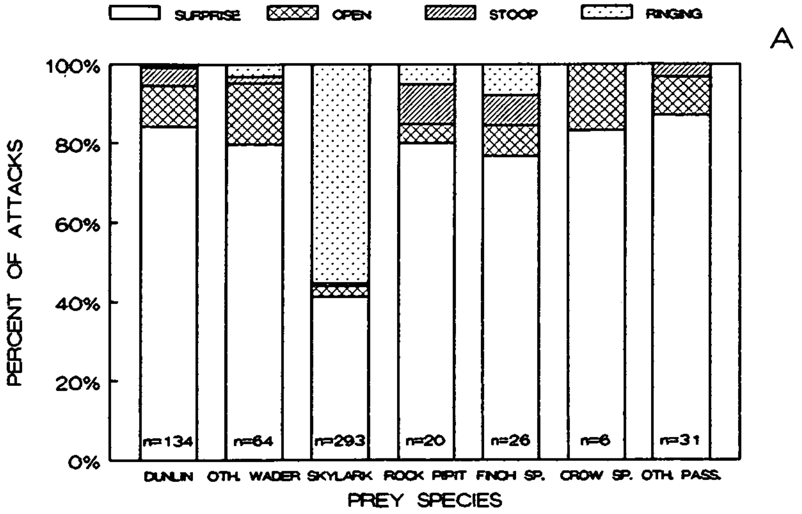


MERLIN HUNTING BEHAVIOUR II.

FIGURE 15

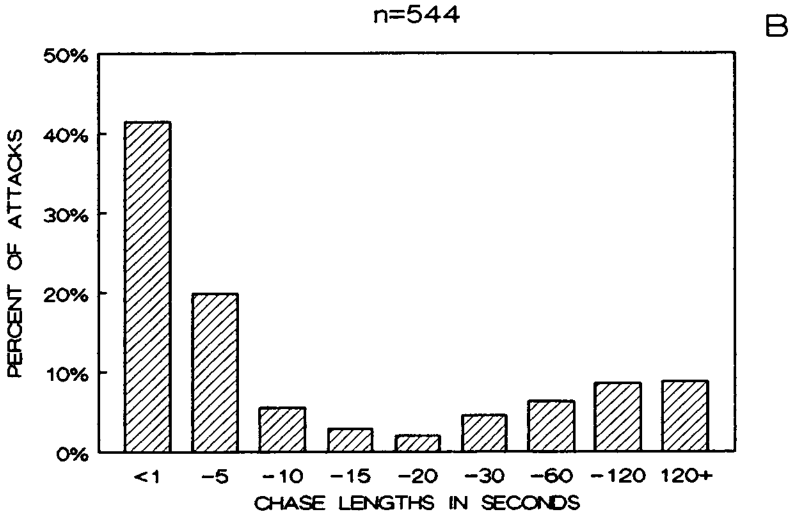
ATTACK TYPES

n=574



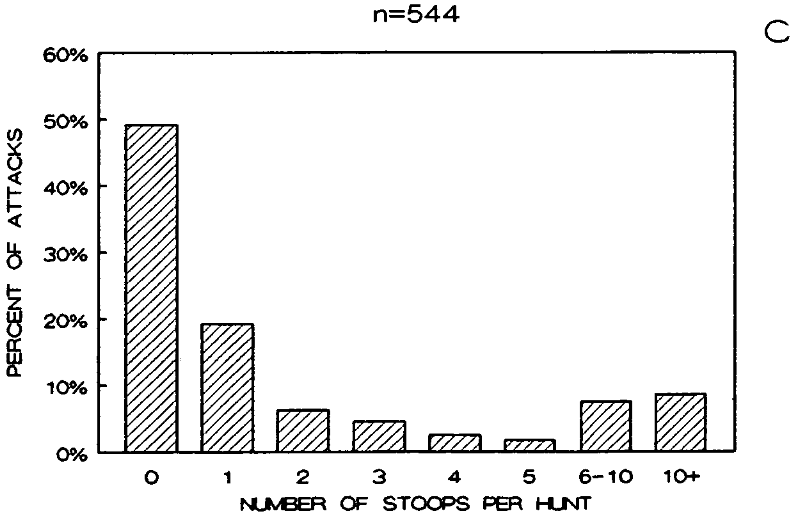
CHASE LENGTHS

n=544



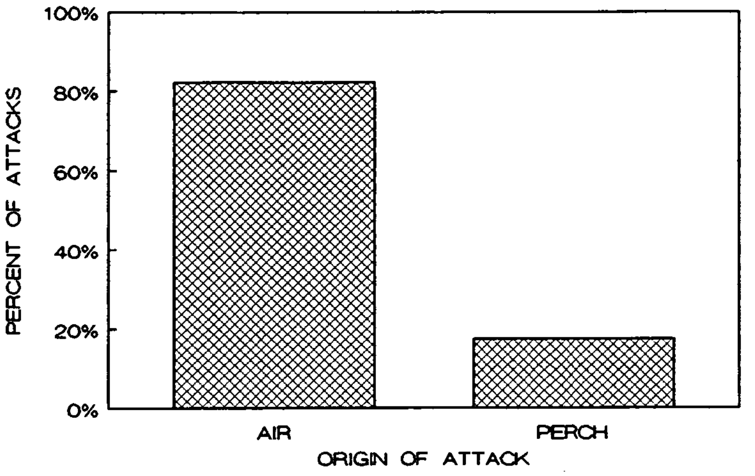
STOOPS PER HUNT

n=544

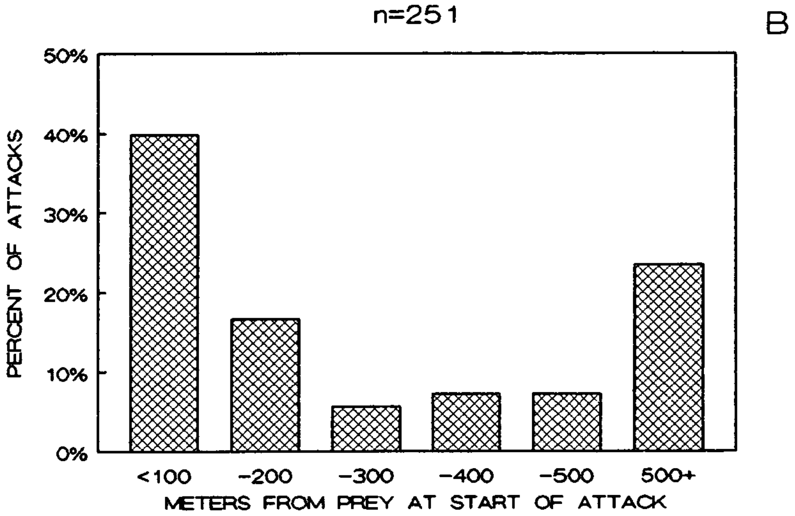


PEREGRINE HUNTING BEHAVIOUR I. FIGURE 16

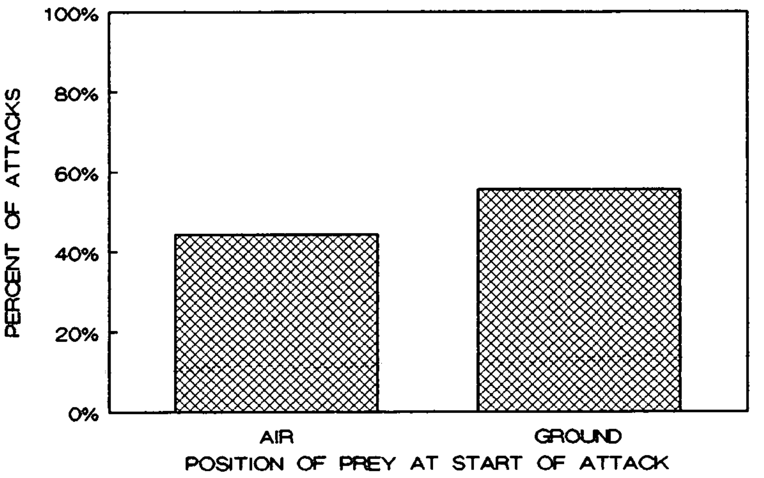
ATTACK ORIGINS
n=478



ATTACK DASH LENGTHS
n=251



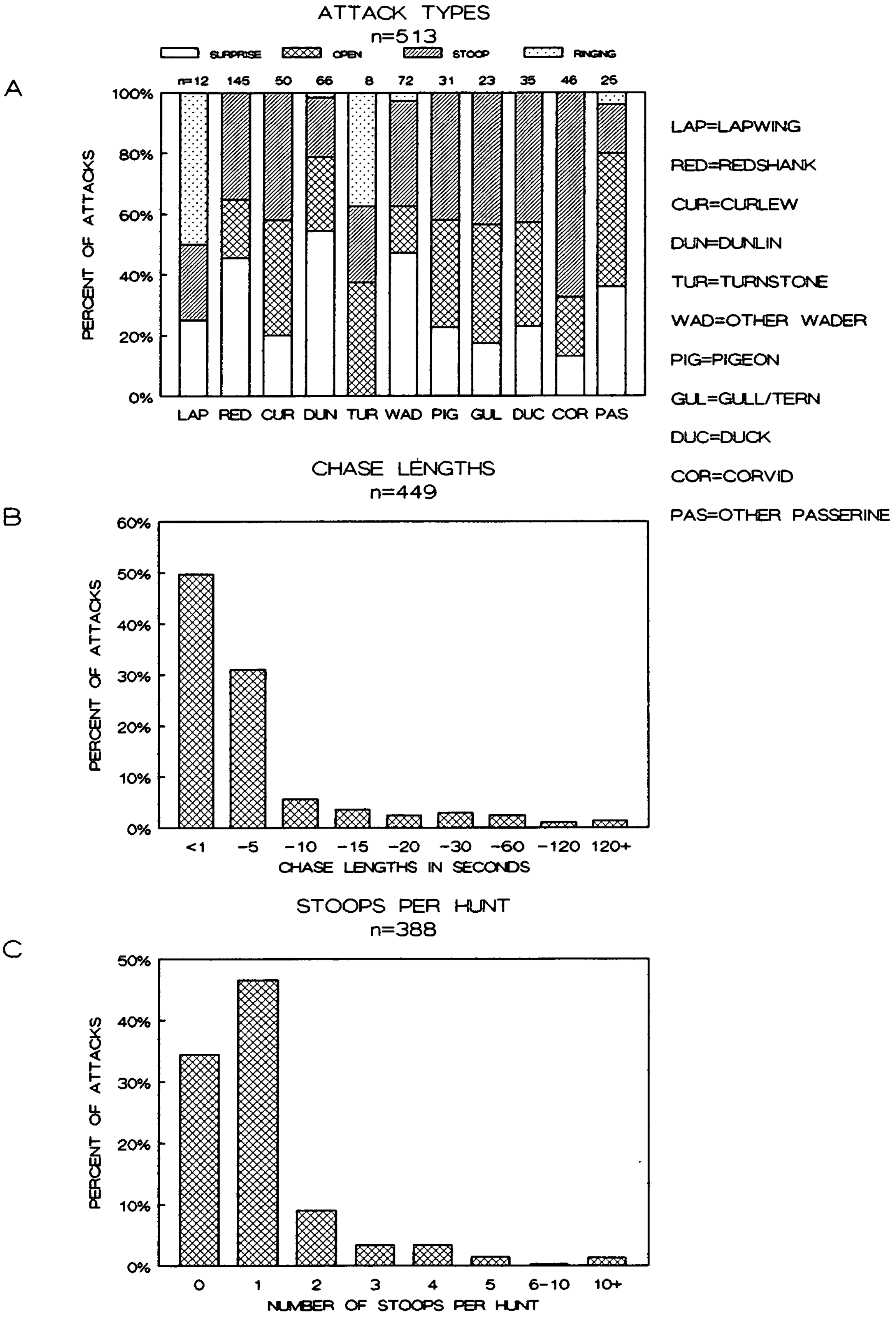
POSITION OF PREY AT START OF ATTACK
n=473



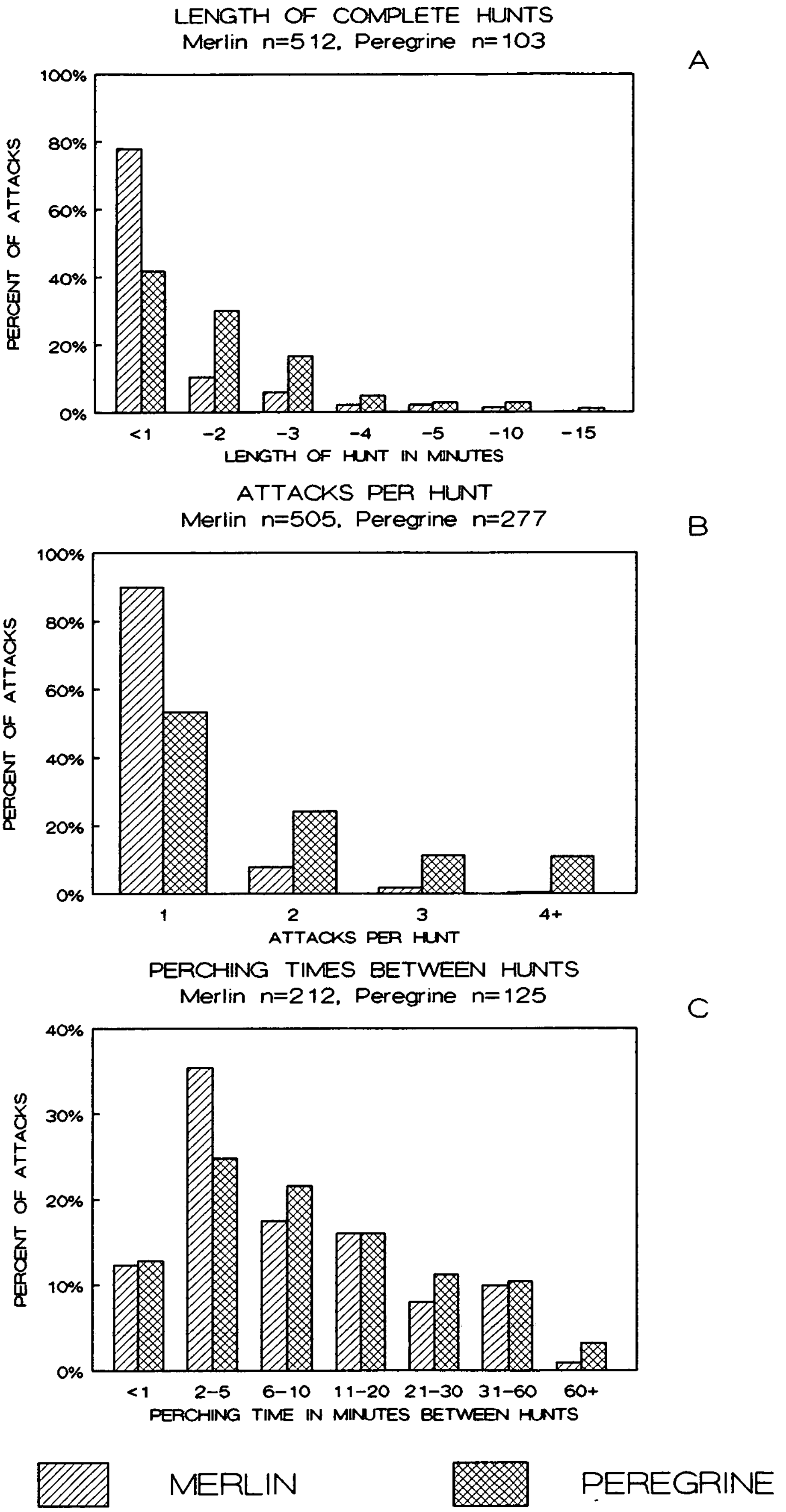
attacks >500m pooled. Prey were occasionally attacked at distances of >1000m (1.6%) and the maximum attack distance recorded was approximately 1,500m. On ten occasions it was possible to time the speed of flight of an attacking peregrine. The peregrine was timed with a stop-watch, from the start of flight, from the same perch (a 20m high tree) until it passed close by a distinctive landmark on the estuary. The distance of flight was then measured on a map: the smallest distance of flight measured was 330m, and the maximum 1650m. The mean attack speed was 82.8+/-4.9km/hour (63.4 to 108 km/hr, and over 1650m a peregrine averaged 90.3 km/hr). The attack type depended on the species attacked (Fig. 17A). Surprise attacks were used most frequently (most stoops were probably surprise attacks), as were open and stoop attacks. Ringing attacks were only recorded in 4 % of passerine attacks, but in 37.5% of turnstone and 50.0% of lapwing attacks. In cases of ringing the prey species flew straight upwards and attempted to stay above the chasing peregrine, and this appeared to be the main escape strategy for lapwing and turnstone. During an attack chase lengths were highly variable but most attacks did not result in chases (Fig. 17B). The longest chases involved ringing, the maximum chase length recorded was of a turnstone for more than 6 minutes before the peregrine was lost still chasing. Occasionally some low level chases lasted over 30 seconds. Most attacks had one or more stoops in them (Fig. 17C) but more than 5 stoops per attack were rare (1.3% of attacks).

The lengths of complete hunts (attack flights between periods of perching or high soaring), rounded up to the nearest minute, were significantly different comparing merlin and peregrine (Fig. 18A):

PEREGRINE HUNTING BEHAVIOUR II. FIGURE 17



MERLIN AND PEREGRINE HUNTING BEHAVIOUR I. FIGURE 18



G=46.1, 6DF, $p<0.001$. The number of attacks per complete hunt was also significantly different comparing merlins and peregrines (Fig. 18B): G=141.3, 3df, $p<0.0001$. Most merlin hunts, 77.9%, were less than 1 minute in length compared to 41.7% of peregrine hunts. Only 10.1% of merlin hunts had more than one attack in them; the maximum number of attacks per complete hunt recorded was 4. Peregrines in contrast had 46.6% of hunts with a second attack in them, the maximum number of attacks per hunt recorded was 11. Perching times between hunts (Fig. 18C) were not significantly different comparing merlins and peregrines (G=6.5, 6DF, $p>0.05$). The modal perching period between hunts was 2-5 minutes, but most perching periods between hunts were greater than 5 minutes.

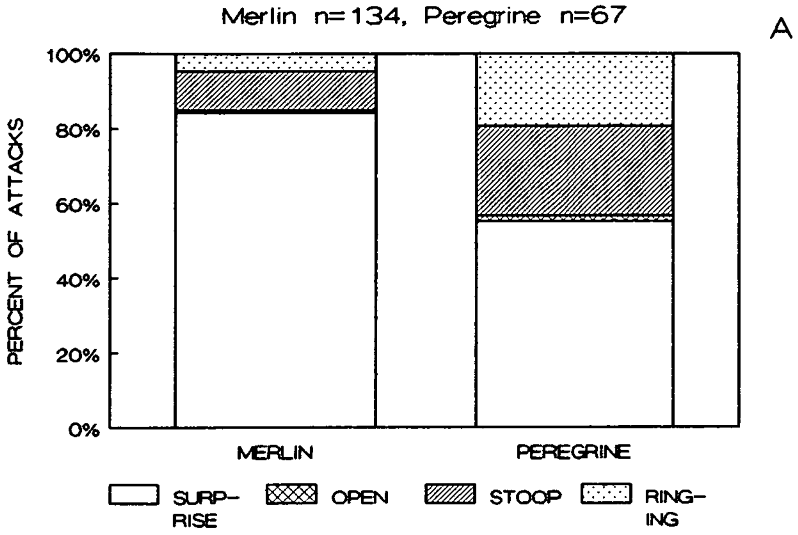
There were significant differences in the relative frequency of attack types used by merlins and peregrines on the same species of prey. Merlins attacked dunlins mainly by surprise, while peregrines used stoops and ringing more frequently (Fig. 19A): G=18.3, 2df, $p<0.001$, alpha=0.05, Sequential Bonferroni, K=3. Merlins attacked redshank mainly by surprise and rarely stooped, while peregrines stooped frequently at redshank (Fig. 19B): G=24.0, 2df, $p<0.0001$, alpha=0.025, Sequential Bonferroni, K=3. Merlins and peregrines used open attacks on redshank with similar frequencies. Merlins attacked skylarks mainly by ringing, while peregrines used open attacks and stoops (Fig. 19C): G=47.3, 3df, $p<0.0001$, alpha=0.016, Sequential Bonferroni, K=3.

There were significant differences in the relative frequency of different positions of prey at the start of an attack comparing merlins and peregrines. For dunlin, merlins rarely attacked birds in

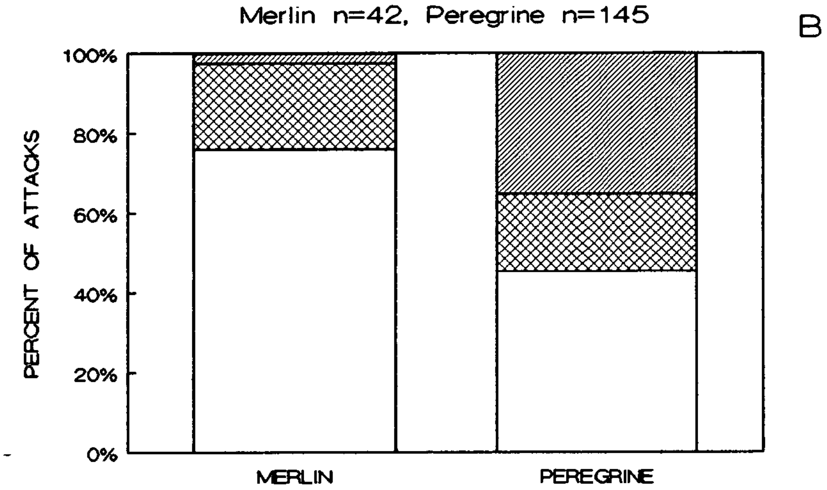
FIGURE 19

MERLIN AND PEREGRINE HUNTING BEHAVIOUR II.

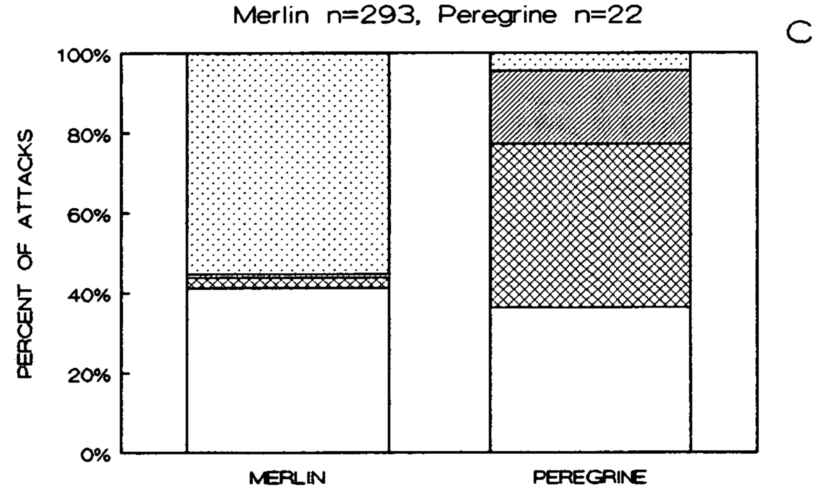
ATTACK TYPES ON DUNLIN
Merlin n=134, Peregrine n=67



ATTACK TYPES ON REDSHANK
Merlin n=42, Peregrine n=145



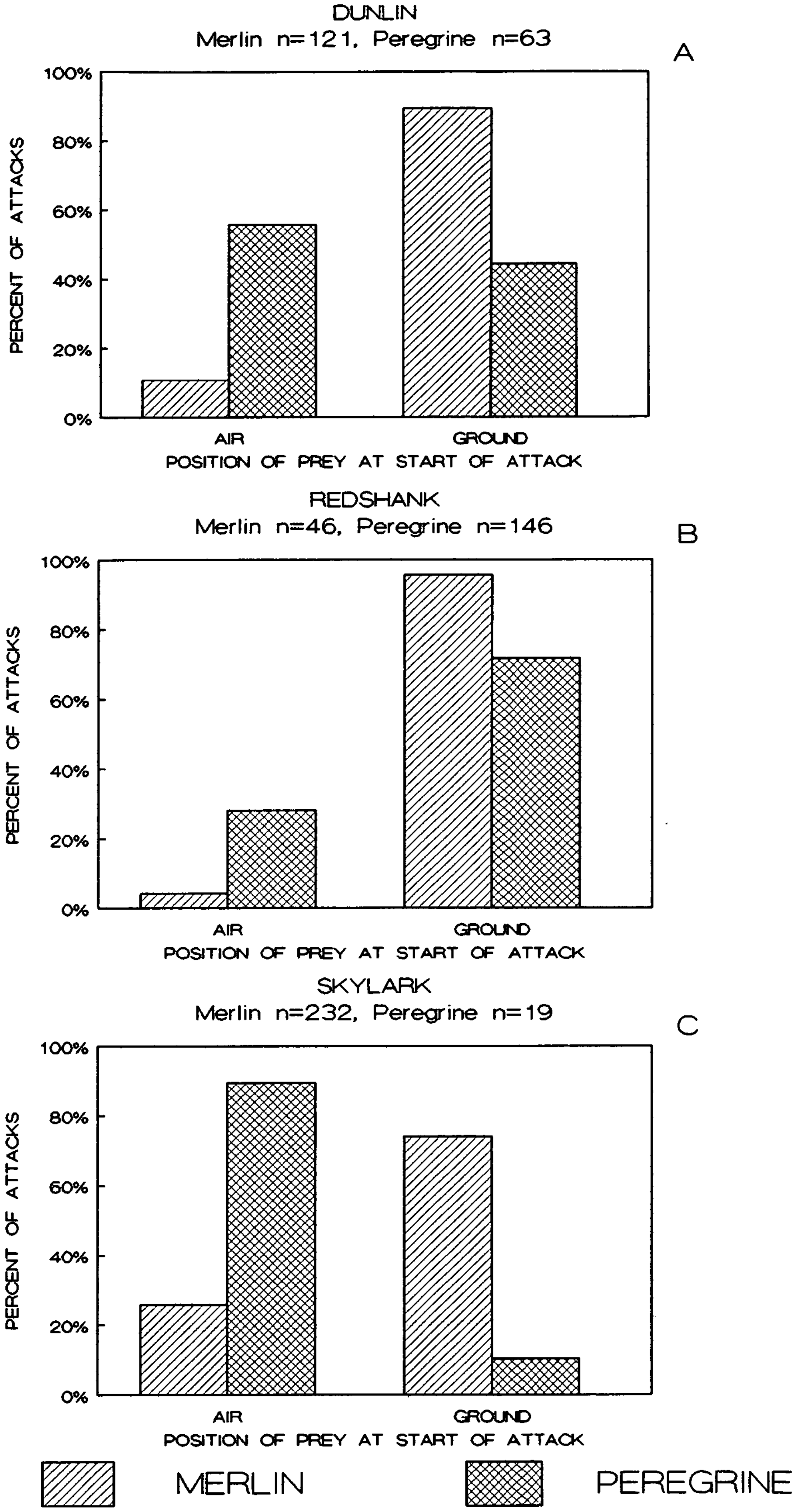
ATTACK TYPES ON SKYLARK
Merlin n=293, Peregrine n=22



flight, but peregrines attacked birds on the ground and in flight with similar frequencies (Fig. 20A): G=41.6, 1df, p<0.0001, alpha=0.016, Sequential Bonferroni, K=3. For redshank, peregrine were more likely to attack birds in flight compared to merlins but both species attacked redshank on the ground most frequently (Fig. 20B): G=14.2, 1df, p<0.001, alpha=0.05, Sequential Bonferroni, K=3. For skylark, merlins attacked birds most frequently on the ground while peregrines attacked birds most frequently in flight (Fig. 20C): G=30.5, 1df, p<0.0001, alpha=0.025, Sequential Bonferroni, K=3.

Merlins and peregrines attacked dunlin commonly at Tyninghame, allowing a comparison to be made of the different behaviours during hunting, controlling for species attacked. Merlins initiated dunlin attacks most frequently from a perch, while peregrines initiated attacks most frequently from the air (Fig. 21A): G=46.1, 1df, p<0.0001. For peregrines, modal distance from the prey at the start of the attack was less than 100m, compared to between 100 and 200m for merlin: 18.5% of peregrine attack distances were of greater than 500m compared to 2.2% of merlins (Fig. 21B): G=13.1, 5df, p<0.05. Peregrine and merlin chase lengths of dunlin were not significantly different (Fig. 21C): G=5.0, 6DF, p>0.05. Most chases were less than 5 seconds, although 1.6% of peregrine and 3.3% of merlin chases exceeded 1 minute. There were no significant differences in the number of stoops comparing merlin and peregrine (G=0.58, 4df, p>0.05); both species rarely stooped at dunlins (Fig. 22A). Merlins and peregrines attacked the different dunlin flock size classes with significantly different frequencies (Fig. 22B): G=22.0, 7df, p<0.01.

MERLIN AND PEREGRINE HUNTING BEHAVIOUR III. FIGURE 20
POSITION OF PREY



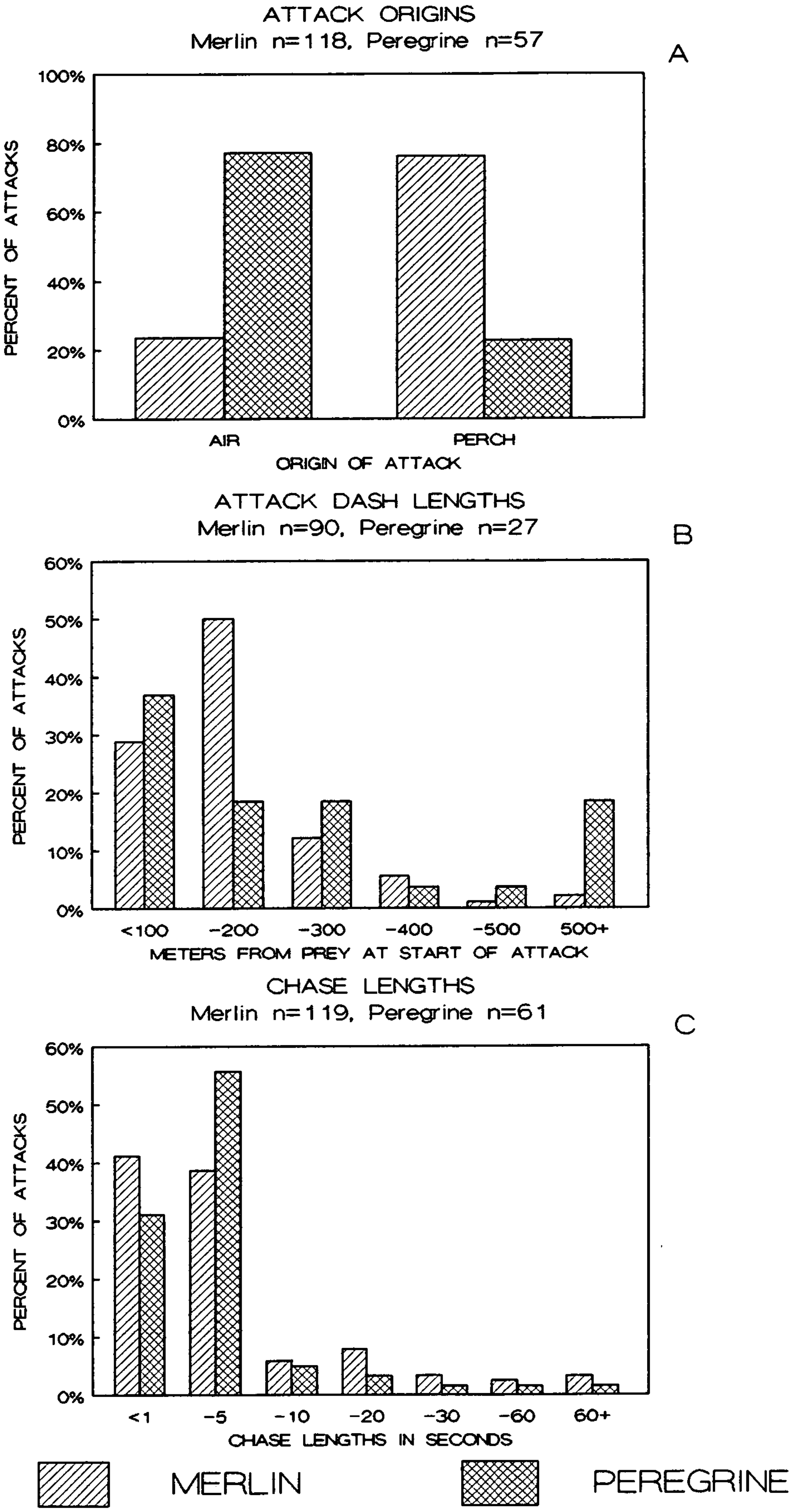
DUNLIN
Merlin n=121, Peregrine n=63

REDSHANK
Merlin n=46, Peregrine n=146

SKYLARK
Merlin n=232, Peregrine n=19

MERLIN AND PEREGRINE HUNTING BEHAVIOUR IV. FIGURE 21

DUNLIN ATTACKS ONLY



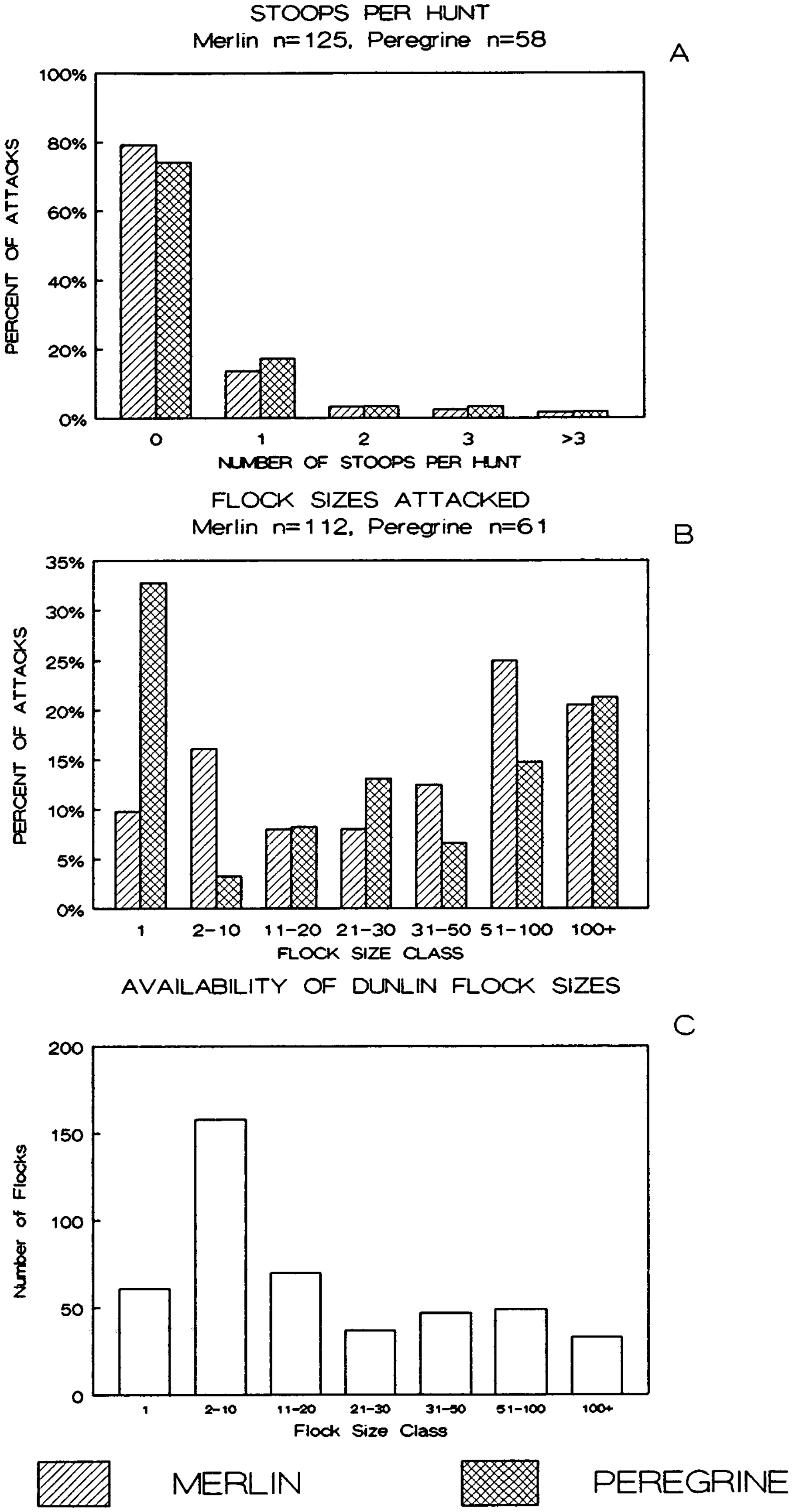
ATTACK ORIGINS
Merlin n=118, Peregrine n=57

ATTACK DASH LENGTHS
Merlin n=90, Peregrine n=27

CHASE LENGTHS
Merlin n=119, Peregrine n=61

MERLIN AND PEREGRINE HUNTING BEHAVIOUR V. FIGURE 22

DUNLIN ATTACKS ONLY



STOOPS PER HUNT
Merlin n=125, Peregrine n=58

FLOCK SIZES ATTACKED
Merlin n=112, Peregrine n=61

AVAILABILITY OF DUNLIN FLOCK SIZES

Peregrines attacked single dunlins more frequently than merlins, while merlins attacked small flocks (2-10) more frequently; both species attacked large flocks with a similar frequency.

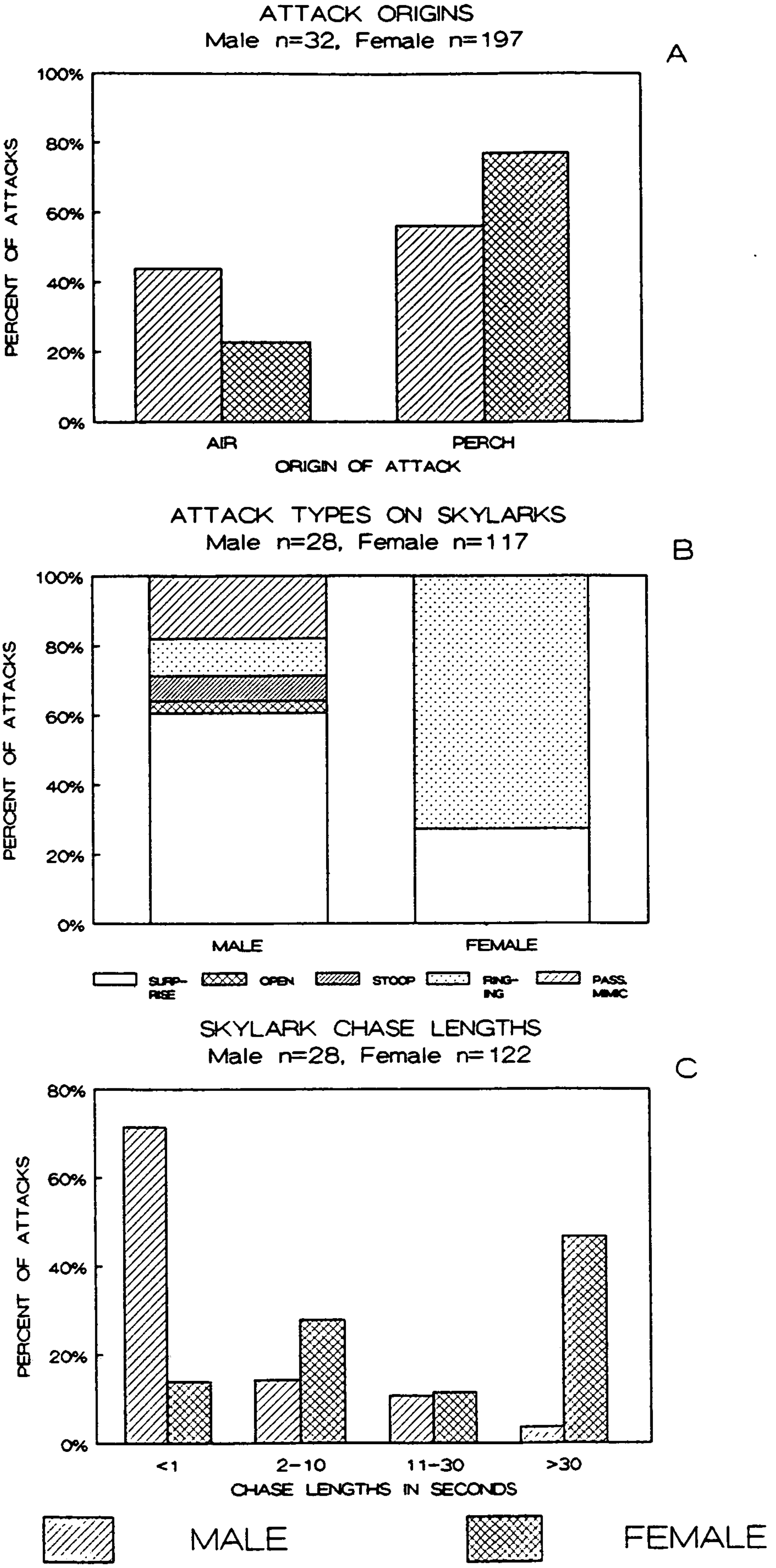
Both merlins and peregrines attacked dunlin flock size classes with significantly different frequencies than would have been expected from the relative occurrence of the different sized flocks (Fig. 22C): merlin x^2=65.0, 6df, p<0.0001; peregrine x^2=56.7, 6df, p<0.0001. For merlin the expected attack frequency was greater than the observed frequency for all flock sizes of less than 30; at flock sizes of greater than 30 expected attack frequency was less than observed. For peregrine there was no consistent pattern; single birds and flocks of greater than 50 were attacked more frequently than expected, but small flocks (2-10) were attacked much less frequently than expected. Sample sizes of kills observed were small, but there were no significant differences in the success rate for the two raptors with different flock sizes of dunlin. Flock sizes were pooled into 1-10, 11-100 and 100+ to spread kills reasonably equally between classes. For merlin, success rate was 20.8% for flock size 1-10 (n=5/19 captures/unsuccessful attacks), 15.1% for 11-100 (n=8/53), and 13.0% for 100+ (n=3/23): G=1.0, 2df, p>0.05. For peregrine success rate was 4.8% for flock size 1-10 (n=1/20), 6.7% for 11-100 (n=2/28), and 15.4% for 100+ (n=2/11): G=1.1, 2df, p>0.05. There was a trend for merlins to be less successful when attacking larger flocks, and vice-versa for peregrine attacks.

Hunting behaviour of male and female merlins was compared. Data from winters 1 and 2 were used as no attacks by males were seen in winter 3. The data analysed probably came from only 2-3 males and 2-

3 females, and was most likely to have come from mainly 2 females and 1 male. Any differences in hunting behaviour may then only reflect differences between individual merlins rather than genuine sex-based differences. There were significant differences in the hunting behaviour by sex. Male merlins attacked significantly more frequently from perches compared to females (Fig. 23A): G=5.6, 1df, $p<0.02$. Male merlins used attack types with significantly different frequencies, when attacking skylarks (G=23.8, 1df, $p<0.001$, surprise attacks compared to ringing). Male merlins attacked mainly by surprise, whereas females used ringing; males used passerine mimicking flight and stooped in some attacks; females were not recorded using these attack methods (Fig. 23B). Males rarely chased skylarks for any length of time, most chases were less than a second, most female chases were greater than 10 seconds, with 46.7% of chases being longer than 30 seconds (Fig. 23C). The chase length distributions for the two sexes were significantly different (G=40.3, 3df, $p<0.0001$).

There were no significant differences in peregrine hunting behaviour split by age or sex. Sample sizes prevented analysis for age controlling for sex. Attack types used by males and females (G=3.2, 2df, $p>0.05$) and adults and immatures (G=2.8, 2df, $p>0.05$) were not significantly different (comparing the relative frequencies of surprise, open and stoop attacks). The position of prey at the start of attack (air or ground) did not differ significantly by sex (G=1.6, 1df, $p>0.05$) or by age (G=2.1, 1df, $p>0.05$). Chase lengths (<1, 2-5, 6-10 and 10+ seconds) were not significantly different split by sex (G=7.3, 3df, $p=0.06$) or by age (G=1.6, 3df, $p>0.05$).

MALE AND FEMALE MERLIN HUNTING BEHAVIOUR FIGURE 23



7.2.9 Kleptoparasitism and Feeding Behaviour

Kleptoparasitism was a minor factor affecting merlin winter hunting behaviour because merlins simply outflew attempted kleptoparasites. In 63 observations of merlins with just-caught prey, 28.6% of cases had kleptoparasitism attempts in them by another bird. Only 1.4% of attempts were successful, when a carrion crow snatched a rock pipit from a flying merlin, just after the merlin had successfully kleptoparasitised a male sparrowhawk, that had just caught a rock pipit. In total there were 8 attempts by other raptors to kleptoparasitise merlins carrying prey (1 by merlin, 4 by sparrowhawk, and 3 by kestrel) and 10 attempts on 8 occasions by carrion crows.

Kleptoparasitism appeared to be a more important factor for peregrines. In 28 observations of peregrines with just-caught prey, 14.3% resulted in another bird gaining the prey: a dunlin, a redshank, a wigeon (Anas penelope) and a teal (Anas crecca) were taken by a great black-backed gull (the dunlin, after the peregrine dropped it due to crows mobbing it) and the other prey by a pair of carrion crows. Of the 11 attempts by carrion crows to kleptoparasitise a peregrine carrying prey, 27.2% were successful, although on two occasions the peregrine had fed on the prey before leaving it to the crows. No other raptor species were seen to attempt to kleptoparasitise a peregrine.

Most merlin feeding was carried out in the open, on the ground or in a conspicuous tree: 73.9% of prey was eaten on the ground, 15.2% in a tree above 3m and 10.9% was plucked on the ground and then cached on the ground (n=46 cases of merlin feeding). Sample sizes of peregrines feeding were small, but more prey was eaten in trees than on the ground (36.4% on the ground, 63.6% in trees, $n=11$ cases of peregrine feeding). Merlins were significantly more likely to eat prey on the ground (including plucking periods prior to caching) than peregrines: $G=9.3$, 1df, $p<0.01$.

The length of complete feeding periods by the two raptors was related to the size of prey caught. For merlin, rock pipits were consumed in $x=18.0$ mins ($n=2$), skylark in $x=25.2$ mins ($n=15$) and dunlin in $x=28.5$ mins ($n=4$); overall the average eating time was $x=25.1$+/-6.0 mins. For peregrine, dunlin were eaten in $x=17.0$ mins ($n=2$) and redshank in $x=21.5$ mins ($n=2$); overall the average eating time was $x=19.3$+/-3.9 mins (20-30 mins in Baker 1967).

Merlins were observed to cache prey frequently. Peregrines were not observed to cache but sample sizes of peregrines eating prey were very small. Of 55 kills seen, merlin cached 9.1% of kills; of 70 occasions of merlins with prey, a merlin was seen to get prey from a cache in 7.1% of cases. Merlins were observed to cache 1 linnet (*Carduelis cannabina*), 3 skylarks and a dunlin, and to recover 4 skylarks and a dunlin from a cache. Typically, cached birds were intact, or headless, or with slight wing plucking, but a merlin was seen to recover a completely plucked skylark on one occasion. Merlins were observed to take up to 3 minutes to re-find caches, checking several adjacent grass clumps before locating the correct one. Some cached prey was not recovered by a merlin for up to 4 days, if at all. Typical cache sites were described in the methods.

7.3 Discussion

7.3.1 Diet

Despite the probable biases in finding mostly only larger peregrine kills, merlins and peregrines probably took prey, on average, of different sizes. The observed range of prey taken, and the mean size of prey taken by the two species agreed well with previous studies for peregrine (267.6g compared to 289g, Ratcliffe 1963), but less so for merlin (51.7g compared to 32.3g Page & Whitacre 1975, 38.3g Warkentin & Oliphant 1990 - both of the studies had a wide range of prey sizes available). Merlins at Tyninghame, which were mostly females (although this was also the case for Page & Whitacre 1975), were apparently habitually taking larger prey on average than previously reported. There was, on average, little overlap in the diet of merlins and peregrines except when hunting dunlin. Dunlin were a relatively minor part of peregrine diet (14.3%), compared to merlin (52.5%): merlins were more likely to be affected by direct competition, than vice-versa. Dunlin were one of the commonest prey species available, and peregrines were unlikely to be reducing the population sufficiently to reduce merlin encounter rates (Chapter 3). Daily hunting by the resident merlin, may have reduced the hunting success of arriving peregrines, by increasing dunlin wariness and flocking behaviour (e.g. Buchanan et al. 1988). Peregrines hunted less frequently than merlins on the estuary and so would affect merlin hunting relatively less. Merlins were probably, therefore, more of a significant competitor for peregrines, than peregrines were for merlins: interference competition having a greater effect than direct competition. The escape responses of dunlin on attack by peregrines or merlins were the same: rapid flight away, and the formation of dense flocks. Previous attacks by merlins would not benefit a hunting peregrine in the same way as with redshanks attacked by sparrowhawks (Chapter 4.2.6).

Male and female peregrines and merlins, attacked prey of different sizes conforming to the hypothesis that the size difference serves to reduce intraspecific competition. The low success rates for the strongly dimorphic raptors reported in this study conform to the hypothesis that the degree of dimorphism is most pronounced in species which hunt low vulnerability, and hence largely unavailable prey (Temeles 1985).

7.3.2 Attack and Hunt Strategies

The main winter hunting strategy used by peregrines and merlins was to surprise prey. Surprise has been shown to be important in most raptor hunts (e.g. Rudebeck 1950, 1951, Page & Whitacre 1975, Dekker 1988). Comparison of merlin and peregrine attack techniques is only really valid when comparing attacks on the same species. When attacking dunlin, the two raptors used very similar attack strategies. The relative frequency of attack types used by merlins and peregrines on waders in a similar habitat in Canada, was very similar to the frequency recorded at Tyninghame: short surprise attacks, c73%, open attacks, c16%, and ringing c3%, in Canada (Dekker 1988), compared to c70-80% surprise or stoop, 15-20% open attacks and c2-3% ringing attacks. Peregrines and merlins had a very similar success rates when hunting dunlin (c13%). The observed differences in attack methods must compensate for any differences in the size of the two raptors, with the raptors only attacking when the probability of capture was above a certain level. The major difference in attack strategy between the two raptors was the position of the prey at the start of the attack. Peregrines were never observed to catch prey on the ground, while merlins frequently did so. Peregrines are capable of catching prey on the ground (Baker 1967, Ratcliffe 1963, Chapter 4) but do so rarely, preferring to catch prey in flight. Attack types by raptors should reflect the escape responses of the prey (Buchanan 1989), but within the constraints of the predator species. One possible functional explanation for the difference is the decrease in manoeuvrability and agility of larger birds of prey compared to smaller birds of prey (Newton 1979). A peregrine which hunts close to the ground may run the risk of injury to a much greater degree than a merlin. Both species of raptor, when attacking low to the ground, usually strike upwards as they approach prey and it flies up before them (Ratcliffe 1980, Cramp & Simmons 1980, this study), which will minimise the risk of hitting the ground. Observed speeds of peregrine attacks were frequently below the maximum speed theoretically possible for a stooping bird (Alerstam 1987, this study). By adopting a moderate stooping speed, raptors may gain in hunting precision (Alerstam 1987).

Peregrines and merlins attacked different sized flocks of dunlins. Merlins specialised in attacking small flocks, while peregrines attacked either single birds or very large flocks. Peregrines also attacked dunlins from greater distances away. This pattern may be a consequence of the relative conspicuousness of the two raptor species. Peregrines may only have been able to use surprise effectively on single birds as the probability of detection is usually lowest for a single bird (Pulliam 1973). As merlins were less conspicuous, they may be able to approach closer to larger flocks before detection. Both raptors attacked very large flocks at a similar rate as might be expected because probability of very early detection would be almost one, even for merlins.

My results clearly showed that merlins and peregrines were relatively 'low efficiency' hunters with low capture success rates. Raptors would be expected to hunt optimally, and many attacks may be discontinued due to the prey being chased being relatively more difficult to catch compared to other available prey, and not because the raptor was incapable of catching the prey, if it had 'pressed home its attack' (Treleaven 1980). The motivational state of an individual peregrine may make it put more effort into chasing prey (Ratcliffe 1980), which may increase its success rate per attack. This increased hunting effort will reflect the tradeoff between the peregrines need to maximise energy gain, while minimising energy expenditure during hunting, and other factors such as the risk of injury, which will be greater in a more intense, longer chase. The whole argument between 'high' and 'low' efficiency may be an artefact of measuring success rate as the proportion of kills per attack/hunt, rather than measuring success rate adaptively as the mass of prey (energy intake) obtained, per unit of time (or energy expended) hunting. However, estimating energy expenditure during hunting by raptors in the field poses severe methodological problems.

7.3.3 Interference and Mobbing

Intra- and interspecific interactions in merlins and peregrines and interactions of the two raptor species with crows and other mobbing species were qualitatively and quantitatively different. Peregrines were more tolerant than merlins to conspecifics, and sightings of non-antagonistic pairs of peregrines may have been pairs which bred in the area (Mearns 1982). Merlins at Tyninghame appeared to be defending home ranges. Merlins only very rarely hunted together, in contrast to up to 30% of hunts in some studies (Cramp & Simmons 1980). Peregrines appeared to mob only other raptor species which were larger than itself (e.g. a buzzard), other interactions with other raptor species were hunts, similar to those described by Rudebeck (1951) and Baker (1967) which resulted in peregrines eating sparrowhawks. Merlins mobbed all raptor species, and attempted to exclude them from their hunting area. The frequency of kleptoparasitism attempts, between raptors, at Tyninghame, was also high. These observations accord with Temeles (1990), who showed that inter-specific territoriality is governed by the ability of an intruding raptor to be kleptoparasitised, or to act as a kleptoparasite.

Merlins appeared to easily outfly other raptors when carrying prey, but this escape ability may be constrained when carrying large prey (e.g. Warkentin 1988). As with sparrowhawks, kleptoparasitism pressure may reduce optimal prey size. Other raptor species did not attempt to kleptoparasitise peregrines probably because there were no species at Tyninghame which were larger than, and not in danger of attack from peregrines (see Beebe 1960).

Merlins were mobbed about 8 times less frequently than peregrines, although the range of species mobbing the two raptor species was very similar. Corvids, other raptor species, and gulls were probably associating with raptors primarily for potential kleptoparasitism opportunities. Gulls regularly kleptoparasitise other gulls (Brockmann & Barnard 1979) and other species, and I observed one incident in which a great black-backed gull kleptoparasitised a peregrine successfully. Overall of 287 observed 'mobbing' incidents for the two raptors, 86.8% may have involved attempted kleptoparasitism, or responses to reduce the risk of kleptoparasitism (e.g. Temeles 1990); for sparrowhawks 98.1% (n=457) of 'mobbing' incidents were probably associated with kleptoparasitism (Chapter 6). Much conventionally described mobbing behaviour (e.g. crows mobbing raptors) does not accord with the definition of mobbing, as defined by Curio (1978). It is very difficult to disentangle the motivation of, for example, carrion crows, when associating with a peregrine, which provides a considerable risk of predation (Cramp & Simmons 1980) as well as kleptoparasitism opportunities. One interesting result of not considering crow or raptor 'mobbing' incidents, is that 'true' mobbing of wintering raptors then becomes extremely rare: merlins less than 0.1% of raptor watch minutes, peregrines 1.5% of raptor watch minutes and sparrowhawks 0.7% of raptor watch minutes. Merlins were mobbed the least which may reflect the small home range used by merlins at Tyninghame (the saltmarsh), sparrowhawks ranged over a much larger area (the whole estuary and adjacent farmland) and peregrines ranged over several estuaries. Each species had a different capacity to respond to mobbing by 'moving on', and the frequency of mobbing reflected this.

7.3.4 Optimal Foraging

The pattern of merlin and peregrine foraging may be interpreted optimally in terms of the change in profitability with time within a patch. Every time a raptor hunts, the prey within a certain radius of the raptor will detect it, and become alert. Prey vigilance declines with time (e.g. see vigilance decay in Chapter 4.2.3.1), but immediately after an attack, most prey within the area will be unlikely to be caught by surprise by a second attack. The optimal raptor strategy would appear to be a single attack, using cover as much as possible, followed by a period of inconspicuously perching. The timing of the next attack would then depend on the vigilance decay period of the prey, and the 'zone of disturbance' caused by an attack. As well as altering the timing between attacks, the raptor can alter the distance away the next attack will be from the first attack. The mean inter-hunt time for merlins and peregrines was similar which suggested that the two raptors were adjusting their attacks according to the 'zone of disturbance' each species caused. Peregrines appear to have a disproportionately large 'zone of disturbance' compared to merlins, considering that the size difference is usually only a factor of 2. The deciding factor in a 'zone of disturbance' is probably due to the size range of prey which can be potentially taken by the two species. Waders, for example, probably use interspecific alarm calls and behaviour as cues for increased alertness (pers. obs.), and so a single wader responding as it detects a raptor can potentially alert all other wader species on the estuary. Every species of bird which occurred at Tyninghame, with the exception of the large gulls, geese and swans was potential peregrine prey and so all birds would potentially have to respond to a peregrine within the area. Only bird species of less than approximately 100g were in any real danger from a merlin and so the probability and scale of response would be much smaller. Merlins could use short distance hunts and cover more effectively to maintain the element of surprise within the estuary.

Peregrines cause very large disturbances when they arrive in an area (Baker 1967, Cramp & Simmons 1980), and their probability of surprising a prey individual probably decreases very quickly. Peregrine hunting must be a trade-off between travel time (and cost) of moving between areas, and the probability of success within an area. The optimum strategy appeared to be frequent movement, and consequent hunting over a very wide area (this was also the pattern observed by Baker 1967). The proportion of time spent in moving flight was significantly greater at low temperatures when peregrines would require more food. Both merlins and sparrowhawks probably ate more food at lower temperatures at Tyninghame. Mueller (1973) showed that captive American kestrels (Falco sparverius), and Warkentin & Oliphant (1990) showed that merlins had a peak of predatory activity in late afternoon and early morning. This was interpreted as a response to the need to feed to maintain body weight over a potentially cold night, when no hunting is possible. The energy costs of active, flapping flight relative to perching and waiting are, for example 13.6x BMR in the American kestrel (Koplin et al.

1980) and 5.3x perched metabolic rate in merlins. Peregrines make frequent use of thermals, and dynamic soaring, so the actual costs of moving flight between an area and staying may be much less. Assuming an average travel speed of 50km/hour (mixing flapping and gliding flight, from Cochran & Applegate 1986), a peregrine can move approximately 2.5km in 5 minutes. This distance would appear to be more than sufficient for a peregrine to move out of its 'zone of disturbance', and reach an 'undisturbed' area. A peregrine's success rate on arriving at a new area (or one in which no peregrine had been hunting in the last hour) was found to be c16.4%, compared to an average success rate of 3% after 5 minutes of perching, after a hunt, within the same area: a relative gain of 5.5 times. If the gain in the probability of capture is greater than the increased cost of moving (i.e. an increase in energy use of less than 5.5), then it would be predicted that peregrines would move between hunts rather than waiting. The energetic costs of perching, relative to flight may increase at lower temperatures (Schmidt-Nielsen 1983), and so the observed pattern of increased movement by peregrines to new areas at lower temperatures was probably a consequence of this. Although in European Kestrels the relative amount of hunting in flight, relative to perch hunting, declined at low temperatures, but the relative costs of hovering compared to perching were very high, compared to the gain in success rate (a 3x gain in success rate; Village 1990). The occurrence of more peregrine moving flight later in the day can be interpreted in terms of a high risk, high gain strategy (e.g. Caraco et al. 1980b). If a peregrine remains in an area, it can expect on average to make a kill once every 2.8 hours, while a peregrine which moves to a new area can expect on average to make a kill every 30 minutes. During the very short daylengths of mid winter, and at low temperatures, a peregrine might be expected to use risk-prone foraging: using more energy in the short term to guarantee a kill before dark.

Raptors should hunt the most profitable prey. Size will be the main determinant of profitability, but as prey gets larger the ability of a raptor to catch and kill the prey diminishes. Merlins showed similar problems to sparrowhawks in killing large prey (Chapter 6.2.7). Of two redshank captures by merlins that I observed, both resulted in the release of the redshank as the merlin tried to adjust its grip on the struggling redshank (see also Dekker 1988). Merlins, and probably also peregrines, regularly attacked very large prey, which in normal circumstances they would not expect to catch. Most large prey is probably unprofitable because the high costs of chase, risks of injury in dealing with large struggling prey and increased risk of kleptoparasitism by not being able to carry very large prey (e.g. Warkentin 1988). Open attacks were probably very low cost, in terms of time and energy expenditure, but potentially of high gain by allowing weak or injured prey individuals to be identified. Rudebeck (1950, 1951) argued that raptors preferentially selected injured birds, and Ruggerio et al. (1979) showed that American Kestrels preferentially attacked prey which was familiar but moving aberrantly. After an initial surprise attack, a raptor may adopt a second strategy of brief, 'testing' attacks.

The trade-off between size of prey, and ease of capture should result in an optimum size of prey. Merlins were equally successful at catching most prey up to and including the size of a dunlin. Dunlin represented the optimal prey and were most frequently taken by merlins at Tyninghame. For peregrines sample sizes of kills were too small to determine whether interspecific success rates were different. However, taking each success rate (Table 9) as the actual success rate, the optimal wader prey was redshank. Although dunlin were killed twice as easily as redshank, redshank weigh on average nearly three times as much as dunlin. Redshank were the wader prey most often taken by peregrine. The optimal prey overall may have been teal, with a high success rate for mass of prey obtained. Teal were found killed fairly frequently by peregrines, but were rarely seen attacked, despite being a relatively common species.

In discussing selection of prey by raptors it is important to distinguish between availability and vulnerability. Conspicuousness of prey is very difficult to quantify (Baker & Parker 1979), particularly when it will vary depending on the choice of habitat, activity and group size of the prey. Baker & Bibby (1987) found no significant relationship between the conspicuousness of prey and risk of predation by merlins. Within the habitat that merlins usually hunted at Tyninghame, most species were relatively conspicuous, and a reasonably high perched merlin would probably be able to see all available prey within a few seconds, except for single skylarks and rock pipits. Skylarks were relatively less conspicuous than dunlin, but merlins still preferentially selected skylarks. Merlins were more specialised, in terms of prey choice, than peregrines, and the co-evolved skylark/merlin pursuit-deterrent behaviour (Chapter 8) indicated that skylarks were generally a common merlin prey. In most cases of merlin hunting, and probably many cases of peregrine hunting relative conspicuousness of prey did not affect choice of prey. Other factors such as specialisation on a prey type or long observation periods before attacks may have reduced conspicuousness to a relatively minor factor. During multiple attack peregrine hunts however, where prey was apparently chosen very quickly and in succession, conspicuousness will have been more important. As success rates were so low for open attacks, the relative selective advantage of being less conspicuous may not have been very great.

Merlins appeared to be using caching to dampen fluctuations of food intake, but observations were too few to quantify. Caching by merlin occurred infrequently, as reported by Page & Whitacre (1975). Prey caching has been documented for many birds of prey and studied extensively in the American kestrel (Collopy 1977) and European kestrel (Village 1990). Despite the different falcon species studied, choice of cache sites, position of cached prey, the apparent difficulty in relocating caches (e.g. search times of up to 3 minutes) and hunting behaviour immediately after caching was very similar to that observed for merlins in this study. Merlins may cache more than other species, such as peregrines, because they are smaller and so have relatively smaller internal food stores available to last for long periods of cold weather. Prey was frequently cached at midday and recovered in late afternoon. Caching prey also allows a merlin to remain at a lower wing loading during more of the day, which will probably allow more efficient hunting. Some merlin caches were probably lost or scavenged (e.g. by carrion crows), so the behaviour may not always have been optimal.

Merlins and peregrines spent, on average, over 85% and 75% of their time perched during the winter. Processing of prey in, for example, a merlin which caught two prey a day, would account for less than 20% of a day's activity (Warkentin & West 1990), so it was unlikely that most raptor inactivity was due to a processing constraint. Peregrines and merlins in winter at Tyninghame did appear to be energy use minimisers, and so correspondingly intake minimisers. Long inter-hunt perching periods and hunting by surprise are the best strategies for energy use minimisation. Long inter-hunt perching periods are most compatible with surprise hunting. Low effort hunting in the winter may contrast with energy maximising, high effort hunting in the summer when the energy requirements for maximal fitness (and the gains from higher risk of injury hunts) are much greater. At Tyninghame it appeared that some raptors were not food stressed and had no problem in obtaining sufficient daily energy intake (with capture rates probably rising as temperature declined). Tyninghame may be a very profitable area, and raptors which hunted in adjacent areas may have had to hunt much more frequently. Hunting experience gained over the winter, and in the first winter particularly, may be essential to maximise reproductive fitness, when energy gained per unit time, will be one of the main determinants of fitness. Raptors may therefore trade-off a low risk, low energy over winter strategy with the need to gain or maintain experience of catching prey.

CHAPTER 8: INTERACTIONS BETWEEN MERLINS AND SKYLARKS

8.1 Introduction

During a hunt a predator must constantly assess its likelihood of successfully capturing prey. Not all prey individuals are of equal fitness because body condition and experience of a prey individual, and consequent escape ability will vary. If a prey individual has a low probability of being caught, it will benefit the prey to communicate this to the predator. Pursuit-deterrent signals (Woodland et al. 1980) evolve when a prey individual can honestly signal to a predator a low probability of capture. Both predator and prey will benefit from such information because both avoid a potentially costly and probably unsuccessful chase. For example, Fitzgibbon & Fanshawe (1988) showed that wild dogs attacked those gazelles in a group which were stotting at a relatively lower frequency, and which were then found to be easier to catch. Rhisiart (1989, cited in Hasson 1991) showed that singing skylarks escape merlin pursuits more frequently than non-singing skylarks, and that merlins learn to avoid singing skylarks as they gain experience.

The frequency of pursuit-deterrent signals by skylarks to hunting merlins and their effect on hunting success has not been quantified in a completely wild situation (Rhisiart used falconry merlins). Observations at the Tyninghame estuary, in southeast Scotland, with a high population of skylarks and frequent merlin attacks provided an opportunity to test the hypothesis that winter singing in skylark acts as a pursuit-deterrent signal to hunting merlins. Specific tests of the hypothesis are (after Hasson 1991):

1) Skylarks will sing only or most frequently when attacked by merlins.

2) The occurrence of song influences chase length and the probability of capture of the skylark by the merlin.

If song does act as an honest "pursuit-deterrent" signal, then this may affect other anti-predation behaviours such as flocking. Flocking may be an effective anti-predation strategy through the 'dilution' effect (Hamilton 1971, Foster & Treherne 1981, Chapter 4.2.1), unless there is an increase in the attack rate on larger flocks by a factor greater than the reciprocal of flock size. If merlins preferentially attack larger flocks, and use song in order to choose which skylark to attack, then there will be no benefit for poor-quality, non-singing skylarks in joining a flock. Skylarks which are unable to deter merlins by singing may have to adopt other anti-predation strategies such as being solitary, and using crypsis and refuges (anecdotal use of refuges by skylark and other prey during merlin hunts has also been documented by Taylor 1986, Booth 1988, Dekker 1988, Chatfield 1992, and Simms 1992). Alternatively if merlins choose a prey victim before any song may or may not be given, then there may still be dilution benefits for non-singing skylarks to join flocks (dependent on the attack rate). Data on the relative occurrence of attacks and the success rate of attacks on flocks of different sizes are needed to assess the 'dilution' effect. Data on when song occurs during a merlin attack are needed to determine whether the decision to join a flock is influenced by the condition of the skylark, and consequent ability to sing.

Merlins can potentially chase for many minutes (Cramp & Simmons 1980, Dickson 1988, Chapter 7.2.8). Reducing the amount of time spent in apparently very costly escape flights will probably be very important to individual skylark, particularly in cold weather, when the risk of starvation is probably high. Skylarks may use specific escape strategies depending on their ability to sing. A skylark which cannot sing on attack may use, for example crypsis as its main anti-predation strategy. Condition-dependent responses have been shown for other bird species (e.g. Buitron 1983, Walters 1990). Skylarks should be expected to use the escape strategy which maximises the probability of escape for the particular attack conditions (e.g. Buchanan _et al._ 1988). The importance of song as a 'pursuit-deterrent' signal to an individual skylark can only be understood relative to any other anti-predation options.

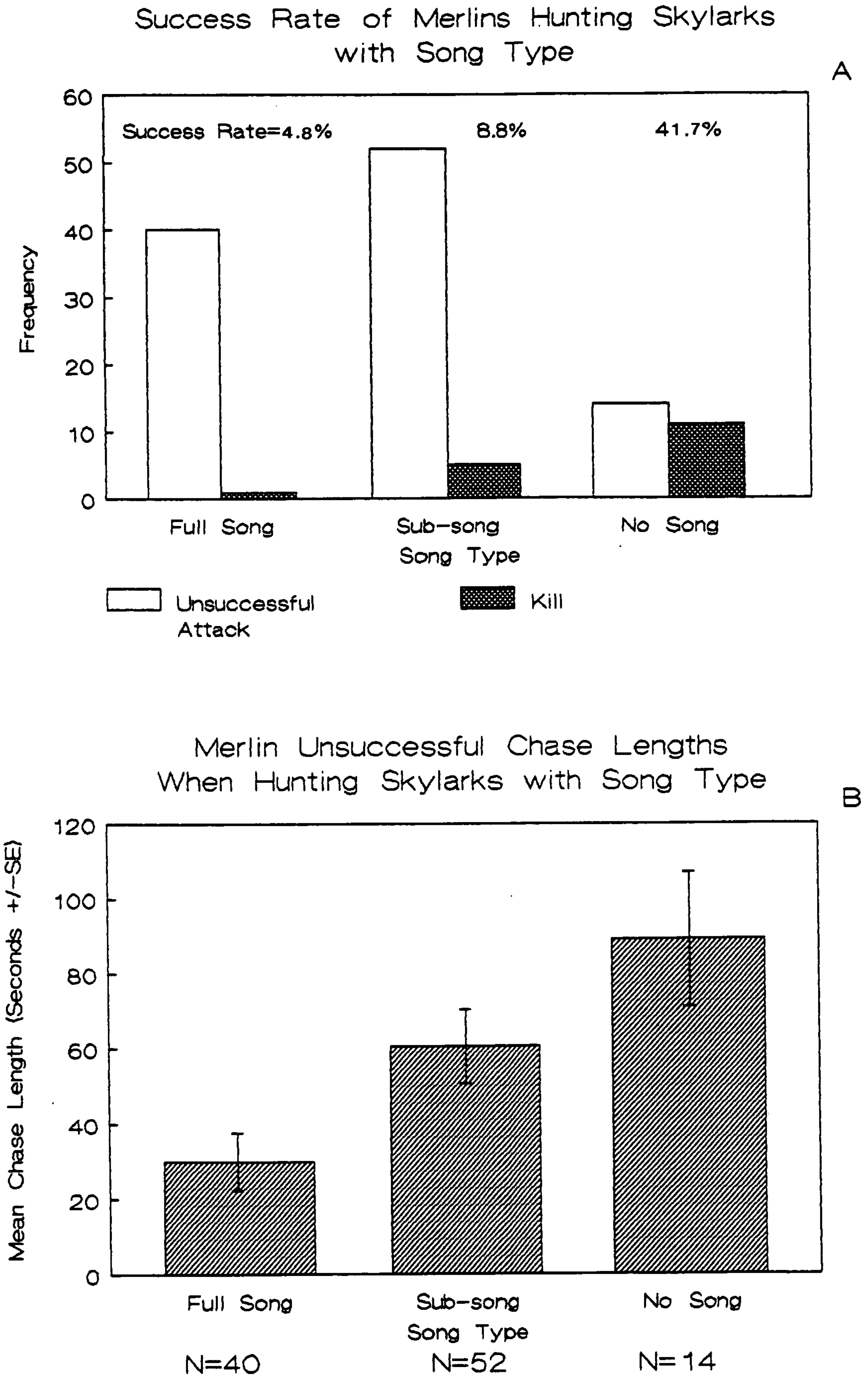
8.2 Results

8.2.1 Song as a 'Pursuit-Deterrent' Signal

There was a significant relationship between the type of song made by an attacked skylark, and the chase length and success rate of the attack by the merlin. A merlin was more likely to catch a skylark which did not sing on attack (41.7%) compared to a skylark which gave short phrases of sub-song (8.8%) compared to a skylark which gave continuous, full territorial song (4.8%) within the first 5 seconds of the attack (Fig. 1A): g=15.0, n=106 unsuccessful attacks, n=17 kills, df=2, p<0.001. The difference in success rate still applies if the data are split into skylarks which made any call

FIGURE

Merlin Success Rates and Chase Lengths of Skylarks with Song Type



or song at all, and skylarks which made no call at all, removing all possible errors in judging song type: g=14.8, df=1, $p<0.001$.

Merlins chased those skylarks which sang poorly or not at all significantly longer than those which sang fully (Fig. 1B): $x^2=14.1$, Kruskall-Wallis 1-way ANOVA, $p<0.001$, n=106 excluding all hunts which led to capture to remove bias due to the higher success rate of capture of non- or poorly singing birds which probably led to earlier capture of those birds. The result still occurred when unsuccessful chase lengths of silent skylarks were compared to skylarks which made any call at all: $x^2=7.4$, Kruskall-Wallis 1-way ANOVA, $p<0.01$. Because non-singing birds were chased for longer the frequency of seeing the outcome of the hunt was lower than for singing skylarks: during long hunts the merlin frequently chased the skylark until both were out of sight. For non-singing skylarks 21.9% of hunts (n=7/25 unknown/known outcome) and for singing skylarks 7.5% of hunts (n=8/98) were of known outcome: g=4.3, df=1, $p<0.05$. Success rates of merlin attacks on non-singing skylarks was therefore probably higher than 41.7%.

There was no indication that temperature, whether measured as mean daily air temperature (MDT) or mean temperature for the previous seven days (ML7DT), affected any of the attack characteristics of merlins and skylarks. If song during an attack was a reliable measure of body condition then song on attack might be expected less frequently in periods of cold weather. There was no significant difference between the frequency of occurrence of the three song types when split by temperature (<5, and >5°C, temperature range chosen to split sample sizes of kills approximately equally): MDT, G=1.8, 2df, P=0.41; ML7DT, G=4.4, 2df, p=0.12 (n=144 attacks). There was no significant difference in the success rate of attack split by temperature (as above): MDT, G=0.92, 1df, P=0.35; ML7DT, G=0.03, 1df, p=0.87 (n=221 unsuccessful attacks, n=29 kills). There was no significant correlation between the chase lengths of unsuccessful attacks and temperature: MDT, T=0.62, p=0.54; ML7DT, T=-1.3, p=0.19; Spearman's Rank Correlation, n=218.

8.2.2 Flocking and 'Pursuit-Deterrence'

Whether a skylark could sing or not on attack by a merlin apparently did not affect flocking behaviour. The relative frequency of the different song types on merlin attack was not significantly different comparing single skylarks and flocks: for single birds, n=21/41/25, and for flocks n=3/7/5, for song types none/sub-song/full song respectively, g=0.18, df=2, p=0.7. Merlins attacked mostly single skylarks (61% of n=251 attacks) and attacked skylarks more frequently on the ground (74.1%) compared to in flight (25.9%): x^2=54.1, 1df, p<0.0001. Single birds were attacked with the same frequency, relative to flocks, whether the attack was on flying skylarks or skylarks on the ground: for ground attacks, n=102/47, and for flight attacks n=29/17, for single birds/flocks respectively; g=0.45, df=1, p=0.5. Song was only ever heard in flight, and usually only when the merlin was very close to the skylark, just after the merlin had begun to chase a clear individual. Merlins were not using the occurrence of song to choose which skylark to attack.

Merlins did not attack skylark flocks in proportion to their occurrence at Tyninghame in winter 3 (Fig. 2A): x^2=682.4, 3df, p<0.0001, comparing the frequency of attacks, with the expected frequency of attacks if the flocks were attacked in the same ratio as their occurrence. Only data from winter 3 was used because skylark flock availability was only censused in that winter. Merlins attacked single skylarks more often than expected (vulnerability index=1.3), avoided mid size flocks (2-30 birds, VI=0.19) but preferentially attacked large flocks (31-100, VI=23.5). The preference for large flocks was sufficient to overcome the dilution effect for an individual within a larger flock (31-100, p=0.004) compared to a medium size flock (11-30, p=0.0004): Figure 2B. The probability of a successful attack was not significantly different across the different flock sizes: single skylarks, 12.8%, n=18/123 kills/unsuccessful attacks; flock size 2-10, 15.0%, n=3/17; flock size 11-30, 9.1%, n=2/20 and flock size 31+, 9.0%, n=6/61 (x^2=1.0, Kruskall-Wallis 1-way ANOVA, p=0.80). Therefore an individual skylark was safest from a merlin within a flock size of 11-30. Most skylarks censused were in flock sizes of 2-10, 52.7%; in the least risky flock size for an individual (11-30), 22.5% of skylarks were present; in the most risky flock size (single birds), 10.6% of skylarks were present. The size of skylark flocks was probably not primarily determined by the risk of attack by merlins.

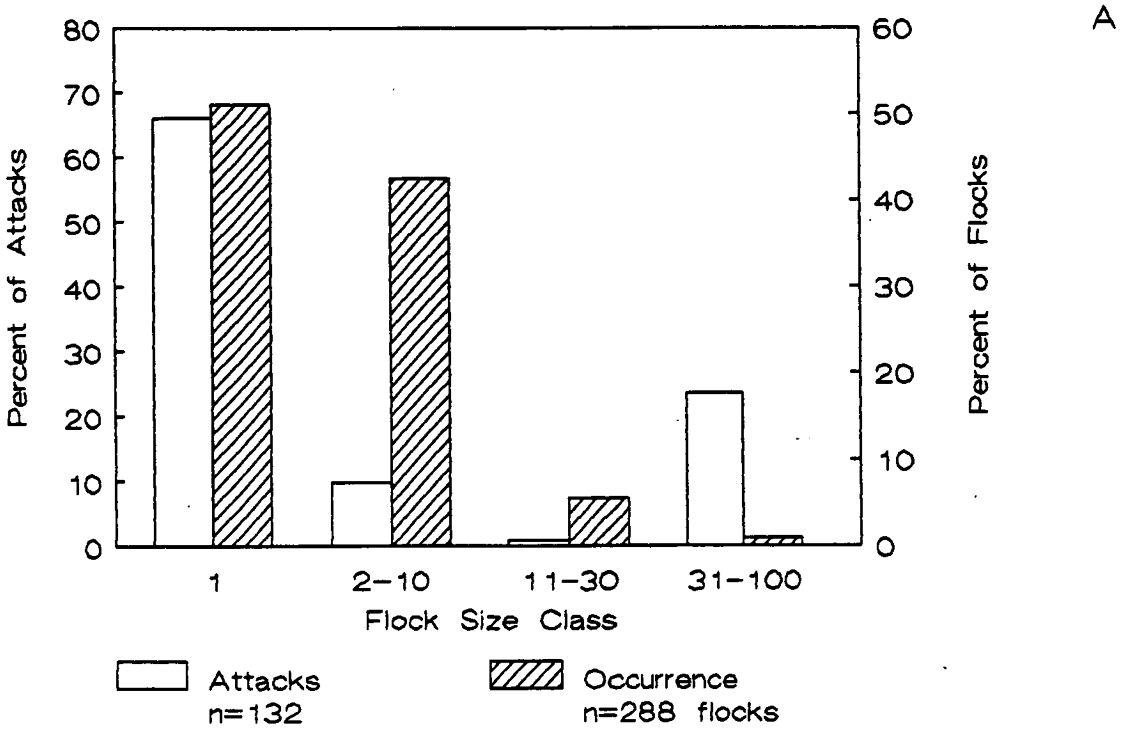
8.2.3 Alternative Escape Strategies

Merlins were most successful when a skylark remained on the ground during an attack (32.3% success rate, n=10/31 kills/unsuccessful

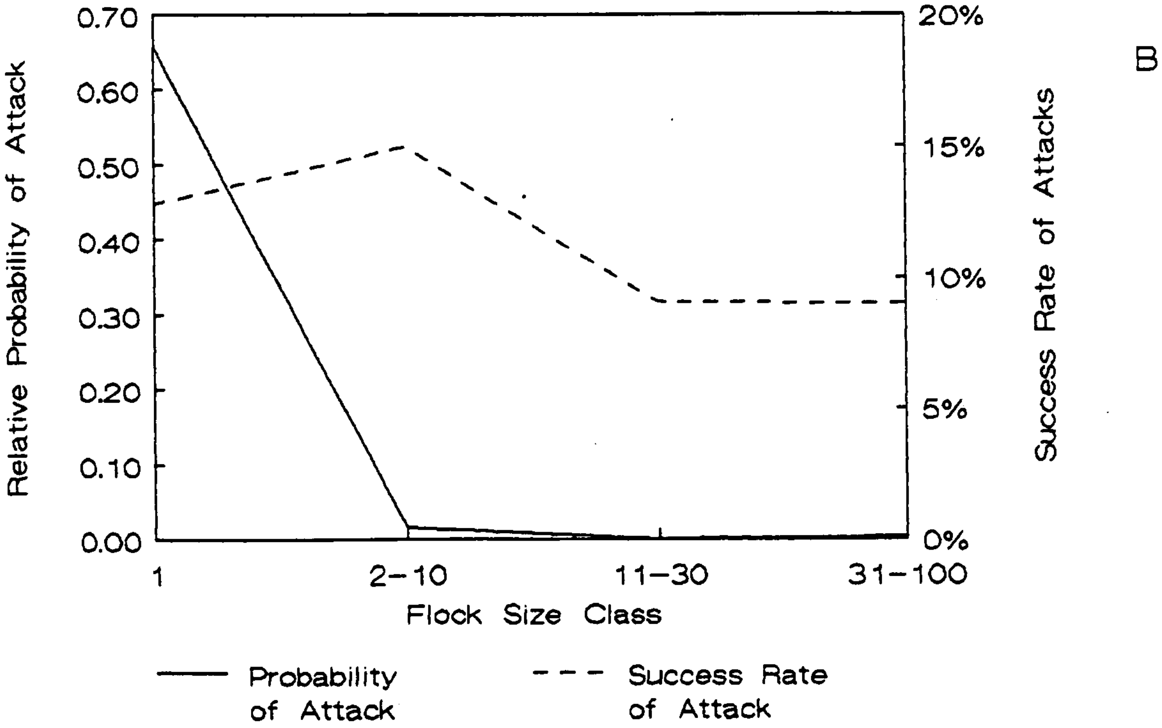
FIGURE 2

The 'Dilution' Effect in Skylark Flocks Attacked by Merlins

Flock Sizes of Skylarks Available
and Attacked by Merlins 1991–92



The Probability of Death From Merlins
of Individual Skylark Within a Flock



attacks for ground/crouch on attack). If a skylark flew from the ground on attack, success rate was lower (8.8% success rate, n=10/114 attacks for ground to fly); success rate was lowest for skylarks which were attacked in flight and remained in flight (2.6% success rate, n=1/38 attacks of flying to flying birds). Success rate for skylarks which ended a chase by diving into trees or bushes (for cover) was also high (21.9% success rate, n=7/32 attacks with a final 'tree dive', after a ground or flight start). The success rate of capture by a merlin was significantly different depending on the initial position of the skylark attacked and the skylark's response: G=12.1, 3df, $p<0.01$.

The optimal escape strategy for a skylark was dependent on its condition as reflected by an individuals ability to sing on attack by a merlin. The null hypotheses that the kill rate of a skylark of a particular song type on attack by a merlin was independent of response was rejected in all cases of reasonable sample size (Table 1). A full song or sub-song singing skylark was less likely to be killed if it flew rather than if it stayed on the ground or used a refuge. A non-singing skylark was equally likely to be killed if it flew compared to an individual that stayed on the ground or used a refuge. The actual kill rates for non-singing skylarks that flew were greater than for a skylark that stayed on the ground or used a refuge, and small sample sizes were probably the reason for the difference not being significant. Skylarks of differing conditions (and consequent singing abilities) might therefore be expected to respond differently on merlin attack. Full singers had the highest frequency of flying (88.1%), sub-song singers flew less frequently

Table 1: The consequences of different escape responses by skylark of different song types on attack by merlins. The escape responses were to fly only (F), or to fly after a period of refuge using or to fly and then attempt to seek a refuge in a bush or tree (BD).

	Full Song	Sub-song	No Song
F Unsuccessful Attacks	37	43	7
F Kills	0	1	8
F Kill Rate	0%	2.5%	53.3%
BD Unsuccessful Attacks	3	9	7
BD Kills	2	4	2
BD Kill Rate	40.0%	30.8%	22.2%

Comparing kill rate if a skylark stayed on the ground or used a refuge:

Full Song	Fisher's Exact Test,	$p=0.022$,	alpha=0.025
Sub-song	$g=7.2$, $df=1$,	$p<0.01$,	alpha=0.016
No Song	$g=2.2$, $df=1$,	$p=0.14$	

(77.1%) and non-singers flew the least frequently (62.5%): g=5.7, df=2, p=0.058; Table 1).

8.3 Discussion

Raptor predation was probably a major selective pressure governing winter behaviour of skylarks at Tyninghame, but skylarks did not gain much dilution benefit from flocking. Merlins hunting at Tyninghame frequently appeared to have difficulties in finding single skylarks and so preferentially attacked flocks. Merlins frequently perched for long periods scanning the saltmarsh before attacking a skylark only a few meters away. I found it impossible to see skylarks feeding on the saltmarsh during censuses until they were flushed, frequently only 2-3m away. The major, and obviously very low cost anti-predator defence for skylarks was crypsis (also described by Simms 1992), but this was lost in large flocks. Merlins frequently caught skylarks on the ground, and these were probably 'frozen' birds. Some skylarks did not fly on attack, but instead ran a short distance and froze again. A merlin would then spend several minutes searching for it by running along the ground like a thrush. Brown (1976) suggested that merlins hunt frequently on the ground, particularly when hunting young gamebirds; these species also freeze and rely on crypsis on approach of predators (pers. obs., Cramp & Simmons 1980). Sparrowhawks, in contrast, hunted skylarks at Tyninghame by quartering the ground like harriers (Chapter 6.2.6). The difference in the hunting methods of the two species probably reflects the lower wing-loading for sparrowhawks, enabling slower flight.

Merlins and skylarks showed a definite co-evolved pattern of predator-prey communication behaviour as shown also by Rhisiart (1989, cited in Hasson 1991). Song was a frequent and successful anti-predation behaviour for a skylark which was forced to fly or attacked in flight. The occurrence of song during a chase was a valid predictor of the outcome of the chase. Both the skylark and merlin benefited from the skylark's communication of its ability to elude capture because both avoided an energetically costly chase. The ability to sing while being chased is not an obvious costly activity compared to other examples of honest indications of condition used as pursuit-deterrent signals, such as stotting in gazelles (C. Fitzgibbon pers. comm., Fitzgibbon & Fanshawe 1988). However, to sing loudly and complexly while a merlin was tail-chasing, only a few meters away, during a very fast directly upward flight, would appear to be a relatively risky strategy. Measurements of the cost of singing in flight, relative to the costs of silent flight are needed. Female skylarks sing (Cramp 1988), but only males make territorial song-flights in the breeding season. The primary selective pressure on female song in skylark is probably due to merlin hunting pressure in the winter: the occurrence of female song in passerines is rare and is usually associated with kin-recognition (Ritchison 1983).

Merlins did not choose skylarks according to song-type, in contrast to Fitzgibbon & Fanshawe's (1988) results. Locating which skylarks within a flock were giving which song-type during an attack would probably be impossible because song is an auditory signal. Also the ability to sing on approach of a merlin is probably not very energetically demanding as singing while being chased, and so would not be a good indicator of the escape abilities of the skylarks in the flock. The main merlin attack strategy appeared to be to catch skylarks on the ground and to avoid a chase, which matches the skylarks' main strategy of avoiding an attack by being inconspicuous. Song as a pursuit-deterrent signal only functions when the merlin starts to chase an individual skylark.

Hasson (1991) predicted that pursuit-deterrent signals would be most expected when they were most likely to change a predator's behaviour: skylarks should sing on attack by a merlin, which can potentially chase for long periods, but not to sparrowhawks, which do not. I was unable to quantify the differential response as there were few sparrowhawk/skylark attacks, observed in good conditions in winter 3 (the only period I was specifically looking for the behaviour in sparrowhawk attacks). For those sparrowhawk-skylark attacks which I did record however, skylark song was rarely heard. One problem was that sparrowhawks attacked very quickly, and rarely chased for more than a few seconds. Hasson (1991) also predicted that the rate of pursuit-deterrent signals should increase as the predator approaches the prey: a skylark should sing only (in winter) when a merlin was approaching it. Silent flying skylarks would start singing as a merlin flew below them, or as it changed direction to fly towards them. It was also noticed that in the later stages of an attack, as the merlin stooped at the skylark after the initial upward, 'ringing' chase, the skylark would utter short loud flight calls on the merlin's closest approach. These were almost invariably heard if the final, close stoops of the attack occurred close to me, even if the skylark had not called or sung at all during the initial ascent. Flight calls may represent a lower cost type of 'pursuit-deterrent' signal. Consequently the low cost calls would be ignored by the merlin, except possibly at the end of a long chase when the merlin already has an idea of the skylarks ability to elude capture. When it is about to give up, even a low cost call may influence a merlin.

Assessment of risk of predation by a prey animal will influence all aspects of behavioural decision making (Lima & Dill 1990). The optimal tradeoff between risk of predation and other priorities such as choice of feeding areas for a skylark probably depended on the condition of an individual and its consequent ability to deter merlin attacks through song. Seeking refuges or staying on the ground inconspicuously was probably the best strategy for poor condition skylarks, while good condition birds could probably feed in more conspicuous areas and fly on attack, as they had a low probability of capture, and the ability to deter a merlin from an energetically costly chase.

Section 9: REFERENCES

Alerstam,A.1987. Radar observations of the stoop of the peregrine falcon (Falco peregrinus) and the goshawk (Accipiter gentilis) Ibis 129:267-273.

Allen,J.A.1988. Frequency-dependent selection by predators. Phil. Trans. R. Soc. Lond. B 319:485-503.

Andersson,M. & Norberg,R.A.1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biol. J. Linn. Soc. 319: 485-503.

Andersson,M. & Wicklund,C.G.1978. Clumping versus spacing out: experiments on nest predation in fieldfares (Turdus pilaris). Anim. Behav. 26:1207-1212.

Anglestam,P.1984. Sexual and seasonal differences in mortality of the black grouse Tetrao tetrix in boreal Sweden. Ornis. Scand. 15:123-134.

Ashmole,N.P.1960. Regulation of numbers of tropical oceanic birds. Ibis 103b:458-473.

Ashmole,N.P.1987. Sparrowhawk caching and returning repeatedly to prey. Scot. Birds 14:182-183.

Baker,J.A.1967. The Peregrine. Collins: London.

Baker,M.C.1971. A comparative study of the foraging ecology of six species of shorebirds (Charadriiformes, charadrii) on their breeding and wintering ranges. Unpubl. Ph.D thesis. Univ. Yale

Baker,R.R.& Bibby,C.J.1987. Merlin (Falco columbarius) predation and theories of the evolution of bird colouration. Ibis 129:259-263.

Baker,R.R.& Hounsome,M.V.1983. Bird colouration: unprofitable prey model supported by ringing data. Anim. Behav. 31:614-615.

Baker,R.R.& Parker,G.A.1979. The evolution of bird colouration. Phil. Trans. R. Soc. Lond. B. 287:63-130.

Bakker,R.T.1983. The deer flees, the wolf pursues: incongruencies in predator-prey coevolution. In Coevolution. Ed. by D.J. Futuyma & M. Slatkin. Sunderland MA: Sinauer Associates.

Balser,D.S.,Dill,H.H. & Nelson,H.K.1968. Effect of predator reduction on waterfowl nesting success. J. Wildl. Man. 32: 669-682.

Barnard,C.J. 1979. Interactions between house sparrows and sparrowhawks. Br. Birds. 72:569-573.

Barnard,C.J.1980. Flock feeding and time budgets in the house sparrow. Anim. Behav. 28:295-309.

Barnard,C.J. & Stephens,H.1981. Prey size selection by lapwing in lapwing/gull associations. Behaviour 77:1-22.

Batten,L.A.,Bibby,C.J.,Clement,P.,Elliot,G.D. & Porter,R.F. 1990. Red Data Birds in Britain. London: Poyser.

Bednarz,J.C.1988. Cooperative hunting in Harris' hawk (Parabuteo unicinctus). Science 239:1525-1527.

Beebe,F.L.1960. The marine peregrines of the north-west Pacific coast. Condor 62:145-189.

Beecroft,R. & Clarke,R.1986. The effect of severe weather in January February 1985 on conditions of redshank on the Orwell estuary. Wader Study Group Bull. 47:20-24.

Bertochi,L.E., Castro,G. & Myers,J.P.1984. Notes on the predators especially the peregrine, of sanderling on the Peruvian coast. Wader Study Group Bull. 42:31-32.

Bertram,B.C.R.1978. Living in groups: predators and prey. In Behavioural Ecology: An Evolutionary Approach. Ed. by J.R. Krebs & N.B. Davies. Oxford: Blackwell Scientific Press.

Bertram,B.C.R.1980. Vigilance and group size in ostriches. Anim. Behav. 28:278-286.

Blick,D.J.1980. Advantages of flocking in some wintering birds. Unpubl. PhD. thesis, Univ. Michigan.

Booth,V. 1988. The grey seals of Donna Nook. In Conservation Management, ed. C. Hutchinson. LSHTNC: Alford, Lancs.

Boyce,D.A.Jr.1985. Merlins and the behaviour of wintering shorebirds. J. Raptor Res. 19:94-96.

Boyd,H.1962. Mortality and fertility of European charadrii. Ibis 104:368-387.

Boyle,G.L.1966. Kestrel taking prey from short-eared owl. Br. Birds 67:474-475.

Broadley,B.J.1985. Unusual method of killing prey by sparrowhawk. Scot. Birds 13:268.

Brockmann,H.J.& Barnard,C.J.1979. Kleptoparasitism in birds. Anim. Behav. 27:487-514.

Brown,J.L.1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160-169.

Brown,L.H.1976. British birds of prey. London: Collins.

Brown,L.H. & Amadon,D.1968. Eagles, hawks and falcons of the world. Feltham: Hamlyn House.

Bryant,J.P. & Kuropat,P.J.1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Ann. Rev. Ecol. Systematics 11:261-285.

Buchanan,J.B., Schick,C.T., Brennan,L.A. & Herman,S.G.1988. Merlin predation on wintering dunlins: hunting success and dunlin escape tactics. Wilson Bull. 100:108-118.

Buitron,D.1983. Variability in the responses of black-billed magpies to natural predators. Behaviour 87:209-236.

Burger,J.1980. Age differences in foraging black-headed stilts in Texas. Auk 97:633-636.

Cade,T.J.1982. The falcons of the world. New York: Cornell University Press.

Caldwell,G.S.1986. Predation as a selective force on foraging herons: effects of plumage colour and flocking. Auk 103:494-505.

Calvert,W.H.,Hedrick,L.E. & Brower,L.P.1979. Mortality of the monarch butterfly, Danaus plexippus: avian predation at five over-wintering sites in Mexico. Science NY 204:847-851.

Campbell,R.W.1975. Hunting tactics of a peregrine falcon on black turnstones. Condor 77:485.

Caraco,T.1979. Time budgetting and group size: a test of theory. Ecology 60:618-627.

Caraco,T., Martindale,S. & Pulliam,H.R.1980a. Avian flocking in the presence of a predator. Nature 285:400-401.

Caraco,T, Martindale,S. & Whitham,T.S.1980b. An empirical demonstration of risk-sensitive foraging preferences. Anim. Behav. 28:820-830.

Carey,H.V.1985. The use of foraging areas by yellow-bellied marmots. Oikos 44:273-279.

Charnov,E.L.1976. Optimal foraging: the marginal value theorem. Theoret. Pop. Biol. 9:129-136.

Charnov,E.L.& Krebs,J.R.1975. The evolution of alarm calls, altruism or manipulation? Am. Nat. 109:107-112.

Chatfield,D.P.G.1992. Meadow pipit evading merlin by settling near human being. Br. Birds 12:670.

Clark,D.A.1980. Age- and sex-dependent foraging strategies of a small mammalian omnivore. J. Anim. Ecol. 49:549-563.

Clarke,J.A.1983. Moonlight's influence on predator/prey interactions between short-eared owls (Asio flammeus) and deermice (Peromyscus maniculatus). Behav. Ecol. Sociobiol. 13: 205-209.

Clark ,N.A.1982a. The effects of severe weather in December 1981 and January 1982 on waders in Britain. Wader Study Group Bull. 34: 5-7.

Clark ,N.A.1982b. The effects of severe weather in December 1981 and January 1982 on waders in Eastern Scotland. Preliminary Report to the NCC.

Clutton-Brock,T.H. & Harvey,P.H.1979. Comparison and adaptation. Proc. R. Soc. Lond. B. 205:547-565.

Cochran,W.W. & Applegate,R.D.1986. Speed of flapping flight of merlins and peregrine falcons. Condor 88:397-398.

Collopy,M.W. 1977. Food caching by female American kestrels in winter. Condor 79:63-68.

Cook,L.M. & Miller,P.1977. Density-dependent selection on polymorphic prey - some data. Am. Nat. 111:594-598.

Cramp,S. & Simmons,K.E.L.1980-1992. The Birds of the Western Palearctic. Vols. 1-6. Oxford: Oxford University Press.

Cresswell,W. a. Flocking is an effective anti-predation strategy in redshank Tringa totanus. Anim. Behav. In press.

Cresswell,W. b. Escape responses by redshank (Tringa totanus) on attack by avian predators. Anim. Behav. In press.

Curio,E.1975. The functional organisation of anti-predator behaviour in the pied flycatcher. A study of avian visual perception. Anim. Behav. 23:1-115.

Curio,E.1976. The Ethology of Predation. Berlin: Spring-Verlag.

Curio,E.1978. The adaptive significance of avian mobbing. Z. Tierpsychol. 48:175-183.

Curio,E., Klump,G. & Regelmann,K.1983. An anti-predator response in the great tit (Parus major): is it tuned to predation risk? Oecologia 60:83-88.

Davidson,N.C.1981a. Seasonal changes in nutritional condition of shorebirds during the non-breeding season. Unpubl. Ph.D. Thesis, University of Durham.

Davidson,N.C.1981b. Survival of shorebirds (Charadrii) during severe weather: the role of nutritional reserves. In: Feeding and Survival Strategies of Estuarine Organisms. (Ed. by N.V. Jones & W.J. Wolff), pp. 231-249. New York: Plenum Press.

Davidson,N.C.1982. Changes in body condition of redshanks during mild winters: an inability to regulate reserves? Ringing and Migration 4:51-63.

Davidson,N.C.& Clark ,N.A.1985. The effects of severe weather in January and February 1985 on waders in Britain. Wader Study Group Bull. 44:10-16.

Davidson,N.C.& Evans,P.R.1982. Mortality of redshank and oystercatcher from starvation during severe weather. Bird Study 29:183-188.

Davies,N.B.1977. Prey selection and social behaviour in wagtails (Aves: Motacillidae). J. Anim. Ecol. 46:37-57.

Davies,N.B. & Houston,A.I.1981. Owners and satellites: the economics of territory defence in the pied wagtail (Motacilla alba). J. Anim. Ecol. 50:157-180.

Davis,J.M.1975. Socially induced flight reactions in pigeons. Anim. Behav. 23:597-601.

Dawkins,M.1971. Perceptual changes in chicks: another look at the 'search image' concept. Anim. Behav. 19:566-574.

Dawkins,R. & Krebs,J.R.1979. Arms races between and within species. Proc. R. Soc. Lond. B 205:489-511.

Dekker,D.1988. Peregrine falcon and merlin predation on small shorebirds and passerines in Alberta. Can. J. Zool. 66: 925-928.

Dickson,R.C.1984. Falcons hunting close to harriers. Br. Birds 77:481-482.

Dickson,R.C.1988. Habitat preferences and prey of merlins in winter. Br. Birds 81:269-274.

Dill,L.M.1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. Can. J. Zool. 66:925-928.

Dill,L.M.1990. Distance-to-cover and the escape decisions of an African cichlid fish, Melanochromis chipokae. Environ. Biol. Fishes 27:147-152.

Dill,L.M. & Fraser,A.H.G.1984. Risk of predation and feeding behaviour of juvenile coho salmon (Onchorhyncus kisutch). Behav. Ecol. Sociobiol. 16:65-71.

Dill,L.M. & Houtman,R.1989. The influence of distance to refuge on the flight-iniation distance in the gray squirrel (Sciurius carolinensis). Can. J. Zool. 67:232-235.

Dill,L.M. & Ydenberg,R.C.1987. The group size-flight distance relationship in waterstriders (Gerris remigis). Can. J. Zool. 65:223-226.

Duncan,P. & Vigne,N.1979. The effect of group size in horses on the rate of attacks by blood-sucking flies. Anim. Behav. 27:623-625.

Dunn,E.K.1972. The effect of age on fishing ability of sandwich terns (Sterna sandvicensis). Ibis 114:360-366.

Edmunds,M.1974. Defence In Animals: A Survey Of Anti-predator Defences. Longmans: London.

Elgar,M.A.1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol. Rev. 64:13-33.

Elgar,M.A. & Catterall,C.P.1981. Flocking and predator surveillance in house sparrows: test of an hypothesis. Anim. Behav. 29:868-872.

Elgar,M.A.,Burren,P.J.& Posen,M.1984. Vigilance and perception of flock size in foraging house sparrows. Behaviour 90:215-223.

Elliot,J.P.,McTaggart Cowan,I., and Holling,C.S.1977. Prey capture in the African lion. Can. J. Zool. 55:1811-1828.

Ellis,D.H.,Bednarz,J.C.,Smith,D.G. & Flemming,S.P.1993. Social foraging classes in raptorial birds. Bioscience 43:14-20.

Elner,R.W. & Hughes,R.N.1978. Energy maximisation in the diet of the shore crab, Carcinu maenas. J. Anim. Ecol. 47:103-116.

Endler,J.A.1986. Natural Selection in the Wild. Princeton: University Press.

Endler,J.A.1991. Interactions between predators and prey. In Behavioural ecology: an evolutionary approach - 3rd ed. Ed. by J.R. Krebs & N.B. Davies. Oxford: Blackwell Scientific Press.

Erlinge,S.1987. Predation and noncyclicity in a Microtine population in southern Sweden. Oikos 50:347-352.

Erlinge,S., Goransson,G., Hansson,L.,Hogstedt,G.,Liberg,O., Nilsson,I.N.,Nilsson,T.,Von Schantz,T. & Sylven,M.1983. Predation as a regulating factor on small rodent populations in southern Sweden. Oikos 40:36-52.

Erlinge,S.,Goransson,G.,Hogstedt,G.,Jansson,G.,Liberg,O., Loman,J.,Nilsson,I.N.,Von Schantz,T. & Sylven,M.1984. Can vertebrate predators regulate their prey? Am. Nat. 123: 125-133.

Errington,P.L.1946. Predation and vertebrate populations. Q. Rev. Biol. 21:144-177,221-245.

Feener,D.H.Jr.1988. Effects of parasite on foraging and defense behaviour of a termitophagous ant, *Pheidole titanus* Wheeler (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 22:421-427.

Ferguson-Lees,J.,Willis,W. & Sharrock,J.T.R. *The Shell Guide to the Birds of Britain and Ireland*. London: Micheal Joseph.

Fienberg,S.E.1970. The analysis of multi-dimensional contingency tables. *Ecology* 51:419-433.

Fish,J.D.& Fish,S.1989. *A student's guide to the seashore*. London: Unwin.

Fis cher,D.L.1985. Piracy behaviour of wintering bald eagles. *Condor* 87:246-251.

Fitzgibbon,C.D. & Fanshawe,J.H.1988. Stotting in Thomson's gazelles: an honest signal of condition. *Behav. Ecol. Sociobiol.* 23:69-74.

Fleischer,R.C.1983. Relationships between tidal oscillations and ruddy turnstone flocking, foraging and vigilance behaviour. *Condor* 85:22-29.

Foster,W.A. & Treherne,J.E.1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* 295:466-467.

Fox,N.1981. Hunting behaviour of trained Goshawks. In *Understanding the Goshawk*. Ed. by R.E. Kenward & I.M. Lindsay. Oxford: The International Association for Falconry and Conservation of Birds of Prey.

Fretwell,S.D. & Lucas,H.L.1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.* 19:16-36.

Futuyma,D.J. & Slatkin,M.1983. *Coevolution*. Sunderland MA: Sinauer Associates.

Gendron,R.P.1986. Searching for cryptic prey: evidence for optimal search rates and the formation of search images in quail. *Anim. Behav.* 34:898-912.

Gendron,R.P. & Staddon,J.E.R.1983. Searching for cryptic prey: the effect of search rate. *Am. Nat.* 121:172-186.

Gilliam,J.F. & Fraser,D.F.1987. Habitat selection when foraging under predation hazard: a model and a test with stream dwelling minnows. *Ecology* 68:1227-1253.

Gill,F.B. & Wolf,L.L.1975. Economics of feeding territoriality in the golden-winged sunbird. *Ecology* 56:333-345.

Goodey,W. & Liley,N.R.1986. The influence of early experience on the escape behaviour in the guppy. *Can. J. Zool.* 64:885-888.

Goss-Custard,J.D.1970a. Feeding dispersion in some overwintering wading birds. In: *Social Behaviour in Birds and Mammals* (Ed J.H. Crook), p3-35. New York: Academic Press.

Goss-Custard,J.D.1970b. The reponses of redshank (*Tringa totanus*) to spatial variations in the density of their prey. *J. Anim. Ecol.* 39:91-113.

Goss-Custard,J.D.1977a. Optimal foraging and the size selection of worms by redshank (Tringa totanus L.) in the field. Anim. Behav. 25:10-29.

Goss-Custard,J.D.1977b. The energetics of prey selection by redshank Tringa totanus (L.), in relation to prey density. J. Anim. Ecol. 46:1-19.

Goss-Custard,J.D.1980. Competition for food and interference among waders. Ardea 68:31-52.

Goss-Custard,J.D.1984. Intake rates and food supply in migrating and wintering shorebirds.In: Shorebirds: migration and foraging behaviour. Ed. by J.Burger & B.L. Olla, pp 271-321. New York: Plenum Press.

Goss-Custard,J.D.,Clarke,R.T. & Durrell,S.E.A.1984. Rates of food intake and aggression of oystercatchers Haematopus ostralegus on the most and least preferred mussel Mytilus edulis beds of the Exe estuary. J. Anim. Ecol. 53:233-246.

Goss-Custard,J.D.,Durrell,S.E.A. le V. dit & Ens,B.1982. Individual differences in aggressiveness and food stealing among wintering oystercatchers Haematopus ostralegus L.. Anim. Behav. 30:917-928.

Goss-Custard,J.D.,Jenyon,R.A.,Jones, R.E.,Newberry, P.E. & Williams,R.B.1977. The ecology of The Wash. II. Seasonal variation in feeding conditions of wading birds. J. Appl. Ecol. 14:701-719.

Gould,S.J. & Lewontin,R.C.1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme. Proc. R. Soc. Lond. B. 205:581-598.

Greenwood,J.J.D. & Elton,R.A.1979. Analysing experiments on frequency-dependent selection by predators. J. Anim. Ecol. 48:721-737.

Grieg-Smith,P.W.1981. Responses to disturbance in relation to flock size in foraging groups of barred ground doves (Geopelia striata). Ibis 23:103-106.

Griffiths,K.S. & Holling,C.S.1969. A competition sub-model for parasites and predators. Can. Entomol. 101:785-818.

Groves,S.1978. Age-related differences in ruddy turnstone foraging and aggressive behaviour. Auk 95:95-103.

Grubb,T.C. & Greenwald,L.1982. Sparrows and a brushpile: different combinations of predation risk and energy cost. Anim. Behav. 30:637-640.

Guildford,T. & Dawkins,M.S.1987. Search images not proven, a reappraisal of recent evidence. Anim. Behav. 35:1838-1845.

Hale,W.G.1971. A revision of the taxonomy of the Redshank, Tringa totanus. Zool. J. Linn. Soc. 50:199-268.

Hale,W.G.1973. The distribution of the redshank Tringa totanus in the winter range. Zool. J. Linn. Soc. 53:177-236.

Hale,W.G.1980. Waders. London: Collins.

Hamilton,W.D.1964. The genetical evolution of social behaviour. I, II. J. Theor. Biol. 7:1-52.

Hamilton,W.D.1971. Geometry for the selfish herd. J. Theor. Biol. 31:295-311.

Hammerstrom,F.1957. The influence of a hawk's appetite on mobbing. Condor 59:192-194.

Hassell,M.P.1978. Foraging strategies, population models and biological control: a case study. J. Anim. Ecol. 49:603-628.

Hassell,M.P.1985. Insect natural enemies as regulating factors. J. Anim. Ecol. 54:323-334.

Hassell,M.P. & May,R.M.1974. Aggregation of predators and insect parasites and its effect on stability. J. Anim. Ecol. 43: 567-594.

Hassell,M.P. & May,R.M.1985. From individual behaviour to population dynamics. In Behavioural Ecology: Ecological Consequences of Adaptive Behaviour. Ed. by R.M. Sibly & R.H. Smith. Oxford: Blackwell Scientific Press.

Hasson,O.1991. Pursuit-deterrent signals: communication between prey and predator. TREE 6:325-329.

Heads,P.A. & Lawton,J.H.1983. Studies on the natural enemy complex of the holly-leaf miner: the effects of scale on the detection of aggregative responses and the implications for biological control. Oikos 40:267-276.

Heppleston,P.B.1971. The feeding ecology of Oystercatchers Haematopus ostralegus L. in winter in northern Scotland. J. Anim. Ecol. 40:651-672.

Hildrew,A.G. & Townsend,C.R.1982. Predators and prey in a patchy environment: a freshwater study. J. Anim. Ecol. 51:797-815.

Holomuzki,J.R.1986. Predator avoidance and diet patterns of microhabitat use by larval tiger salamanders. Ecology 67:737-748.

Holmes,W.G.1984. Predation risk and foraging behaviour of the hoary marmot in Alaska. Behav. Ecol. Sociobiol. 15:293-301.

Holmes,W.G.1991. Predator risk affects foraging behaviour of pikas: observational and experimental evidence. Anim. Behav. 42:111-119.

Holling,C.S.1959a. The components of predation, as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91:293-332.

Holling,C.S.1959b. Some characteristics of simple types of predation. Can. Entomol. 91:385-398.

Holling,C.S.1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 45:11-60.

Holt,R.D.1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. Am. Nat. 124:377-406.

Hoogland,J.L.1983. Nepotism and alarm calling in the black-tailed prairie dog (Cynomys ludovicianus). Anim. Behav. 31:472-479.

Hudson,P.1986. Red Grouse. The Biology and Management of a Wild Gamebird. The Game Conservancy Trust. Bournemouth: Bourne Press.

Janetos,A.C. & Cole,B.J.1981. Imperfectly optimal animals. Behav. Ecol. Sociobiol. 9:203-210.

Jennings,T. & Evans,S.M.1980. Influence of position in the flock and flock size on vigilance in the starling, *Sturnus vulgaris*. Anim. Behav. 28:634-635.

Jones,A.M.1987. Hen sparrowhawk taking rabbit carrion. Scot. Birds 14:210-211.

Kacelnik,A.1984. Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. J. Anim. Ecol. 53:283-299.

Keith,L.B.,Todd,A.W.,Brand,C.J.,Adamcik,R.S. & Rusch,D.H.1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. Proc. Int. Congr. Game Biol. 13:151-175.

Kemp,J.B.1992 Harrier-like hunting technique of female sparrowhawk. Br. Birds 85:377.

Kennedy,P.L. & Johnson,D.R.1986. Prey-size selection in nesting male and female cooper's hawks. Wilson Bull. 98:110-115.

Kenward,R.E.1978. Hawks and doves: factors affecting success and selection in goshawk attacks on pigeons. J. Anim.Ecol., 47:449-460.

Kenward,R.E.1982. Goshawk hunting behaviour and range size as a function of food and habitat availability. J. Anim. Ecol. 51: 69-80.

Kenward,R.E., Marcstrom,V. & Karlbom,M.1981. Goshawk winter ecology in Swedish pheasant habitats. J. Wildl. Manag. 45: 397-408.

Klem Jr.,D.,Hillegass,B.S. & Peters,B.A.1985. Raptors killing raptors. Wilson Bull. 97:230-231.

Klump,G.M.,Kretzschmar,E.& Curio,E.1986. The hearing of an avian predator and its avian prey. Behav. Ecol. Sociobiol. 18:317-323.

Koplin,J.R.,Collopy,M.W.,Bamann,A.R. & Levenson,H.1980. Energetics of two wintering raptors. Auk 97:795-806.

Krebs,J.R.1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). Behaviour 51:99-134.

Krebs,J.R.1978. Optimal foraging: decision rules for predators. In *Behavioural Ecology: An Evolutionary Approach*, Ed. by J.R. Krebs & N.B. Davies. Oxford: Blackwell Scientific Publications.

Krebs,J.R.1980. Optimal foraging, predation risk and territory defence. Ardea 68:83-90.

Krebs,J.R. & Davies,N.B.1987. *An Introduction to Behavioural Ecology*, 2nd Ed. Oxford: Blackwell Scientific Press.

Krebs,J.R. & Kacelnik,A.1991. Decision making. In *Behavioural Ecology: An Evolutionary Approach* 3rd Ed. Ed. by J.R. Krebs & N.B. Davies. Oxford: Blackwell Scientific Publications.

Krebs,J.R. & McCleery,R.H.1984. Optimization. In *Behavioural Ecology: An Evolutionary Approach* 2nd Edition. Ed. by J.R. Krebs & N.B. Davies. Oxford: Blackwell Scientific Publications.

Krebs,J.R.,Erichsen,J.T.,Webber,M.I. & Charnov,E.L.1977. Optimal prey selection in the great tit (Parus major). Anim. Behav. 25:30-38.

Kus,B.E.1985. Flocking and predator avoidance in wintering shorebirds. Unpubl. PhD. thesis, Univ. California, Davis.

Kus,B.E.,Ashman,P.,Page,G.W.& Stenzel.L.E.1984. Age-related mortality in a wintering population of dunlin. Auk 101: 69-73.

Harvey,P.H. & Greenwood,P.J.1978. Anti-predator defence strategies: some evolutionary problems. In Behavioural Ecology: An Evolutionary Approach. Ed. by J.R. Krebs & N.B. Davies. Oxford: Blackwell Scientific Publications.

Lack,D.1954. The natural regulation of animal numbers. Oxford: University Press.

Lack,P.1986. The Atlas of Wintering Birds in Britain and Ireland. Calton: Poyser.

LaGory,K.E.1986. Habitat, group size and behaviour of white-tailed deer. Behaviour 98:168-179.

LaGory,K.E.1987. The influence of habitat and group characteristics on the alarm and flight response of the white-tailed deer. Anim. Behav. 35:20-25.

Lazarus,J.1979. The early warning function of flocking in birds: an experimental study with captive quelea. Anim. Behav. 27:855-865.

Lindstrom,A.1989. Finch flock size and risk of hawk predation at a migratory stopover site. Auk 106:225-232.

Lima,S.L. & Dill,L.M.1990. Behavioural decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68:619-640.

Lima,S.L. & Valone,T.J.1986. Influence of predation risk on diet selection: a simple example in the grey squirrel. Anim. Behav. 34:536-544.

Lima,S.L., Valone,T.J. & Caraco,T.1985. Foraging efficiency - predation risk tradeoff in the grey squirrel. Anim. Behav. 33: 155-165.

Lindstrom,A.1989. Finch flock size and risk of hawk predation at a migratory stopover site. Auk 106:225-232.

MacArthur,R.H. & Pianka,E.R.1966. On optimal use of a patchy enviroment. Am. Nat. 100:603-609.

Madsen,J.1988. Goshawk harassing and killing brent geese. Dansk Orn. Foren. 82:57-58.

Mallory,E.P. & Schneider,D.C.1979. Antagonistic behaviour in short-billed dowitchers feeding on a patchy resource. Wilson Bull. 91:271-278.

Marler,P.1955. Characteristics of some animal calls. Nature 176:6-8.

Marquiss,M.& Newton,I.1981.A radio-tracking study of the ranging behaviour and dispersion of European sparrowhawks. J. Anim. Ecol. 51:111-133.

Marquiss,M.& Newton,I.1982. Habitat preference in male and female sparrowhawks. Ibis 124:324-328.

Marr,T.G. & McWhirter,D.W.1982. Differential hunting success in a group of short-eared owls. Wilson Bull. 94:82-83.

Masman,D. & Haasen,M.1987. Energy expenditure during free flight in trained and free-living Eurasian Kestrels (Falco tinnunculus). Auk 104:603-616.

Masman,D.,Daan,S. & Beldhuis,H.1988. Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly-labled water methods. Ardea 76:64-81.

May,R.M.1978. Host-parasitoid systems in patchy enviroments: a phenomenological model. J. Anim. Ecol. 47:833-844.

McLusky,D.S.1981. Estuarine Ecology. Blackie: Glasgow.

Mearns,R.1982. Winter occupation of breeding territories and winter diet of peregrines in South Scotland. Ornis. Scand. 13: 79-83.

Mech,L.D.1970. The Wolf. Garden City: Natural History Press.

Melzack,R.1961. On survival of mallard ducks after "habituation" to the hawk-shaped figure. Behaviour 17:9-16.

Metcalfe,N.B.1984. The effects of habitat on the vigilance of shorebirds: is visibility important? Anim. Behav. 32:981-985.

Metcalfe,N.B. & Furness,R.W.1984. Changing priorities: the effect of premigration fattening on the trade-off between foraging and vigilance. Behav. Ecol. Sociobiol. 15:203-206.

Millinski,M.& Heller,R.1978. The influence of a predator on the optimal foraging behaviour of sticklebacks. Nature 275:642-644

Monaghan,P.1980. Dominance and dispersal between feeding sites in the herring gull (Larus argentatus). Anim. Behav. 28:521-527.

Morse,D.H.1973.Interactions between tit flocks and sparrowhawks. Ibis 115:591-593.

Mueller,H.C.1973. The relationship of hunger to predatory behaviour in hawks (Falco sparverius) and (Buteo platypterus). Anim. Behav. 21:513-520.

Mueller,H.C. & Berger,D.D.1970. Prey preferences in the sharp-shinned hawk. The roles of sex, experience and motivation. Auk 87:453-457.

Mueller,H.C.,Berger,D.D. & Allez,G.1981. Age and sex differences in wing loading and other aerodynamic characteristics of sharp-shinned hawks. Wilson Bull. 93:491-499.

Murton,R.K.,Isaacson,A.J. & Westwood,N.J.1971. The significance of gregarious feeding behaviour and adrenal stress in a population of woodpigeons Columba palumbus. J. Zool. Lond. 165:53-84.

Myers,J.P.1980. Territoriality and flocking by buff-breasted sandpipers: variation in nonbreeding dispersion. Condor 82:241-250.

Myers,J.P.1984. Spacing behaviour of nonbreeding shorebirds. In *Shorebirds: Migration and Foraging Behaviour*. Ed. by J. Burger & B.L. Olla. pp 271-321. New York: Plenum Press.

Naunton,C.R.1973. Unusual hunting behaviour of sparrowhawks. *Br. Birds* 66:396-397.

Neill,S.R.St.J. & Cullen,J.M.1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *J. Zool. London* 172:549-569.

Nettleship,D.N.1973. Breeding ecology of turnstones *Arenaria interpres* at Hazen Camp, Ellesmere Island, N.W.T. *Ibis* 115:202-217.

Newton,I.1979. *Population Ecology of Raptors*. Calton: Poyser.

Newton,I.1986. *The Sparrowhawk*. Calton: Poyser.

Newton,I. & Haas,M.B.1984. The return of the sparrowhawk. *Br. Birds* 77:47-70.

Newton,I & Marquiss,M.1982. Food, predation and breeding season in the Sparrowhawk *Accipiter nisus*. *J. Zool. Lond.* 197:221-240.

Newton,I.,Meek,E.R., & Little,B.1984. Breeding season foods of merlins *Falco columbarius* in Northhumbria. *Bird Study* 31:49-56.

Nie,N.H.,Hull,C.H.,Jenkins,J.G.,Steinbrenner,K. & Bent,D.H.1975. *SPSS: Statistical Package for the Social Sciences*. New York: McGraw-Hill.

Norusis,M.J.1990. *SPSS/PC+ Advanced Statistics 4.0.* Gorinchem: SPSSInc.

Oaten,A. & Murdoch,W.W.1975a. Switching, functional response, and stability in predator-prey systems. *Am. Nat.* 109:299-318.

Oaten,A. & Murdoch,W.W.1975b. Functional response and stability in predator prey systems. *Am. Nat.* 109:289-298.

Owen,J.H.1932. The hunting of the sparrowhawk. *Br. Birds* 25:151-155.

Owens,N.W.& Goss-Custard,J.D.1976. The adaptive significance of alarm calls given by shorebirds on their winter feeding grounds. *Evolution* 30:397-398.

Page,G. & Whitacre,D.F.1975. Raptor predation on wintering shorebirds. *Condor* 77:73-83.

Partridge,L. & Green,P.1985. Intraspecific feeding specialisations and population dynamics. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*. Ed. by R.M. Sibly & R.H. Smith. Oxford: Blackwell Scientific Press.

Pereira,M.E. & Macedonia,J.M.1991. Ring-tailed lemur anti-predator calls denote predator class not response urgency. *Anim. Behav.* 41:543-544.

Peters,R.H.1983. *The Ecological Implications of Body Size*. Cambridge: University Press.

Pettifor,R.A.1990. The effects of avian mobbing on a potential, predator the European kestrel (*Falco tinnunculus*). *Anim. Behav.* 39:821-827.

Porter,R.F.,Willis,I.,Christensen,S., & Pors Nielsen,B.1981. Flight Identification of European Raptors. Calton: Poyser.

Potts,G.R.1980. The effects of modern agriculture, nest predation and game management on the population ecology of partridges (Perdix perdix and Alectoris rufa). Adv. Ecol. Res. 11:2-81.

Poysa,H.1987a. Numerical and escape responses of foraging teals (Anas crecca) to predation risk. Bird Behav. 7:87-92.

Poysa,H.1987b. Feeding-vigilance trade-off in the teal: effects of feeding method and predation risk. Behaviour 103:108-122.

Prater,A.J.,Marchant,J.H. & Vuorinen,J.1977. Guide to the Identification and Ageing of Holarctic Waders. Tring: BTO Guide No. 17.

Pulliam,H.R.1973. On the advantages of flocking. J. Theor. Biol. 38:419-422.

Pulliam,H.R. & Caraco,T.1984. Living in groups: is there an optimal group size? In Behavioural Ecology: An Evolutionary Approach. 2nd Ed. Ed. by J.R. Krebs & N.B. Davies. Oxford: Blackwell Scientific Press.

Pyke,G.H.,Pulliam,H.R. & Charnov,E.L.1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52:137-154.

Ratcliffe,R.1963. The status of the peregrine in Great Britain. Bird Study 10:56-90.

Ratcliffe,R.1980. The Peregrine Falcon. Calton: Poyser.

Recher,H.F. & Recher,J.A.1969. Some aspects of the ecology of migrant shorebirds. II Aggression. Wilson Bull. 81:140-154.

Rice,W.R.1989. Analyzing tables of statistical tests. Evolution 43:223-225.

Ridpath,M.G.1972. The Tasmanian Native Hen (Tribonyx mortierii) I. Patterns of behaviour. CSIRO Wildl. Res. 17:1-5.

Ritchison,G.1983. The function of singing in female black-headed grosbeaks (Pheucticus melanocephalus): family group maintenance. Auk 100:105-116.

Roalkvam,R.1985. How effective are hunting peregrines? J. Raptor Res. 19:27-29.

Rosenzweig,M.L.1978. Aspects of biological exploitation. Q. Rev. Biol. 52:371-380.

Rosenzweig,M.L. & MacArthur,R.1963. Graphical representation and stability conditions of predator-prey interactions. Am. Nat. 97:209-223.

Rudebeck,G.1950 and 1951. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. Oikos 2: 65-88 & 3: 200-231.

Ruggerio,L.F.,Cheney,C.D.& Knowlton,F.F.,1979. Interacting prey characteristics effects on kestrel predatory behaviour. Am. Nat. 113:749-757.

Sage,B.1963. Magpie robbing kestrel. Br. Birds 50: 353.

Salomonsen,F.1954. The migration of the European Redshanks (*Tringa totanus*) (L.). *Dansk Orn. Foren. Tidsskr.* 48: 94-112.

Salt,G.W.1974. Predator and prey densities as controls of the rate of capture by the predator *Didinium nasutum*. *Ecology* 55:434-439.

Salt,G.W. & Willard,D.E.1971. The hunting behaviour and success of Forster's tern. *Ecology* 52:989-999.

Savino,J.F. & Stein,R.A.1989. Behavioural interactions between fish predators and their prey: effects of plant density. *Anim. Behav.* 37:311-321.

Schaller,G.B.1967. *The Deer and the Tiger*. Chicago: University Press.

Schaller,G.B.1972. *The Serengeti Lion*. Chicago: University Press.

Schmidt-Kielsen,K.1983. *Animal physiology: adaptation and enviroment*. Cambridge: University Press.

Schoener,T.W.1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2:369-404.

Seyfarth,R.M.,Cheney,D.L. & Marler,P.1980. Vervet monkey alarm calls: evidence of predator classification and semantic communication. *Science* 210:801-803.

Shanewise,S. & Herman,S.G.1979. Flocking behaviour in wintering Dunlin. *Stud. Avian Biol.* 2:191.

Sharrock, J.T.R.1976. *The Atlas of Breeding Birds in Britain and Ireland*. Calton: Poyser.

Siegfried,W.R.1972. Aspects of the feeding ecology of cattle egrets (*Ardeola ibis*) in South Africa. *J. Anim. Ecol.* 41:71-78

Sih,A.1980. Optimal behaviour: can foragers balance two conflicting demands. *Science* 210:1041-1043.

Sih,A.1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* 63:786-796.

Sih,A.1984. Optimal behaviour and density-dependent predation. *Am. Nat.* 123:314-326.

Simmons,K.1968. Food hiding by rooks and other crows. *Br. Birds* 61:228-229.

Simmons,K.1970. Further observations on food hiding in the Corvidae. *Br. Birds* 63:175-177.

Simms,E.1992. *British larks, pipits and wagtails.* London: HarperCollins.

Sokal,R.R. & Rohlf,F.J.1981. *Biometry*. New York: W. H. Freeman and Company.

Sonerud,G.A.1985. Brood movements in grouse and waders as defense against win-stay search in their predators. *Oikos* 44:287-300.

Sordahl,T.A.1990. The risk of avian mobbing and distraction behaviour: an anecdotal review. *Wilson Bull.* 102:349-352.

Speakman,J.R.1984. The energetics of foraging in wading birds (Charadrii). Unpublished Ph.D Thesis. Univ. of Stirling.

Speakman,J.R.1987. Apparent absorbtion efficiencies for redshank (Tringa totanus L.) and oystercatcher (Haematopus ostralegus L.): implications for the predictions of optimal foraging models. Am. Nat. 130:677-691.

Speakman,J.R.1991.The impact of predation by birds on bat populations in the British Isles. Mammal Rev. 21:123-142.

Stephens,D.W. & Krebs,J.R.1986. Foraging Theory. Princeton: University Press.

Stinson,C.H.1988. Does mixed-species flocking increase vigilance or skittishness. Ibis 130:303-304.

Storer,R.W.1966. Sexual dimorphism and food habits of three North American Accipiters. Auk 83:423-436.

Suhonen,J.,Halonen,M. & Mappes,T. Predation risk and the organisation of the Parus guild. Oikos 66:94-100.

Summers,R.W. & Underhill,L.G.1991. The relationship between body size and time of breeding in Icelandic Redshanks (Tringa t. robusta).Ibis 133:134-139.

Sullivan,K.A.1988. Ontogeny of time budgets in yellow-eyed juncos: adaptation to ecology constraints. Ecology 69:118-124.

Sutherland,W.J.1982. Spatial variations in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. II The pattern of predation. J. Anim. Ecol. 51:491-500.

Sutherland,W.J. & Parker,G.A.1985. Distribution of unequal competitors. In Behavioural Ecology: Ecological Consequences of Adaptive Behaviour. Ed. by R.M. Sibly & R.H. Smith. pp. 255-273. Oxford: Blackwell Scientific Publications.

Taylor,M.E.1986. Skylarks using human beings as a refuge. Br. Birds 79:592.

Taylor,R.J.1984. Predation - (Population and Community Biology). London: Chapman & Hall.

Temeles,E.J.1985. Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. Am. Nat. 125:485-499.

Temeles,E.J.1989. Effect of prey consumption on foraging activity of northern harriers. Auk 106:353-357.

Temeles,E.J.1990. Interspecific territoriality of northern harriers: the role of kleptoparasitism. Anim. Behav. 41: 285-294.

Thompson,D.B.A. & Barnard,C.J.1983. Anti-predator responses in mixed species associations of lapwings, golden plovers and black-headed gulls. Anim. Behav. 31:585-593.

Thompson,D.B.A. & Barnard,C.J.1984. Prey selection by plovers: optimal foraging in mixed groups. Anim. Behav. 32:554-563.

Thompson,P.S. & Hale,W.G.1989. Breeding site fidelity and natal philopatry in the Redshank (Tringa totanus). Ibis 131: 214-224.

Thiollay,J.M. & Clobert,J.1990. Comparative foraging adaptations of small raptors in a dense African savannah. Ibis 132:42-57.

Tinbergen,N.1953. Carrion crow striking lapwing in the air. Br. Birds 66:377.

Tinning,P.& Tinning,P.1970. Hooded crows robbing merlin of prey. Br. Birds 63:83.

Toland,B.1986. Hunting success of some Missouri raptors. Wilson Bull. 98:116-125.

Townshend,D.J.1984. The effects of predators upon shorebird populations in the non-breeding season. Wader Study Group Bull. 40:51-54.

Treleaven,R.B.1980. High and low intensity hunting in raptors. Z. Tierpsychol. 54:339-345.

Underwood,R.1982. Vigilance behaviour in grazing African antelopes Behaviour 79:81-107.

Valone,T.J. & Lima,S.L.1987. Carrying food items to cover for consumption: the behaviour of ten bird species feeding under the risk of predation. Oecologia 71:286-294.

Vermeij,G.I.1987. Evolution and Escalation; An Ecological History of Life. Princeton: University Press.

Village,A.1990. The Kestrel. Calton: Poyser.

Virnstein,R.W.1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58:1199-1217.

Waage,J.K.1979. Foraging for patchily distributed hosts by the parasitoid Nemeritis canescens. J. Anim. Ecol. 48:353-371.

Waddington,K.D. & Heinrich,B.1979. The foraging movements of bumblebees on vertical 'inflorescences': an experimental analysis. J. Comp. Physiol. 134:113-117.

Walters,J.R.1990. Anti-predatory behaviour of lapwings: field evidence of discriminative abilities. Wilson Bull. 102:49-70.

Warkentin,I.G.1988. Seasonal predation of large prey by merlins. Wilson Bull. 100:137-139.

Warkentin,I.G. & Oliphant,L.W.1990. Habitat use and foraging behaviour of urban merlins in winter. J. Zool. Lond. 221:539-563.

Warkentin,I.G.& West,N.H.1990. The ecological energetics of wintering merlins. Physiol. Zool. 63:334-352.

Watson,J.1979. Foods of merlins nesting in young conifer forests. Bird Study 26:253-258.

Wellborn,G.A. & Robinson,J.V.1987. Microhabitat selection as an anti-predator strategy in an aquatic insect Pachydiplex longipennis Burmeister. (Odonata: Libellulidae). Oecologia 71:185-189.

Welty,J.C.1963. The Life of Birds. New York: Alfred A. Knopf.

Whitfield,D.P.1985a. Raptor predation on wintering waders in southeast Scotland. Ibis 127:554-558.

Whitfield,D.P.1985b. Social organisation and feeding behaviour of wintering turnstone (Arenaria interpres). Unpubl. PhD. thesis, Univ. of Edinburgh.

Whitfield,D.P.1988. Sparrowhawks Accipiter nisus affect the spacing behaviour of wintering Turnstone Arenaria interpres and Redshank Tringa totanus. Ibis 130:284-287.

Whitfield,D.P.,Evans A.D,& Whitfield,P.A.1988. The impact of raptor predation on wintering waders. Proc. Int. Orn. Congr. 19:674-687.

Wilson,J. & Weir,A.G.1989. Hunting behaviour and attack success of a female sparrowhawk between October 1987 and April 1988. Scot. Birds 15:126-130.

Woodland,D.J.,Jaafer,Z. & Knight,M.L.1980. The "pursuit deterrent" function of alarm signals. Am. Nat. 115:748-753.

Ydenberg,R.C. & Dill,L.M.1986. The economics of fleeing from predators. Adv. Study Behav. 16:229-249.

Zach,R.1979. Shell dropping:decision making and optimal foraging in Northwestern crows. Behaviour 68:106-117.

Zwarts,L. & Bloomert,A.1990. Selectivity of whimbrels feeding on fiddler crabs explained by components of specific digestibilities. Ardea 78:193-208.

APPENDIX 10.1: Radio-tracking of Sparrowhawks at Tyninghame

Attempts were made to capture and radio-track sparrowhawks in November and December, winter 2. This was abandoned as no females could be caught, and those birds which were caught provided little useful data, compared to the time invested. The aim was to tag those sparrowhawks which were hunting in the study area. As these birds were fairly successful wader specialists it was probably not surprising that they would not enter the traps.

Double-compartment cage traps were used. A lower compartment contained two house sparrows (Passer domesticus), and the upper compartment had an open top which was released and closed as a raptor attempted to catch the sparrows by landing on a perch below the entrance. Two traps were placed out overnight along woodland rides of the Tyninghame Estate, and left in operation until 1pm the following day. Trapping was not carried out on successive days. In total 16 trapping days were carried out with both traps placed in various areas around the estuary where sparrowhawks were frequently seen hunting.

Two immature males and an adult male sparrowhawk were captured and tagged according to the procedure in Kenward (1978). Tags all weighed less than 4.5g. The sparrowhawks were found to be only casual visitors to the estuary. I had two subsequent visual sightings of one immature within the study site, 14 and 15 days after capture, and radio data from both immatures only for about a day after release. The adult could be only sporadically tracked and all locations were well out of the study area. The adult (with the transmitter on its tail making it distinctive) was reported as hunting around Tyninghame village the following February. The immature sparrowhawks were not seen after mid-December.

Sample sizes of captured birds were too small to determine whether the capture and tagging procedure resulted in the immature birds leaving the estuary area, or whether the observed pattern reflected occasional use of the estuary by male sparrowhawks.

Kenward,R.E.1978. Radio-transmitters tail-mounted on hawks. Ornis. Scand. 9:220-223.

APPENDIX 10.2: Cannon-netting Redshank at Tyninghame

Two successful cannon-nets were carried out during winter 2, capturing 47 redshank. No other species were captured. All redshank were captured unharmed. The first catch was under the supervision of Graham Appleton, on October 7th, and 7 juveniles and 5 adults were captured. The second catch was under the supervision of Ian Bainbridge, on March 3rd, and 9 juveniles and 26 adults were captured.

Catches were both carried out with two approximately 30m nets placed next to each other on the spring, high tide line. The nets fired over flat saltmarsh grass in late afternoon as the tide approached about 5.7m in height. Nets were located at the back of the Heckie's Hole saltmarsh and fired over an area of grass used by up to 250 redshank on spring tides. After capture the redshank were all individually colour-ringed with 6 Darvic rings (according to a scheme issued by the Wader Study Group). Maximum wing chord, tarsus, tarsus and toe, bill, weight, and head and bill were measured using standard methods. All redshank were processed and released within 2 hours of capture.

In March 1992 (over 1 year after capture), 68% of the redshank colour-ringed were still present in the study area.

APPENDIX 10.3: Bird Species Recorded at Tyninghame During the Study

Great Northern Diver
Black-throated Diver
Red-throated Diver
Little Grebe
Gannet
Fulmar
Shag
Comorant
Grey Heron
Whooper Swan
Bewick's Swan
Mute Swan
Pink-footed Goose
Greylag Goose
White-fronted Goose
Canada Goose
Barnacle Goose
Brent Goose
Shelduck
Wigeon
Gadwall
Teal
Mallard
Pintail
Shoveller
Tufted Duck
Scaup
Eider
Long-tailed Duck
Common Scoter
Velvet Scoter
Goldeneye
Red-breasted Merganser
Goosander
Buzzard
Marsh Harrier
Hen Harrier
Sparrowhawk
Kestrel
Merlin
Peregrine
Grey Partridge
Pheasant
Moorhen
Coot
Oystercatcher
Avocet
Ringed Plover
Golden Plover
Grey Plover
Lapwing
Sanderling
Little stint
Knot
Purple sandpiper
Curlew Sandpiper
Dunlin
Ruff
Jack Snipe
Snipe
Woodcock
Black-tailed Godwit
Bar-tailed Godwit
Whimbrel
Curlew
Turnstone
Spotted Redshank
Redshank
Greenshank
Green Sandpiper
Common Sandpiper
Great Skua
Long-tailed Skua
Arctic Skua
Mediterranean Gull
Black-headed Gull
Common Gull
Herring Gull
L. Black-backed Gull
G. Black-backed Gull
Kittiwake
Arctic Tern
Common Tern
Sandwich Tern
Little Tern
Black Tern
Guillemot
Razorbill
Black Guillemot
Little Auk
Rock Dove/Feral Pigeon
Stock Dove
Woodpigeon
Collared Dove
Tawny Owl
Long-eared Owl
Short-eared Owl
Kingfisher
Green Woodpecker
Great Spotted Woodpecker
Skylark
Shore Lark
Swift
Sand Martin
Swallow
House martin
Tree Pipit
Meadow Pipit
Water Pipit
Rock Pipit
Yellow Wagtail
Pied and White Wagtail
Grey Wagtail
Waxwing
Wren
Dipper
Dunnock
Robin
Redstart
Whinchat
Stonechat
Wheatear
Fieldfare
Mistle Thrush
Blackbird
Song Thrush
Redwing
Ring Ouzel
Grasshopper Warbler
Sedge Warbler
Lesser Whitethroat
Whitethroat
Blackcap
Chiffchaff
Willow Warbler
Spotted Flycatcher
Goldcrest
Long-tailed Tit
Coal Tit
Blue Tit
Great Tit
Treecreeper
Jay
Carrion Crow
(Hooded Crow)
Rook
Magpie
Jackdaw
Starling
Tree Sparrow
House Sparrow
Chaffinch
Brambling
Bullfinch
Greenfinch
Goldfinch
Siskin
Redpoll
Linnet
Twite
Crossbill
Lapland Bunting
Snow Bunting
Yellowhammer
Reed Bunting