

Raptor predation on non-breeding shorebirds: some thoughts for the future

D.P. WHITFIELD

Scottish Natural Heritage, 2 Anderson Place, Edinburgh EH6 5NP, UK, e-mail: phil.whitfield@snh.gov.uk

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This brief review highlights the importance of studies of raptor predation on non-breeding shorebirds and considers selected aspects where future work could be directed. Aspects covered include the recording of raptor activity and predation risk, geographical variation in predation risk, the effects of predation on shorebird population dynamics, and the possible role of competition within predator assemblages in affecting shorebird abundance.

INTRODUCTION

Why should shorebird biologists be interested in raptor predation and why is raptor predation of shorebirds a “big issue”? Well, we should all be interested in what influences shorebird abundance, since the conservation of shorebirds is essentially about maintaining or increasing their abundance. And shorebird abundance is most influenced by changes in adult mortality, and raptors are probably one of the major causes of adult shorebird mortality. But there are other reasons why this subject deserves our attention.

Finding enough food to eat and avoiding being eaten have long been recognised as two of the most potent forces of natural selection (e.g. Lack 1954, Krebs & Davies 1978). Reflecting this, there is a vast literature on the ecology and behaviour of obtaining food. But predation is more poorly represented. In part this may be because predators are usually rarer than their prey, and so predation events become rarer as one moves up the “food chain”, making their study more difficult. An elevated position in the food chain was probably also indirectly responsible for causing an even greater scarcity of many raptors in the 1960s and 1970s due to the accumulation of pesticides, primarily through adverse effects on reproduction. What also has not helped is that raptors are often seen as competitors for food or sport by humans, and so are killed. Their naturally low numbers make them vulnerable to such killing and in extreme cases predators have been driven to extinction (e.g. UK Raptor Working Group 2000). Although many raptor populations still suffer from a range of other detrimental factors from electrocution at power poles to habitat loss, and several raptor populations are still well below their potential, at least some species in the northern hemisphere have shown population recoveries in recent decades (e.g. Ferrer & Hiraldo 1991, Ratcliffe 1993, Real & Mañosa 1997, Pedrini & Sergio 2001).

As many raptors have become more common in areas where most researchers live, there are few traits of small birds that are not now thought to be influenced by the effects of predation, and there has been a huge expansion in the research that has been devoted to the subject in the last 10–20 years (e.g. Lima 2002). Much of this research, however, has made assumptions about how predators behave and there is

a danger that such assumptions are incorrect because very few studies actually record the interactions between raptors and their prey in the field. Lima (2002), for example, has pointed out that despite the many studies on the mass changes of small passerines and the assumption of the role of Accipiter hawk attack and evasive take-off speed, this paradigm has not benefited from any study of actual attacks by Accipiters on small passerines. This is probably in large part due to the difficulty in observing Accipiter behaviour in the field: most of the few studies of Accipiter attacks on passerines have been made during the migration of hawks where they are seasonally abundant (e.g. Lindström 1989).

By contrast, starting with the work by Page & Whitacre (1975) there have been several field studies of raptor predation on their non-breeding shorebird prey. The typically open habitats inhabited by shorebirds make it relatively easy to observe interactions with raptors. Therefore research focusing on this issue is well placed to make substantial contributions to knowledge of predator–prey evolution, behaviour and ecology, and to knowledge of those factors that affect shorebird abundance. Given the relative ease in observing raptor–shorebird interactions it will be important to see if results obtained from shorebird prey are applicable to other taxa in other circumstances (e.g. mass-dependent predation: Whitfield *et al.* 1999). Below I consider a few of the many possible areas where such future work could be directed.

RECORDING PREDATOR ACTIVITY AND RISK OF PREDATION

I define predation risk as the probability of being killed by a predator. Therefore predation rate (or mortality rate due to the predator) is the probability of being killed by the predator, or predation risk, over a given time period. Predation rate is therefore an expression of the selective force imposed on a prey by the predator and a measure of predation risk over time. It may be tempting to use sighting rates of raptors, since they are easily measured, as a means of estimating predation “risk” but sighting rates are fraught with potential methodological and interpretational difficulties. Not only are there potential differences in the likelihood of seeing raptors due to observer experience or skill (many raptors are probably



under strong selection to remain undetected by both their prey and persecuting humans), but also according to how records are taken. An observer concentrating on shorebirds will experience a different perspective to an observer concentrating on raptors; the former will tend to experience brief observations when raptors are most active, whereas the latter will experience temporally lengthy observations involving long periods of raptor inactivity (e.g. Cresswell 1996). It is possible to arrive at a measure of predation risk from both methods (Whitfield *et al.* 1988), but "sighting rates" between the two types of observation will not be comparable. It is important, therefore, that observation protocols are comparable across studies or sites.

Even using the same protocol, sighting rates may not be a representative measure of risk, as different shorebird species on the same site clearly differ in their vulnerability to predation (e.g. Whitfield 1985, Cresswell 1995). This is also illustrated by a study of Eurasian Sparrowhawks *Accipiter nisus* and Common Redshanks *Tringa totanus* at two sites in southeast Scotland, one on the south Firth of Forth shore at Scoughall (Whitfield 1985, 1988, 2003a) and a second on the north Firth of Forth shore at Dalgety Bay (D.P. Whitfield unpublished data). Sighting rates of hawks did not differ but Redshank mortality rates due to Sparrowhawk predation were markedly different (e.g. for first winter Redshanks, predation rates per winter were over three times higher at Scoughall in the four winters when both sites were studied). Across years at Scoughall, sighting rate did not correlate with the number of Redshanks killed but attack rates did (sighting rate: Spearman's $r = 0.293$, $P = 0.38$; attack rate: Spearman's $r = 0.704$, $P = 0.02$). This indicates that in the absence of information on mortality due to predation, attack rates and/or attack success rates are probably better measures of predation risk than raptor sighting rates.

For several raptors, we might expect such a finding on theoretical grounds. Predators can make two fundamental responses to differences in prey density: the functional response describes how predation rates of individual predators respond to prey density, whereas the numerical response describes changes in predator density (Holling 1959, Sonerud 1992). In so-called generalist predators such as the Sparrowhawk that take a large number of different prey species, functional responses where hawks make frequency-dependent switches between prey species appear to be more prevalent than numerical responses (e.g. Redpath & Thirgood 1999). We might expect therefore that the number of Sparrowhawks that are seen in an area is not necessarily a good reflection of a prey's risk of predation. This expectation probably also holds for those generalist falcon species that are likely to be the most frequent predators of adult shorebirds globally.

GEOGRAPHICAL VARIATION IN PREDATION RISK

Variation in predation risk may reflect differences in a predatory response to prey density *per se*, but other factors such as prey body size and the propensity of prey to feed in geographical areas where raptor attack may be favoured can also be influential. Geographical variation in predation risk is a well-documented feature experienced by a huge range of taxa, including shorebirds, although typically it refers to a small scale covering metres (e.g. Cresswell 1994a, Dierschke 1998, Whitfield 2003b). Whitfield *et al.* (1988) suggested that

ably occur across a range of scales and landscape or "between-site" differences have subsequently been described (e.g. Ydenberg *et al.* 2002). The possibility that raptor predation may influence shorebird choice of feeding grounds at a still larger scale, such that a migration route or national patterns of abundance of wintering birds is affected, has not been investigated (Butler *et al.*, this volume). This deserves to be looked at, especially as a recent study has suggested that large scale processes need to be considered in wintering shorebird populations (Gill *et al.* 2001).

The interplay between avoiding raptor predation and failing to obtain sufficient food (e.g. to avoid starvation, to avoid a shortfall in migratory fuel supplies) should not be viewed in isolation. It seems likely that it is the interplay between these two factors that influences mortality of small shorebirds and affects many of the decisions that are made by individuals when not breeding. So if we want to understand why shorebirds are more common in some areas than others we should not just consider geographical variation in food supplies (see also Butler *et al.*, this volume). Wintering shorebirds should prefer to feed in low predation risk areas, even if these areas are low in food, so long as there is sufficient food to avoid starvation. When there is not sufficient food, through competition or because individual requirements are raised, for example, then areas with a high predation risk will be increasingly used, especially if there is a high food gain (e.g. Cresswell 1994a, Dierschke 1998, Whitfield 2003b). This has important consequences for population dynamics, to which I will return later.

But what makes an area risky with regard to raptor predation? Surprise is probably an important component of success in raptor attacks (Cresswell 1996), and so any area where the chance of approaching prey unseen is increased will be favoured by the predator. In part, how surprise is gained will depend on which species of raptor is involved, and at least for some raptor species this will depend on site topography and habitat. Accipiter hawks often make low rapid attack flights from the cover of terrestrial or intertidal vegetation or "dead ground" and so prey feeding close to cover appear to be more at risk of predation (contrast this with what is considered to be risky for small passerines) (e.g. Whitfield 1985, 2003b, Cresswell 1994a, 1996). Merlins *Falco columbarius* and Peregrines *F. peregrinus* can also rely on similar features for surprise, making low rapid flights using the cover of saltmarsh, for example (Page & Whitacre 1975, Dekker 1988). Comparative morphology would suggest that sustained pursuit flights of prey should be more likely in falcons than in the slower but more manoeuvrable Accipiter hawks (e.g. Brown & Amadon 1969) and field observations confirm this (Cresswell 1996). Other aspects of hunting behaviour differ between raptors, such as the propensity to take aerial prey, a feature most often associated with the Peregrine. We might expect therefore that geographical variation in predation risk may depend on the raptor involved, so that, for example, an area that is safe from Accipiter hawk attack may not be safe from Peregrine attack. If we can understand those features associated with differential predation risk sufficiently well so that predation risk can be predicted and mapped, then recording individual shorebirds' use of areas of different risk may give readily measured surrogates of mortality. Such surrogates may then have a potential use in recent models that predict population consequences from simple measures of individual behaviour (Stillman *et al.* 2000).



THE EFFECTS OF RAPTOR PREDATION ON SHORE-BIRD POPULATION DYNAMICS

Increasingly it is realised that predators can have an impact on the population dynamics of their prey and that predation mortality can be additive and not just compensatory for other sources of death by removal of a "doomed surplus". For small shorebirds, as described earlier, if obtaining enough food to survive (or migrate) and avoiding predation are linked but antagonistic processes then, whenever a shortage in food supplies occurs, mortality through predation should increase. If increasing competition for food occurs through increased shorebird density, then density-dependent mortality through raptor predation can occur. Density-dependent mortality is an important process since it means that population abundance is regulated. Hence, it also has major implications for understanding how habitat loss can affect shorebird numbers (e.g. Goss-Custard *et al.* 1995a,b, Goss-Custard, this volume).

At Scoughall in southeast Scotland, Sparrowhawks regulate the numbers of Redshank and Dunlin *Calidris alpina* through density-dependent predation (Whitfield 2003a,c). Sparrowhawk predation also causes density-dependent mortality in Turnstone *Arenaria interpres* at this rocky shore site (D.P. Whitfield unpublished) and in Redshank at a neighbouring estuarine site (D.P. Whitfield & W. Cresswell unpublished). The mechanism, at least for Redshank and Turnstone, is that as competition for use of predation-safe feeding areas increases, more use is made of predation-risky (but food rich) areas. What is also interesting is that the three species have markedly different social behaviour mediating the competitive interactions affecting predation risk: the Redshank has a territorial system with non-territorial floaters/flocks and Turnstone flocks have stable membership with a rigid dominance hierarchy which appear to be absent from Dunlin flocks. So it is likely that both exploitative and interference competition can lead to density-dependent mortality through raptor predation (Whitfield 2003c).

At some sites, shorebirds may be relatively invulnerable to attack by a particular raptor species at any density (Whitfield *et al.* 1988), and density-dependence may be mediated at a larger geographic scale. So we should not expect density-dependent mortality to be evident at every study site. The scale at which density-dependence may be operating should reflect the scale at which gradients of predation risk are greatest (Whitfield 2003a) or, in other words, the scale at which the "buffer effect" (Brown 1969) operates. The "buffer effect" occurs when areas differ in their quality so that areas of poor quality (in this example, high predation risk) experience large changes in numbers but good quality areas (low predation risk) experience small changes in numbers. Therefore the poor areas "buffer" the good ones. In this example the demographic cost of using the poor quality area (increased mortality due to raptor predation) leads to density-dependent changes in mortality, and the buffer effect operates over a scale of metres or hundreds of metres at the study sites in southeast Scotland. Differences in Sparrowhawk predation between sites (Whitfield *et al.* 1988) and the ranging behaviour of wintering Peregrines (McGrady *et al.* 2002) may indicate that the buffer effect may also operate at the landscape scale (Whitfield 2003a). Gill *et al.* (2001) have shown that it can probably operate at an even larger scale.

DIFFERENT PREDATORS, DIFFERENT PREY BEHAVIOUR AND INTERACTIONS WITHIN PREDATOR GUILDS

Differences between raptors in the way they hunt have already been touched on. Probably because of this variation in attack tactics, shorebirds can also react differently when attacked by different species or by the same raptor species under different circumstances (e.g. Michaelsen & Byrkjedal 2002). At the southeast Scotland sites, shorebirds react to Sparrowhawk attack by flying away at speed, but the response to Peregrine attack is often to crouch to the ground (Cresswell 1993, D.P. Whitfield unpublished data). Making a mistake in response type can be costly (Cresswell 1993), and so it should be important for a shorebird to be able to make a rapid identification of an attacking raptor. Cresswell (1993) has suggested that having the time for identification is a critical aspect of an escape response. The intriguing notion that follows from this is whether a raptor species may benefit from the presence of another raptor species with a different attack method, if this increases the chance that prey may make the wrong type of response.

On the other hand, if other predators are exploiting the same prey, any benefit of inappropriate escape response may be offset by the increased sensitivity of the prey to any attack, as prey may be more difficult to catch by any predator after they have been attacked (e.g. Whitfield 1988, Cresswell 1994b). Like any other foragers, raptors will be sensitive to prey availability and this will decline with an increased rate of attack as surprise will be increasingly difficult to attain. Such potential exploitative competition has been documented within raptor species (e.g. Ferrer 1993), but it is less clear if it is important interspecifically. Interference competition has also been documented between breeding raptor species, where one species may actively attempt to exclude a second from feeding areas (Fernández & Insausti 1990). This may be unusual as other interspecific processes may be more prevalent.

More extreme interspecific interference between raptor species may also be worth examination in the context of how this may affect predation on shorebirds. The positive effect on the numbers of a prey species through the influence of a larger predator on a smaller predator (so-called mesopredator release) is being increasingly documented in carnivores (Caro & Stoner 2003). A recent study has found that breeding communities of raptors may be affected by the presence of the largest species and that this may have an effect on numbers of some prey species (Fielding *et al.* in press). Direct predation on a smaller species by a larger species is often cited as an influence on the abundance of the smaller predator. A predator may also be adversely affected by a second if kleptoparasitism (stealing the kills of another) is common enough to lower prey consumption rates below requirements. In extreme cases the "subordinate species" may actively avoid areas used by the "dominant species".

Carion Crows *Corvus corone* can be frequent kleptoparasites of the kills of Sparrowhawks (Cresswell & Whitfield 1994). In theory, if crows are sufficiently common, kleptoparasitism may render it unprofitable for Sparrowhawks to catch prey. This may explain why hawk predation of Redshanks at Dalgety Bay was much lower than at Scoughall (see earlier). The low predation of Redshanks at Dalgety



Bay was surprising because Redshanks frequently fed close to cover and cover was extensive: superficially ideal conditions for successful Sparrowhawk attacks. Although Sparrowhawks were seen with equal frequency in both areas, mobbing of hawks by crows was much more common at Dalgety Bay (Scoughall, 0% of 287 hawk sightings; Dalgety Bay, 41% of 64 hawk sightings) where there was a much higher density of crows (crow density was almost 25 times higher at Dalgety Bay than at Scoughall across three winters when counts were made at both sites). Site differences in crow density may be explicable by the relatively high abundance of mussels *Mytilus edulis* at Dalgety Bay, which the crows fed on themselves or stole from Eurasian Oystercatchers *Haematopus ostralegus*. It is also probable that Crow numbers at Scoughall were kept low because they were killed by a gamekeeper.

The scope for further studies of raptor predation on shorebirds is enormous. This brief review has only skimmed the surface of what is potentially a very large subject. Many other aspects, such as the effect of predation on shorebird mass changes or shorebirds as sources of pollutants in raptors, have not been covered. This is an important field of study, so it should benefit from more research in future.

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