

Western sandpipers have altered migration tactics as peregrine falcon populations have recovered

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The presence of top predators can affect prey behaviour, morphology and life history, and thereby can produce indirect population consequences greater and further reaching than direct depredation would have alone. Raptor species in the Americas are recovering since restrictions on the use of dichlorodiphenyltrichloroethane (DDT) and the implementation of conservation measures, in effect constituting a hemisphere-wide predator-reintroduction experiment, and profound effects on populations of their prey are to be expected. Here, we document changes in the behaviour of western sandpipers (*Calidris mauri*) at migratory stopover sites over two decades. Since 1985, migratory body mass and stopover durations of western sandpipers have fallen steadily at some stopovers in the Strait of Georgia, British Columbia. Comparisons between years, sites and seasons strongly implicate increasing danger from the recovery of peregrine falcons (*Falco peregrinus*) as a causal factor. A decade-long ongoing steep decline in sandpiper numbers censused on our study site is explained entirely by the shortening stopover duration, rather than fewer individuals using the site. Such behavioural changes are probably general among migratory shorebird species, and may be contributing to the widespread census declines reported in North America.

Keywords: predation danger; sandpiper migration tactics; stopovers; falcon population recovery; migration

1. INTRODUCTION

Safety from predators is an important selective factor in the evolutionary ecology of avian migration (Alerstam & Lindström 1990). Raptors, particularly falcons, are dangerous for shorebirds (Page & Whitacre 1975; Kus *et al.* 1984; Whitfield 1985; Bijlsma 1990; Cresswell & Whitfield 1994; Cresswell 1995). Merlins (*Falco columbarius*) and peregrines (*F. peregrinus*) rely on stealth and speed to capture sandpipers (Dekker 1988, 1998), and hence sandpipers are especially vulnerable at migratory stopover sites, where flight performance attributes important in predator escape and evasion, such as take-off, acceleration and manoeuvrability, are diminished by the large fuel reserves necessary for long migratory flights (Kullberg *et al.* 1996; Lind *et al.* 1999). Burns & Ydenberg (2002) showed that more heavily wing-loaded individual western sandpipers (*Calidris mauri*) and least sandpipers (*C. minutilla*) were slower on take-off. The best explanatory variable was wing loading, suggesting that the escape performance of individual birds falls they increase their fuel reserves.

In North America and Europe, populations of predatory birds were reduced greatly in abundance over the past century by persecution and especially by the widespread agricultural use of dichlorodiphenyltrichloroethane (DDT) beginning after World War II (Newton 1979). Some, such as the peregrine, were even threatened with

extinction. The restriction on DDT use in 1973 and other conservation measures spurred a recovery of peregrines beginning in the 1980s (Cade *et al.* 1988), and it was removed from the endangered species list in the United States in 1999.

The ongoing recovery of raptor populations provides an excellent opportunity to investigate the effects of predation danger on the behaviour of prey animals. Previously, Gosler *et al.* (1995) documented decreases in overwintering body mass of great tits, *Parus major*, as the sparrowhawk, *Accipiter nisus*, returned to the landscapes of Great Britain. Similarly, Piersma *et al.* (2003) have documented changes in the mid-winter peak mass of golden plovers (*Pluvialis apricaria*) wintering in The Netherlands associated with the recovery of peregrine and goshawk (*Accipiter gentilis*) numbers. In both cases, the body mass changes were interpreted as resulting from behavioural tactics of individual birds made to mitigate the danger posed by these predators.

The recovery of raptor populations has undoubtedly caused an increase in the level of danger experienced by migrants, and we might expect concomitant changes in a variety of migratory tactics. Individuals are predicted to reduce their vulnerability by lowering the amount of fuel reserves carried, to shorten stopover duration to reduce their exposure to predators, and potentially to shift from longer-distance to shorter-distance flights between stopover sites (Alerstam & Lindström 1990; Fransson & Weber 1997; Houston 1998). Sandpipers on stopover should avoid sites or habitat types that are especially

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dangerous (Alerstam & Lindström 1990; Lindström 1990), even if those sites are richer in food (Ydenberg *et al.* 2002). In this paper, we test some of these predictions about danger-mitigating changes in migratory behaviour with data on western sandpipers collected over two decades at stopover sites in the Strait of Georgia, southwestern British Columbia.

2. METHODS

We have studied migrant western sandpipers in the Strait of Georgia in southwestern British Columbia since 1978. In the spring, these birds stop over while northbound to Alaskan and Siberian breeding areas. After breeding, adult sandpipers depart the Arctic and make a direct flight to the Strait of Georgia, where they again stop *en route* to southern temperate and tropical non-breeding areas. Juveniles (young-of-the-year) pass through our study areas in August, about one month later than adults. Dates for the three migration periods used in analyses below are: (i) spring northwards 15 April–20 May; (ii) adult southwards 24 June–5 August; and (iii) juvenile southwards 1 August–15 September. The dates for (ii) and (iii) enclose 98% of adult and 95% of juvenile western sandpiper passage, respectively, based on 997 adults and 1752 juveniles aged by plumage coloration.

Unlike the staging periods of several weeks recorded in the literature for some migrating shorebirds (see, for example, Gudmundsson *et al.* 1991), the length of stay (LOS) of each individual western sandpiper in the Strait of Georgia is brief. Consequently, we do not observe large seasonal changes in mean body mass, as is observed when an entire cohort of birds stages for several weeks to put on fuel. Instead the body masses recorded from day to day cluster around a well-defined mean, and birds transit our study areas continuously during each of the above periods, with arrivals and departures taking place on most days.

We collected data at several locations in the Strait of Georgia (see map in Ydenberg *et al.* 2002). Two large tidal flats (Boundary Bay and Robert's Bank; both more than 5000 ha) located 10 km apart on the delta of the Fraser River are known collectively as the 'Fraser estuary' stopover site. A smaller (*ca.* 100 ha) stopover site is located on Sidney Island in the middle of the Strait, *ca.* 40 km distant. Sandpipers were captured in mist-nests during both northward and southward migrations on the Fraser estuary site, but at Sidney Island during southward migration only, as small sites like this are little used during the northward migration (O'Reilly & Wingfield 1995). Captured western sandpipers ($n = 13\,682$) were weighed, measured and banded following standard procedures (Ydenberg *et al.* 2002).

Peregrine abundance was indexed by the number of peregrines sighted during standardized near-daily surveys made beginning in 1986 at the George C. Reifel Migratory Bird Sanctuary, located on the Fraser estuary. The index was derived by averaging the daily number of sightings during each migratory period in each year. Statistical comparisons of falcon indexes and sandpiper morphometrics were made using type III sums-of-squares comparisons in general linear models. The data presented here were gathered between 1978 and 2001, which frames the recovery period of peregrines (see below).

Stopover or LOS times of western sandpipers were estimated on Sidney Island during southward migration, 1992–2001. Mist-netted birds ($n = 282$ adults and 1021 juveniles) received a unique combination of colour bands, and the mudflat was

searched by telescope for marked individuals on most days. Resighting and survey effort data were used to estimate LOS using Cormack–Jolly–Seber mark–recapture methodology (Lebreton *et al.* 1992). (The large size of the Fraser estuary stopover sites makes resighting difficult, making this methodology for estimating LOS impractical. Our LOS estimates are restricted to Sidney Island.) We constructed a 63 day (3 July–3 September) encounter history (White & Burnham 1999) for each colour-banded bird. The probability of resighting was set to zero for non-surveyed days (on average, 66% of days in each year were surveyed; range 37–81%; no July surveys for adults in 1994 or 2001), and was set to unity on 3 September in each year to reflect the observation that no western sandpipers ever resided at Sidney Island beyond that date. The probability that a newly banded bird remained local to the banding site for one day was calculated, and used to estimate mean residence time ($-1/\ln[\text{daily local residence}]$) at that site, under the assumption that true survival is 100% over the short residency period. We generated many models to explain variation in the LOS measures, which included all possible combinations of year, age class and various seasonal effects, and compared their performance using Akaike's Information Criterion (AIC_c). The model presented here was chosen based on its highest rank (lowest AIC_c) in a formal model selection protocol (Burnham & Anderson 1998).

3. PREDICTIONS

Our general hypothesis is that western sandpiper migratory tactics, in this paper those that affect body mass and LOS at stopover sites, are profoundly affected by the danger posed by peregrines. We assert that the increase in falcon numbers since the early 1980s (see below) has created a steady increase in the danger experienced by migrating western sandpipers.

Peregrine occurrence in our study area shows a marked annual cycle (see fig. 3 in Lank *et al.* (2002)), being relatively high during the northward migration period of western sandpipers owing to the movement of falcons northwards to their own breeding areas in the northern regions of the continent. However, few peregrines breed in the Strait of Georgia region, and after their northward passage peregrines are generally absent until late in July, during which time most adult sandpipers migrate southward. Peregrine abundance rises steeply from late July until September, as they disperse from their breeding areas to coastal wintering sites, and they become increasingly common as the southward migration period of sandpipers progresses.

Stopover sites in the Strait of Georgia also vary in the level of 'danger' they pose for migrating western sandpipers, defined in this context by Lank & Ydenberg (2003). Danger is set by inherent attributes of the ecological situation that affect the potential attack rate, such as the amount of cover and abundance of predators. Peregrines can be observed hunting sandpipers on all the stopover sites that we studied, and during migration periods are sighted at rates of $0.1\text{--}0.4\text{ h}^{-1}$ (R. C. Ydenberg, unpublished data). However, the Sidney Island stopover is more dangerous (*sensu* Lank & Ydenberg 2003) than the Fraser estuary sites, because its small size exposes sandpipers to surprise attacks from cover by raptors, which are much more effective than are attacks made in

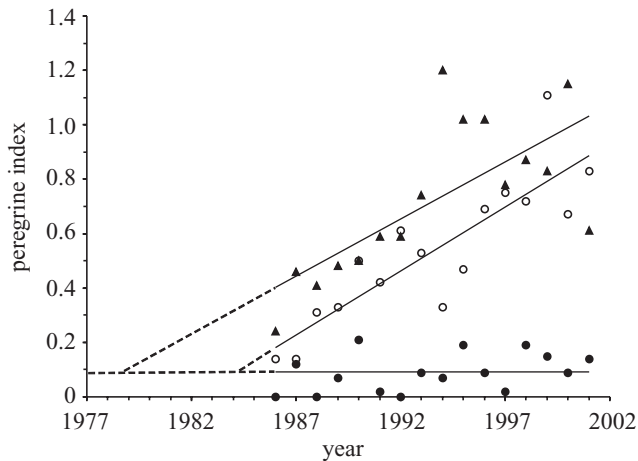


Figure 1. Peregrine abundance index 1986–2001, during the northbound (spring, open circles), adult southbound (July, filled circles) and juvenile southbound (August, filled triangles) migration periods of western sandpipers through the Strait of Georgia. Dashed lines project peregrine abundance backwards to suggest that recovery began between 1979 (August) and 1984 (spring).

the open (Cresswell 1996; Dekker & Ydenberg 2004). By contrast, sandpipers at the large Fraser estuary sites can spend almost all of their feeding time far from cover and hence are safer than at Sidney Island (Ydenberg *et al.* 2002).

We test predictions of danger mitigation hypotheses by making comparisons across years, among stopover sites, and between migratory periods within each year. We examine historical trends in stopover behaviour of western sandpipers on our two study sites, in general predicting that body mass and LOS have fallen as peregrine populations have recovered and made migration more dangerous. Specifically we: (i) compare the Fraser estuary and Sidney Island sites during the southward migration, predicting a stronger decrease in mass over years at the more dangerous site (Sidney Island); (ii) compare the body masses of adults on the Fraser estuary between northward and southward migrations, predicting a stronger decline in body mass on the northward migration when it is more dangerous; and (iii) examine the historical trend in LOS estimates at Sidney Island, where we have made annual estimates between 1992 and 2001, predicting shorter stays in more recent years as the danger has increased.

Reducing the LOS in response to predation danger makes sense only if other stopover sites offer lower danger. For western sandpipers at Sidney Island, the nearby (*ca.* 40 km) Fraser estuary site is less dangerous, and we suspect that many individuals move there after a few days' feeding at Sidney Island (Ydenberg *et al.* 2002). Alternatively, because peregrine migration moves southwards at *ca.* 172 km d⁻¹ (see fig. 2 in Lank *et al.* (2002)), western sandpipers can gain safety by moving ahead of the danger zone with several hours' southward flight.

4. RESULTS

We consider first, all the data pertaining to population recovery of peregrines. The peregrine abundance index in the Strait of Georgia increases significantly over years (figure 1), rising at nearly identical rates during the

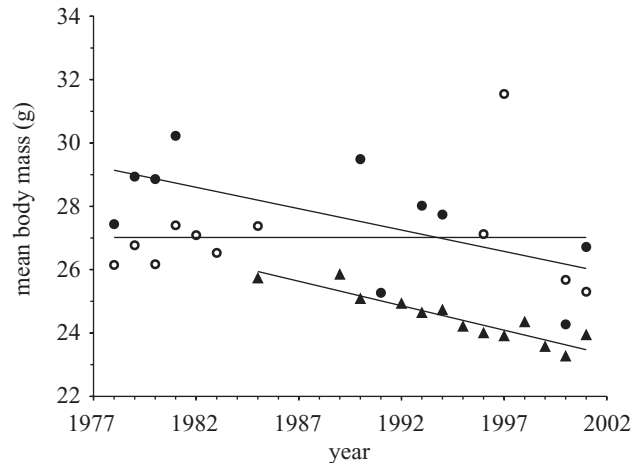


Figure 2. Annual mean body masses of northbound adult sandpipers on the Fraser estuary (filled circles; $n = 1846$ in 10 years since 1978); southbound migrants on the Fraser estuary (open circles; $n = 10\ 111$ in 11 years since 1978); and southbound migrants at Sidney Island (filled triangles; $n = 1725$ in 13 years since 1985). The annual rate of decline in body mass does not differ from zero for southbound migrants on the Fraser estuary ($p = 0.71$), but falls at a rate of 0.154 g yr⁻¹ at Sidney Island ($p < 0.0001$) and at a rate of 0.135 g yr⁻¹ ($p = 0.052$) for northbound migrants on the Fraser estuary. For clarity, 95% confidence intervals (CI) are not shown; they range from ± 0.16 g to ± 0.84 g, with an overall average value of ± 0.45 g.

northward ($r^2 = 0.75$, $p < 0.0001$) and juvenile southward ($r^2 = 0.51$, $p < 0.002$) sandpiper migration periods. The rates of increase do not differ between these periods (pairwise linear contrasts: $p = 0.69$; common slope is 0.045). No increase in the peregrine index is evident during the period that adult sandpipers migrate southwards, when peregrines are scarce in the Strait of Georgia ($r^2 = 0.17$, n.s.; rates of increase during the other two periods are significantly greater, $p < 0.01$). These comparisons confirm that, for adult sandpipers, exposure to peregrines when northbound has become progressively greater relative to southward migration since 1986, when our measurements began. The fact that the peregrine index for the northward and juvenile southward migration periods falls to near zero in the late 1970s or early 1980s (see figure 1) suggests that our observations begin near the onset of peregrine recovery. Historical data on the intensity of peregrine migratory passage in western North America (Hoffman & Smith 2003) and on the number and occupancy of peregrine aeries in Canada (Carrière *et al.* 2003; Rowell *et al.* 2003) support this assertion.

We next consider sandpiper body mass. Our first prediction is that western sandpiper body mass should show a stronger interannual decrease at dangerous (Sidney Island) than at safer stopover sites (Fraser estuary). At present, southbound western sandpipers stopping at Sidney Island are lighter in body mass than those captured on the Fraser estuary, as we reported earlier (Lissimore *et al.* 1999; Ydenberg *et al.* 2002). The mass difference is found within every age and gender class, and is not attributable to structural size differences of birds at the two sites (Lissimore *et al.* 1999). However, near the onset of peregrine recovery in the mid-1980s, body masses of southbound migrants on the two sites are almost identical

(figure 2). The current difference has arisen owing to the steady fall in mean body mass on Sidney Island since 1985, which amounts in total to *ca.* 2.5 g. By contrast, body masses of southbound birds at the safer Fraser estuary have not changed systematically over this period (rate of decline does not differ from zero, $p = 0.648$), although the variation in annual means is great. Body mass on Sidney Island has fallen at a rate of 0.154 g yr^{-1} ($p < 0.0001$).

Our second prediction compares migratory body masses of adults on the northward and southward migrations on the Fraser estuary. The peregrine abundance index shows that since 1986, northward migration through the Strait of Georgia for adult sandpipers has become more dangerous relative to southward migration. Ignoring the predicted effects of predation danger, one might expect adults to be lighter when southbound, because they arrive in the Strait after a long flight (*ca.* 2900 km) directly from Alaska (Lank *et al.* 2002), whereas on the northbound migration western sandpipers make much shorter flights of 500–1500 km (Warnock & Bishop 1998). In line with this expectation, the average southbound adult on the Fraser estuary in 1978 was indeed *ca.* 2 g lighter than a northbound adult. However, and as predicted, body mass patterns across the years differ strikingly between these migrations. Whereas the annual mean body mass has not changed systematically since 1978 for southbound adults, it has fallen at a rate of 0.135 g yr^{-1} ($p = 0.047$; figure 2) for northbound migrants, so that by 2001, the average northbound migrant was 1 g lighter than when southbound. The rate of decline is strikingly similar to that measured on Sidney Island for the southward migration.

These decadal-scale changes represent well over 10% of lean body mass. Both cases seem entirely attributable to changes in the size of the fuel reserve, as western sandpipers have not changed in structural size over this period (change in mean culmen length over years for southbound adults, Sidney Island: $n = 12$ years, slope = -0.07 mm yr^{-1} , $p = 0.23$; for southbound juveniles, Sidney Island: $n = 13$ years, slope = -0.02 mm yr^{-1} , $p = 0.55$; for southbound adults, Fraser estuary: $n = 11$ years, slope = -0.01 mm yr^{-1} , $p = 0.45$; for southbound juveniles, Fraser estuary: $n = 11$ years, slope = 0.02 mm yr^{-1} , $p = 0.16$; for northbound adults, Fraser estuary: $n = 10$ years, slope = 0.02 mm yr^{-1} , $p = 0.48$).

Our third prediction was that the LOS on Sidney Island should shorten in association with the increase in the peregrine index. Coincident with the decline in body mass, the LOS for southbound western sandpipers on Sidney Island declined by 68% between 1992 (mean LOS 8.4 days) and 2001 (2.7 days; figure 3). LOS estimates are not available for southbound migrants on the Fraser estuary, but for northbound migrants, stopover times based on radio telemetry data show that the LOS of northbound adults is also short (1992: 3.6 days, s.e.m. = 0.66, $n = 10$ (Iverson *et al.* 1996); 1995/1996: 2.2 days, s.e.m. = 0.23, $n = 25$ (Warnock & Bishop 1998)).

5. DISCUSSION

The data presented here on migrant western sandpipers in the Strait of Georgia over the past 25 years indicate no temporal trend in body mass of southbound adults

stopping over on the large and open mudflats of the Fraser estuary. In sharp contrast, the body masses of northbound adults at the same sites in the spring, and of southbound adults during the same time at Sidney Island, show significant downtrends in mean annual body mass of almost identical magnitude (0.135 and 0.154 g yr^{-1} , respectively). Independent data suggest that the last two situations are more dangerous than the first. Further, the LOS of migrants at Sidney Island has shortened substantially since 1992. Overall, these results confirm the changes in both body mass and LOS predicted by the danger mitigation hypothesis, and implicate the recovery of peregrine populations as a causal factor.

Another hypothesis attributes the changes in annual mean body mass to declines in the quantity or quality of food at Sidney Island. However, this hypothesis cannot—on its own, at least—account for many of the features of our results. For example, to explain the spatio-temporal pattern of mean annual body mass declines on this hypothesis would require that food has: (i) declined over years during the spring; but (ii) not during the summer at Fraser estuary; whereas (iii) it has declined during the summer at Sidney Island. Unfortunately, we lack the measurements to address this directly. Our measures of fattening rates (Ydenberg *et al.* 2002) and prey densities (Wolf 2001) both show that Sidney Island is a better feeding site, and not a poorer site as any hypothesis relating body mass directly to food abundance would imply. Previously, we (Ydenberg *et al.* 2002) concluded that the mass difference measured between the Fraser estuary and Sidney Island arises by condition-dependent site choice, as individuals with smaller fuel reserves and hence lower vulnerability take advantage of the better feeding at Sidney Island, despite its higher level of danger (Ydenberg *et al.* 2002). Thus, we acknowledge an important role for food availability in migratory behaviour, but maintain that it is unlikely to provide a satisfactory account without an explicit consideration of danger.

We have not made predictions that compare adults and juveniles. Because juvenile southward migration takes place with much greater exposure to peregrines than does adult migration (see Lank *et al.* 2002), one might suppose that danger mitigation tactics would be more strongly expressed by the former. Both adults and juveniles show body mass declines on Sidney Island (adults: 0.17 g yr^{-1} , $p = 0.05$; juveniles: -0.31 g yr^{-1} , $p = 0.0006$), but that of juveniles is not significantly greater. Neither age class shows changes on the Fraser estuary (adults: 0.03 g yr^{-1} ; $p = 0.52$; juveniles: 0.01 g yr^{-1} ; $p = 0.87$). This might indicate that the site difference in danger is stronger than the seasonal difference in predation risk between periods, but there are other differences between adult and juvenile migrations that complicate such interpretations. For example, adults undergo a wing moult at the end (or even during) their southward journey, whereas juveniles fly on newly grown plumage and do not moult. Juveniles have different organ sizes (Guglielmo & Williams 2003) and are less experienced. All these factors complicate predictions about differences between adults and juveniles.

Though by no means definitive, our results suggest that the changes in body mass and LOS result from behavioural adjustments made by individual birds, rather than from selective changes resulting from mortality as a result

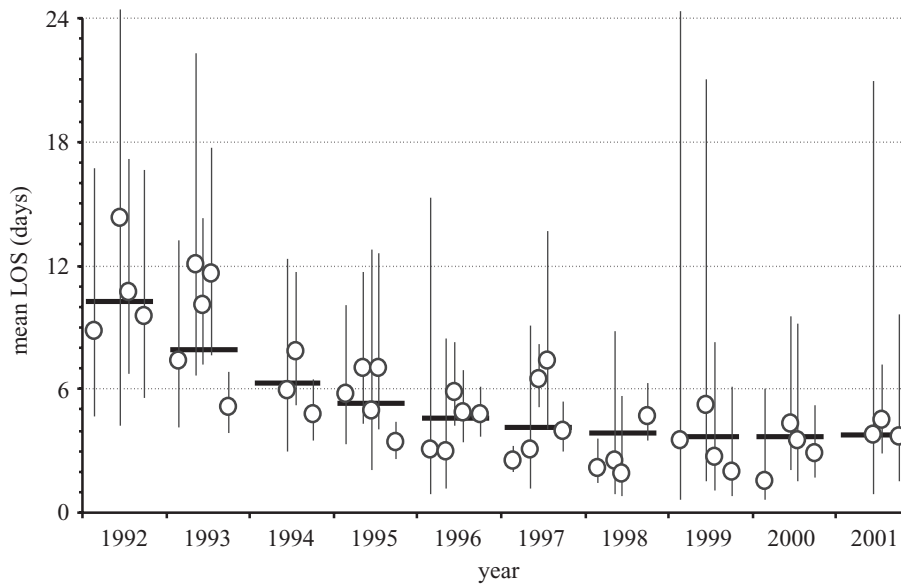


Figure 3. LOS of marked southbound western sandpipers on Sidney Island. The plot portrays a persistent decrease from 1992 to 2001, falling from an annual average of 8.4 to 2.7 days, based on capture–mark–resightings of 282 adults and 1021 juveniles. Points are estimates for LOS for individual week–year data cells with their 95% CI (light lines). In cases with low sample size, adjacent cells were pooled; generally the first few and the last few cells were combined. The model (mean LOS, heavy lines) was chosen based on its highest rank (lowest AIC_C) in a formal model selection protocol (Burnham & Anderson 1998).

of falcons. Evidently, upon arrival in the Strait of Georgia, individuals with small fuel reserves feed at Sidney Island (and similar small sites) until increased wing loading (Burns & Ydenberg 2002) makes further residence too dangerous, at which point they either move to the Fraser estuary, or, if a favourable wind is available, move southwards. Our interpretation of the data presented here is that the rising abundance of falcons has lowered the point at which this transition is advantageous. In this sense the declining body mass and shortening LOS at Sidney Island are closely related, and are not independent tactics to mitigate danger. Though some features of our data do not seem to be adequately explained by the hypothesis here (i.e. that southbound adults show any increase in danger mitigation tactics), overall our results bolster the idea that safety has been an important selective factor in the evolution of migration. The features we examine here are local, but Lank *et al.* (2002) and Butler *et al.* (2003) consider some of the implications for the evolution of migration on a continental scale.

Our understanding of the importance of predators to many aspects of ecology has been significantly enhanced over the past decade by theoretical work and large-scale field experiments demonstrating that the mere presence of predators causes prey to alter behaviour, morphology and life-history traits (Lima & Dill 1990). These ‘non-lethal’ effects not only mitigate the danger posed by predators, but can have population consequences for prey species that are greater and more far-reaching than direct depredation would have alone (Peacor & Werner 2001). The effects may cascade to affect the structure of entire ecological communities (Schmitz 1998; Sinclair *et al.* 2000; McQueen *et al.* 2001). We anticipate that the recovery of raptors in North America and Europe is exerting such effects.

Our results also have implications for the collection and interpretation of data on shorebird population trends.

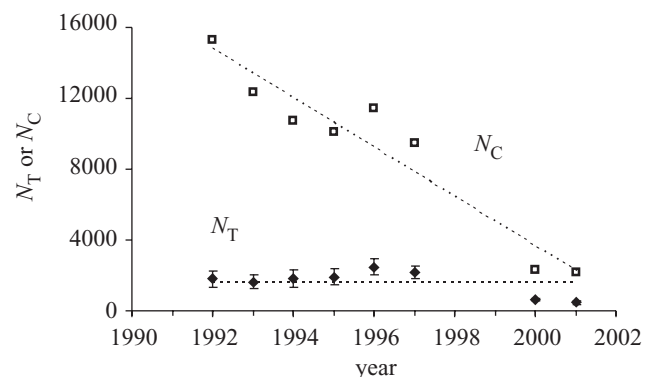


Figure 4. Comparison of annual cumulative daily counts (N_C) of western sandpipers stopping over at Sidney Island between 1992 and 2001, with estimates of the true number (N_T). Estimates of N_T report an s.e.m. associated with the uncertainty in estimating LOS. The values for N_C indicate a significantly declining trend of ca. 18% per year. By contrast, estimates of N_T indicate no significant decline ($p = 0.24$). The method for estimating N_T is explained in the text.

North American shorebird species, especially long-distance migrants, are reported to have declined in abundance during the 1980s and 1990s (Howe *et al.* 1989; Morrison *et al.* 1994, 2001). Proposed causes include climate change, loss of critical habitat, pollution and disturbance. Consistent with the continent-wide trend, the number of western sandpipers censused on Sidney Island (sum of daily counts, called N_C) has declined at ca. 18% per year, based on the most extensive and regular counts made since censuses were initiated in 1992 (figure 4), leading to an overall drop of 83%.

It is well known that estimates of population size based on such census data are sensitive to estimates of the LOS

of migrants at a site (Bishop *et al.* 2000). Less well recognized is that changes in the LOS alter the number of birds censused, even if the total population does not change. To estimate the true number of birds (N_T) stopping over at Sidney Island, we incorporated our LOS estimates with the N_C values in an arrival-stopover-departure model (Frederiksen *et al.* 2001). The outcome (figure 4) provides no evidence for a drop in N_T . The steep decline in N_C can be explained entirely or almost entirely by the shortening stopover times of southbound migrants; perhaps N_T in 2000 and 2001 is somewhat reduced. Thus the strongly declining trend indicated by the census data is created by behavioural changes of the sandpipers, and there is little or no evidence at Sidney Island to support the hypothesis of a true population decline.

Population estimates and trend analyses of shorebirds and other neotropical migrants often use indices (e.g. mean, sum, maximum counts) based on repeated censuses made at one or more stopover sites, raising the possibility that shortened LOS 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 in North America (Donaldson *et al.* 2000; Brown *et al.* 2001) to monitor populations of neotropical migrants need to take this possibility into account.

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REFERENCES

- Alerstam, T. & Lindström, Å. 1990 Optimal bird migration: the relative importance of time, energy and safety. In *Bird migration: physiology and ecophysiology* (ed. E. Gwinner), pp. 331–351. Berlin: Springer.
- Bijlsma, R. G. 1990 Predation by large falcons on wintering waders on the Banc d'Arguin, Mauritania. *Ardea* **78**, 75–82.
- Bishop, M. A., Meyers, J. P. & McNeley, P. F. 2000 A method to estimate migrant shorebird numbers on the Copper River delta, Alaska. *Field Ornithol.* **71**, 627–637.
- Brown, S., Hickey, C., Harrington, B. & Gill, R. (eds) 2001 *The US shorebird conservation plan*, 2nd edn. Manomet, MA: Manomet Center for Conservation Sciences.
- Burnham, K. P. & Anderson, D. R. 1998 *Model selection and inference: a practical information-theoretic approach*. New York: Springer.
- Burns, J. G. & Ydenberg, R. C. 2002 The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). *Behav. Ecol. Sociobiol.* **52**, 128–136.
- Butler, R. W., Ydenberg, R. C. & Lank, D. B. 2003 Wader migration on the changing predator landscape. *Wader Study Group Bull.* **100**, 130–133.
- Cade, T. J., Enderson, J. H., Thelander, C. G. & White, C. M. 1988 *Peregrine falcon populations: their management and recovery*. Boise, ID: Peregrine Fund Inc.
- Carrière, S., Abernathy, D., Bradley, M., Bromley, R. G., Matthews, S. B., Obst, J. & Settingington, M. 2003 Raptor trends in the Northwest Territories and Nunavut: a peregrine falcon case study. *Bird Trends* **9**, 57–62.
- Cresswell, W. 1995 Selection of prey by wintering sparrowhawks *Accipiter nisus* wintering in southern Scotland. *Ardea* **83**, 381–389.
- Cresswell, W. 1996 Surprise as a winter hunting strategy in sparrowhawks *Accipiter nisus*, peregrines *Falco peregrinus* and merlins *F. columbarius*. *Ibis* **138**, 684–692.
- Cresswell, W. & Whitfield, D. P. 1994 The effects of raptor predation on wintering wader populations at the Tynningame estuary, southeast Scotland. *Ibis* **136**, 223–232.
- Dekker, D. 1988 Peregrine falcon and merlin predation on small shorebirds and passerines in Alberta. *Can. J. Zool.* **66**, 925–928.
- Dekker, D. 1998 Over-ocean flocking by dunlins, *Calidris alpina*, and the effect of raptor predation at Boundary Bay, British Columbia. *Can. Field Nat.* **112**, 694–697.
- Dekker, D. & Ydenberg, R. C. 2004 Raptor predation on wintering dunlins in relation to the tidal cycle. *Condor* **106**, 415–419.
- Donaldson, G. M., Hyslop, C., Morrison, R. I. G., Dickson, H. L. & Davidson, I. (eds) 2000 *Canadian shorebird conservation plan*. Canadian Wildlife Service Special Publication. Minister of Public Works and Government Services Canada, catalogue no. CW69-15/5-2000E. Ottawa, Ontario: Authority of the Minister of Environment, Canadian Wildlife Service.
- Fransson, T. & Weber, T. P. 1997 Migratory fuelling in blackcaps (*Sylvia atricapilla*) under perceived risk of predation. *Behav. Ecol. Sociobiol.* **41**, 75–80.
- Frederiksen, M., Fox, A. D., Madsen, J. & Colhoun, K. 2001 Estimating the total number of birds using a staging site. *J. Wildl. Mgmt* **65**, 282–289.
- Gosler, A. G., Greenwood, J. J. D. & Perrins, C. 1995 Predation risk and the cost of being fat. *Nature* **337**, 621–623.
- Gudmundsson, G. A., Lindstrom, A. & Alerstam, T. 1991 Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, sanderlings *Calidris alba* and turnstones *Arenaria interpres*. *Ibis* **133**, 140–152.
- Guglielmo, C. G. & Williams, T. D. 2003 Phenotypic flexibility of body composition in relation to migratory state, age and sex in the western sandpiper. *Physiol. Biochem. Zool.* **76**, 84–98.
- Hoffman, S. W. & Smith, J. P. 2003 Population trends of migratory raptors in western North America, 1977–2001. *Condor* **105**, 397–419.
- Houston, A. I. 1998 Models of optimal avian migration: state, time and predation. *J. Avian Biol.* **29**, 395–404.
- Howe, M. A., Geissler, H. & Harrington, B. A. 1989 Population trends of North American shorebirds based on the international shorebird survey. *Biol. Conserv.* **49**, 185–199.
- Iverson, G. C., Warnock, S. E., Butler, R. W., Bishop, M. A. & Warnock, N. 1996 Spring migration of western sandpipers along the Pacific coast of North America: a telemetry study. *Condor* **98**, 10–21.
- Kullberg, C., Fransson, T. & Jacobsson, S. 1996 Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). *Proc. R. Soc. Lond. B* **265**, 1659–1664.
- 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.
- Lank, D. B. & Ydenberg, R. C. 2003 Death and danger at migratory stopovers: problems with predation risk. *J. Avian Biol.* **34**, 225–228.
- Lank, D. B., Butler, R. W., Ireland, J. & Ydenberg, R. C. 2002 Effects of predation danger on migration strategies of sandpipers. *Oikos* **103**, 303–319.

- Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992 Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. *Ecol. Monogr.* **62**, 67–118.
- Lima, S. L. & Dill, L. M. 1990 Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–640.
- Lind, J., Fransson, T., Jacobsson, S. & Kullberg, C. 1999 Reduced take-off ability in robins due to migratory fuel load. *Behav. Ecol. Sociobiol.* **46**, 65–70.
- Lindström, Å. 1990 The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. *Behav. Ecol.* **1**, 102–106.
- Lissimore, D., Lemon, M., Lank, D. B., Butler, R. W. & Ydenberg, R. C. 1999 Large and consistent body mass differences of migrating small calidrid sandpipers at adjacent stopover sites. *Wader Study Group Bull.* **88**, 55–58.
- McQueen, D. J., Ramcharan, C. W. & Yan, N. D. 2001 Summary and emergent properties. *Arch. Hydrobiol.* **56**(Special Issue *Adv. Limnol.*), 257–288.
- Morrison, R. I. G., Downes, C. & Collins, B. 1994 Population trends of shorebirds on fall migration in eastern Canada 1974–1991. *Wilson Bull.* **106**, 431–447.
- Morrison, R. I. G., Abry, Y., Butler, R. W., Beyersbergen, G. W., Donaldson, G. M., Gratto-Trevor, C. L., Hicklin, P. W., Johnston, V. H. & Ross, R. K. 2001 Declines in North American shorebird populations. *Wader Study Group Bull.* **94**, 39–43.
- Newton, I. 1979 *Population ecology of raptors*. Vermillion, SD: Buteo Books.
- O'Reilly, K. M. & Wingfield, J. C. 1995 Spring and autumn migration in Arctic shorebirds: same distance, different strategies. *Am. Zool.* **35**, 222–233.
- Page, G. & Whitacre, D. F. 1975 Raptor predation on wintering shorebirds. *Condor* **77**, 73–83.
- Peacor, S. D. & Werner, E. E. 2001 The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Natl Acad. Sci. USA* **98**, 3904–3908.
- Piersma, T., Koolhaas, A. & Jukema, J. 2003 Seasonal body mass changes in Eurasian golden plovers staging in The Netherlands: decline in late autumn mass peak correlates with increase in raptor numbers. *Ibis* **145**, 565–571.
- Rowell, P., Holroyd, G. L. & Banasch, U. 2003 Summary of the 2000 Canadian peregrine falcon survey. *Bird Trends* **9**, 52–56.
- Schmitz, O. J. 1998 Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Nat.* **151**, 327–342.
- Sinclair, A. R. E., Krebs, C. J., Fryxell, J. M., Turkington, R., Boutin, S., Boonstra, R., Secombe-Hett, P., Lundberg, P. & Oksanen, L. 2000 Testing hypotheses of trophic level interactions: a boreal forest ecosystem. *Oikos* **89**, 313–328.
- Warnock, N. & Bishop, M. A. 1998 Spring stopover ecology of migrant western sandpipers. *Condor* **100**, 456–467.
- White, G. C. & Burnham, K. P. 1999 Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**(Suppl.), 120–138.
- Whitfield, D. P. 1985 Raptor predation on wintering waders in southeast Scotland. *Ibis* **127**, 554–558.
- Wolf, N. 2001 Foraging ecology and site selection in western sandpipers during their fall migration through southwestern British Columbia. MSc thesis, Simon Fraser University, Burnaby, British Columbia.
- Ydenberg, R. C., Butler, R. W., Lank, D. B., Guglielmo, C. G., Lemon, M. & Wolf, N. 2002 Trade-offs, condition-dependence and stopover site selection by migrating sandpipers. *J. Avian Biol.* **33**, 47–55.

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