

Wader migration on the changing predator landscape

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We suggest that the spatial and temporal patterns of danger arising from the annual migration of birds of prey has important implications for patterns of habitat use and for the evolution of wader annual movement patterns and annual cycles. We discuss how waders might respond to danger by their choice of migration routes, the time of year they choose to migrate, the quantity of fuel they carry, the length of time they spend at staging and stop over sites, the duration of the breeding season and parental care, and the timing and location of feather moult.

INTRODUCTION

The field of ecology gained stature as a professional discipline in the 20th century. It expanded rapidly after WWII, but it did so in a predator vacuum. Persecution and pesticide poisoning had largely erased raptors from the landscape in North America and Europe – and from the consciousness of most ecologists. But as raptor populations began to recover after DDT was banned and other conservation measures were enacted (Bildstein 1998), ecologists began to understand that it is not necessary that predators kill prey to exert an influence (Lima 1986, 1993, Brown *et al.* 1999). The “risk” (or “danger”, as we prefer to say now) posed by predators is by itself a powerful force. When danger lurks, prey alter their behaviour to gain safety, and these behavioural changes directly affect population dynamics, and cascade through entire ecological communities by indirect effects on other species.

The significance of predation for the evolution and ecology of avian migration has also gone largely unseen. Most work has focussed on food and foraging, the ecological and physiological demands of long flights, and how these factors interact to regulate migration (Drent & Piersma 1990, Ens *et al.* 1990, 1994, Piersma 1994, Alerstam & Hedenström 1998). Writings by Lindström (1989, 1990), Alerstam & Lindström (1990), and Walter (1979) were among the first to discuss the potential importance of predators for migrants.

In this paper we suggest the role that predators and predation danger may play in the evolutionary ecology of wader migration, and describe how wader populations might respond to the changing risk posed by the post-DDT era recovery of raptor populations. We do so primarily with reference to our own studies of the Western Sandpiper *Calidris mauri*, a species that has been studied at stopover sites in the Strait of Georgia, in southwestern British Columbia, since 1978. Like many other small waders, these small (25 g) birds perform an annual return migration between Arctic breeding areas and tropical or subtropical nonbreeding areas, which in the case of the Western Sandpiper may be 12,000 km dis-

tant. During this migration, Western Sandpipers are susceptible to avian predators.

THE PREDATOR LANDSCAPE

Western Sandpipers live in a landscape filled with danger. On breeding areas, foxes and jaegers consume sandpiper eggs, chicks and adults. In the course of migrating between breeding and nonbreeding locales, sandpipers are heavily hunted by raptors while at stopover sites (Ydenberg *et al.* 2002). Wintering sites are also dangerous (Buchanan *et al.* 1988, Dekker 1995, 1998). Page & Whitacre (1975) estimated that a single Merlin *Falco columbarius* captured about 6.6% of the total wintering population of sandpipers at Bolinas Lagoon in California, including 7.5% of the Western Sandpipers. The danger level varies in both time and space, creating what we refer to as its “predator landscape”, with valleys of relative safety when and where falcons are sparse, and high treacherous peaks that must be avoided. The work we present here has been guided by the idea that Western Sandpiper migration across the predator landscape has been adjusted by natural selection, with mitigation of danger being a prime fitness consideration.

A variety of important ecological factors combine to create the major features of the predator landscape. The first of these is that many predators are themselves migratory, which produces strong fluctuations in the number of predators at any locality in the course of each annual cycle (Lank *et al.* 2003). In the Strait of Georgia where we work, two predator “waves” pass through the Strait each year. In the spring, Peregrine *F. peregrinus* numbers reach a peak in late April and early May as they move toward breeding sites in the vast tundra and boreal regions of western North America. In late summer and early autumn, post-breeding adult Peregrines and the young-of-the-year from the north arrive as a raptor “tsunami” that surges through the Strait in August and September, and builds southward toward the winter quarters in Mexico, and Central and South America.

A second major feature of the predator landscape in North

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America is a strong east–west gradient in the timing of this southward raptor tsunami. The raptor tsunami east of the Rockies occurs 4–6 weeks later than in the west. Different raptor species vary in the timing of their southward migrations. For example, Peregrine migration peaks about a week ahead of Merlin migration (e.g. Heintzelman 1975). Feeding locations with proximate cover, such as small mudflats or along dykes where falcons can spring surprise attacks are very dangerous places for waders (Cresswell 1994, Ydenberg *et al.* 2002). Thus, a third major feature is that the level of danger varies locally due to the nature of stopover sites.

WADERS ON THE PREDATOR LANDSCAPE

We believe that several features of wader biology and behaviour are in response to the game they play out with predators on the predator landscape. One of those features is choice of migration routes. Some Western Sandpipers migrate south-eastward, rather than due south across the North American continent (Butler *et al.* 1996). One possible explanation for this choice of route is that sandpipers making a cross continent flight gain time on the later raptor tsunami on the east coast. On the east coast, both raptors and many of the abundant species of shorebirds arrive 4–6 weeks later than on the west coast, and prepare for their transoceanic flight at a time when few raptors are present (Lank *et al.* 2003). The 4,000 km oceanic flight from the Canadian Maritime provinces and New England states to northern South America by Semipalmated Sandpipers *C. pusilla* (Hicklin 1987) might have arisen as a tactic to avoid the raptor tsunami from tracking them south along the Atlantic seaboard.

Eloping falcons depends on quick reflexes, fast take-off, and high manoeuvrability. While large fat reserves improve migratory range, they also impair escape ability (Alerstam & Lindström 1990; Houston 1998; see van der Veen 1999, van der Veen & Lindström 2000), as shown for passerines (Kullberg 1998, Kullberg *et al.* 1996, Lind *et al.* 1999) and Western Sandpipers (Burns & Ydenberg 2002). The danger is enhanced if waders have to linger at dangerous staging sites to load fuel reserves for long flights.

The migrations of sandpipers have many mysterious features. For example, why do Western Sandpipers spend so little time rearing their young, after having flown all the way to the Arctic from the tropics? Females desert their broods only a few days after they hatch, and even males terminate parental care before the young can fly. Adult Western Sandpipers begin to depart the breeding areas in mid-summer, and most adults have passed the Strait of Georgia by the third week of July.

The predator landscape suggests a hypothesis. In late July the danger in the Strait of Georgia begins to increase sharply as migratory Peregrines begin to arrive. From late May to the end of June, there is a period of relative safety through which adult Western Sandpipers can pass through all the way to the tropics and moult their wing feathers in relative safety (Lank *et al.* 2003). Extending the duration of parental care would necessarily delay departure and expose parents to greater danger on the entire southward route and during the moult. The increasing danger of later migration explains why adult Western Sandpipers leave Alaska while there is 24h of light and an abundance of food, and puts the parental care decision firmly in a life history context (Webb *et al.* 2002). It also provides a ready hypothesis for Gratto-Trevor's (1991) observation that the duration of post-hatch care by both male

and female Semipalmated Sandpipers declines in later-nesting birds, which also occurs in Western Sandpipers (Neville 2002, Rauthrauff 2002). We note that predation danger is not on the current list of possible costs to parental care in waders compiled by Reynolds & Székely (1997).

What about juveniles? Anyone who has watched wader migration knows that juvenile migrants behave differently from adults; a fact the literature generally attributes to inexperience or naiveté. On the predator landscape, however, the salient fact is not that these individuals make the trip without the benefit of parental experience, but that the calidridines at least, undertake the journey a month later than do their parents (Holmes 1971, 1972, Sandercock 1997). Consequently, their exposure to predators is much greater overall. We suspect that the explanation for the apparent stupidity of juvenile waders lies not with their lack of experience, but in the different ecological situation they face by virtue of their migration schedule. For example, food availability and the risk of predation are likely to differ between the juvenile and adult migrations (Lank *et al.* 2003).

The timing of falcon migrations results in adult Western Sandpipers being relatively safer on the southward than on the northward journey. Consequently, a number of behavioural differences between north- and southbound adults can be explained in the context of these migrations. Falcons migrate northward with Western Sandpipers and trail them on the southward migration. For example, spring flocks are much larger, and confined mostly to large mudflats, whereas southbound birds occur in small, widely dispersed flocks in many places and habitats seldom used in spring. Like many other waders, Western Sandpipers follow different routes when north and southbound. Southbound migrants appear to make a direct flight to the Strait of Georgia. But northbound migrants make several stops along the coast, even though calculations show that a direct flight would save time (Lank *et al.* 2003). The difference between these two migration strategies lies in the risk of spending time getting fat in an already dangerous place. The 2,852 km trans-Gulf flight in spring would require a large fuel reserve to be built up in the Strait, just at the time that danger from falcons is high. On the southbound leg of the flight, falcons and other raptors are busy on their breeding grounds and relatively sparse along the coastal sites used by sandpipers in western Alaska where fuel is accumulated prior to the southbound jump to southern British Columbia. We suspect that the increased vulnerability of heavily wingloaded migrants may be a key factor in selecting for “hop, skip or jump” routing (Piersma 1987). A similar explanation may apply to the “coastal effect”, whereby southbound immature passerines follow a route along the Gulf of Mexico coastline, rather than making a trans-Gulf jump as adult birds do. Existing hypotheses invoke inferior navigation or competitive abilities of young birds (Rappole 1995).

Timing of wing moult strongly affects vulnerability to predation. Moulting birds must contend with increased wing loading which we assert translates into increased danger, and which in turn affects the evolution of moult and migration timing. Adult Western Sandpipers make a quick dash for the winter quarters, arriving in Panama about one month ahead of falcons (B. Watts, pers. comm.). About 30 days is required to complete wing moult. Individuals that choose to migrate across the North American continent, gain enough time to complete a wing moult on the Atlantic seaboard before the arrival of large numbers of falcons (Bruce Peterjohn, pers.



comm.). The race of Dunlins *C. alpina pacifica* that winters along the northwest coast of North America displays an alternative strategy. These birds undergo a complete wing moult in the relative safety of the breeding grounds, remaining there for two months after the departure of Western Sandpipers (O'Hara *et al.* 2002). Dunlins arrive on the winter quarters fully feathered (Warnock & Gill 1996) – and after the peak of the raptor tsunami. The risk of predation on the south-bound leg of migration might also limit how far north a species breeds. More northerly breeding birds might have insufficient time to migrate, breed and moult ahead of the raptor tsunami.

So far we have considered features of wader migration that we suppose have been selected for in evolutionary time – but what about behavioural responses? Could waders be showing behavioural adjustments to their migratory patterns in response to increasing predator populations? We believe that many such behavioural adjustments are being made under our very noses. To mitigate predation danger, migrants could lower the amount of fuel reserves carried, and shorten stopover duration. In addition, they may avoid sites or habitat types that are especially dangerous, even if those sites are richer in food (Ydenberg *et al.* 2001). Site avoidance tactics are condition-dependent, since individuals with smaller fat reserves, and thus lower vulnerability, are better able to take advantage of the feeding opportunities at more dangerous sites. Other possible responses to a variable predator landscape are shifts in migration routes and timing.

Our data show that Western Sandpipers have been shortening their stopovers as well as reducing their migratory mass for the past decade at one of our main study sites (Butler *et al.*, unpubl. data). Moreover, the data strongly indicate that these changes are due specifically to the increase in danger posed by increasing falcon presence. Owing to the reduced stopover duration, an observer censusing the birds would record a decline in the numbers of shorebirds counted at a site. Indeed, this is what our censuses show. However, our data reveal that the decade-long 18% rate of decline of Western Sandpipers counted at a highly risky site on Sidney Island can be entirely accounted for by the shorter stay that migrants make now, compared to a decade ago, and that the actual number of birds migrating has probably changed little!

If this effect is widespread, it has tremendous implications for the collection and interpretation of data on shorebird population trends. North American wader species, especially long-distance migrants, declined in abundance in censuses during the 1980s and 1990s (Morrison *et al.* 1994, 2001). Most population estimates of shorebirds and other neotropical migrants use indices (e.g., mean, sum or maximum counts) based on repeated censuses made at one or more stopover sites, raising the possibility that shortened lengths-of-stay and other danger-mitigation tactics such as site avoidance are contributing to the reported declines. As raptor population recovery is taking place on a continental scale, this mechanism has the potential to be general. Protocols being developed by conservation agencies worldwide to monitor populations of migrant birds need to take this possibility into account.

Of course, a change in stopover duration at one site cannot be considered in isolation, because it means that the arrival time and the migratory mass at the next site are both affected. Thinking about the suite of decision factors throughout the entire annual cycle is essential, because changes at one time or place affect all later stages. Optimisation mod-

elling provides an opportunity to explore these interactions (Clark & Butler 1999).

Recently, Ibanez *et al.* (2001) reported that the greater nocturnal bat *Nyctalus lasiopterus* specialized at catching migrant songbirds on the wing and at night. This wholly unsuspected natural history discovery epitomizes the current state of our understanding about the importance of predators for the evolution of avian migration. Even for tiny songbirds migrating at night, migration is a danger-filled journey across the predator landscape.

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