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Effects of Predation Danger on Migration Strategies of Sandpipers

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Abstract

We examine the potential selective importance of predation danger on the evolution of migration strategies of arctic-breeding calidrid sandpipers. Adult calidrids truncate parental care for reasons not obviously related to levels of food abundance on the breeding areas or at migratory stopover sites, suggesting that a different trade-off occurs between providing additional care and adult survivorship. The southward migrations of adult western sandpipers precede those of migratory peregrine falcons by almost a month. By moving early and quickly, adults remain ahead of migrant falcons all the way to their non-breeding areas, where they rapidly moult flight feathers. They complete the moult just as falcons arrive in late September-October. By migrating early, they avoid exposure to falcons when they are unusually vulnerable, due to the requirements for fuelling migratory flight and to wing feather moult. Juvenile western sandpipers migrate south just as falcon numbers start to increase, but do not moult flight feathers in their first winter. Pacific dunlin use an alternative strategy of remaining and moulting in Alaska after falcons depart, and migrating to their overwintering sites after migrants have passed. East of the Rocky Mountains, the southbound migration of falcons begins 4–6 weeks later. Southbound semipalmated sandpipers make extended migratory stopovers, but their lengths of stay shorten prior to falcon migration to the sites in September. Predation danger also may affect the evolution of migration routes. Southbound western sandpipers fly directly from Alaska to southern British Columbia, in contrast to the multi-stage journey northward along the Alaska panhandle. We estimate that a direct flight would be more economical on northward migration, but may be avoided because it would expose sandpipers to higher mass-dependent predation danger from migratory falcons, which travel north with sandpipers. By contrast, few raptors are present in Alaska during preparation for the southward flight. A temporal and spatial window of safety may also permit semipalmated sandpipers to become extremely vulnerable while preparing for trans-Atlantic southward flights. Danger management may account for the these previously enigmatic features of calidrid migration strategies, and aspects of those of other birds.

Introduction

Alerstam and Lindström (1990) identified time, energy, and safety as three primary considerations governing avian migration strategies. The preponderance of theoretical and empirical recent research in this field has concentrated on quantifying effects of and testing hypotheses derived from the first two factors, examining in what ecological situations predictions of “time-minimisation” versus “energy rate maximising” appear to be strategies used by migrants in different ecological conditions (e.g. Gudmundsson et al. 1991, Lindström and Alerstam 1992, Lyons and Haig 1995, Farmer and Weins 1999, Weber et al. 1999). The few studies focusing specifically on safety concentrate on how sensitivity to predation danger may alter local stopover foraging and habitat use, resulting in slower (Lindström 1990, Ydenberg et al. 2002) or faster (Fransson and Weber 1997) fattening rates (Bednekoff and Houston 1994), and thereby altering migration speeds (Weber et al. 1998). The effects of safety have been thought of primarily as modifying time or energy considerations, rather than considered in their own right. In this paper, we explore situations in which safety and its opposite, danger, may account for some quite general features of calidrid sandpiper migration that appear enigmatic from the perspective of temporal and energetic considerations alone, as well as accounting for certain quite specific aspects of the migration behaviour of three species. Our general thesis is that *spatial and temporal patterns of the presence of falcons and other raptors have profoundly influenced the evolution of the sandpiper migration*, in ways not previously considered. We apply the general paradigm outlined by Lima and Dill (1990), and refer to adaptive strategies of “danger management”, parallel to the term “energy management” used to describe allocation decisions in that dimension (Ricklefs 1996). We are not ignoring other factors, and consider shifting trade-offs between predation danger and feeding opportunities as essential to our understanding of migratory and non-breeding habitat choice (Ydenberg et al. 2002). However, in this paper, we are primarily developing and testing predictions from danger-based explanations, bringing together data from the literature and our own results from a variety of studies. Topics considered include: the timing of parental abandonment of young; the timing of southward migration and post-breeding wing moult of adults; seasonal variation in residence times at migratory stopovers; and differences in migration strategies, including routes, taken on northward and southward migration, or migration routes of different age classes.

Danger management by sandpipers and the predator landscape

The most significant predators on small shorebirds outside of the breeding season are raptors, particularly medium-sized falcons and accipiters (e.g. Page and Whitacre 1975, Kus et al. 1984, Cresswell and Whitfield 1994). Both employ a variety of techniques when hunting shorebirds but the most successful tactic combines stealth and speed to surprise sandpipers on the ground or just after they launch into an escape flight (e.g., Cresswell 1996, Dekker 1998, 1999). Aerial pursuits, involving high-speed manoeuvres by predator and prey, are more time consuming and substantially less likely per attempt to produce a kill. Such chases typically involve raptors attempting to quarry individual sandpipers that they have managed to separate from a flock (Buchanan et al. 1988, Dekker 1998). Sandpiper survival thus depends on quick reflexes, fast take-off, and high manoeuvrability (Lima 1993).

Three points follow from these facts. Most importantly, sandpipers that are slower to take off are at greater risk of being caught on or near the ground (Cresswell 1996), and those less manoeuvrable are at greater risk when in the air. This applies to both performance relative to the raptor and for performance relative to other sandpipers in a flock, particularly during aerial

chases. Wing moult is a time when flight performance is impaired (Hedenström and Sunada 1999), and evidence is accumulating that birds often lighten their body masses to maintain flight performance during moult (Lind and Jakobsson 2001).

Secondly, birds with less than maximal flight performance will particularly benefit from avoiding close encounters with falcons altogether, if possible. One behavioural tactic birds may use to do so is to forage in larger open sites, such as extensive mudflats, which provide safety for feeding or roosting shorebirds, rather than smaller sites surrounded by vegetation, which facilitates stealthy approaches by falcons or other raptors (Ydenberg et al. 2002). A more profound strategic approach, if possible, is to adjust the annual schedule of times and places when flight performance is impaired to occur when contact with raptors is less likely (O'Hara et al. 2002).

Finally, the body reserves needed to fuel migratory flights are likely to impair a bird's flight performance, and for this reason alone migration carries with it higher levels of intrinsic risk than during residential times of year (see Stillet and Holmes 2002). Kullberg et al. (1996) and Lind et al. (1999) showed that fat reserves lowered the escape speed of two migratory passerines. Burns and Ydenberg (2002) measured a similar effect in western and least (*Calidris minutilla*) sandpipers. To the extent that fat reserves impair escape ability, long flights requiring such reserves, and the long periods of exposure at stopover sites when building them, should be avoided when they entail substantially increased exposure to predation danger (Houston 1998). Conversely, times and locations where predation danger is low will be permissive for optimising migration strategies based on minimising the time spent on migration, which theoretically favours larger fuel loads and fewer more lengthy flights (Alerstam and Lindström 1990).

The spatial and temporal predator landscape

The seasonal distributions of falcons create dramatic, but predictable, spatial and temporal patterns of danger and windows of safety for small shorebirds, which we refer to as the “predator landscape”. In North America, adult peregrines and merlins migrate northward more or less coincident with northward shorebird migration, and disperse thinly across temperate and arctic sites on the continent during their breeding season. Adults spend a minimum of two and half months to complete a breeding attempt through fledging. Following the breeding season, migratory falcons concentrate, with their fledged young, along sandpiper migration routes, including coastlines. A “wave” of peregrines proceeds southward, leaving some birds behind to become residents thinly distributed across suitable temperate and subtropical non-breeding sites (Fig. 1). In North America, the peregrine migratory races *anatum* and *tundrius* migrate from arctic areas to spread across non-breeding areas in Central and South America, as far as Chile (Fuller et al. 1998), while members of the other non-migratory races (e.g. *pealei* on the northwest Pacific Coast) disperse more locally to wintering locations.

The predator landscape in North America has particular spatial and temporal attributes. First, the shape of the continent funnels and concentrates migratory raptors, including birds from Greenland (Fuller et al. 1998), as they move southward. Second, the timing of southward migration differs across the continent (Fig. 2). On the west coast, peregrine numbers in southern Canada and the northern US rise in late July and August, and these raptors arrive in northern Mexico by mid-September. Peregrine falcons banded in west-central Canada, and recovered farther south, pass through the northern US during mid-late September and early October (Schmutz et al. 1991). In eastern North America, peregrine passage at Hawk Mountain in Pennsylvania peaks in the first or second week of October (Heintzelman 1975: Fig. 6). Thus,

there is a strong west to east lag in the timing of peregrine migration. Other major shorebird predators, such as merlins and prairie falcons (*Falco mexicanus*), migrate later than peregrines at a given longitude (Heintzelman 1975, Schmutz et al. 1991).

The movements described here create regular seasonal abundance patterns of falcons at particular locations. As an example from a single migration stopover site, we plot the annual cycle of peregrine abundance observed in the Strait of Georgia, southern British Columbia (Fig. 3). The northward movement of peregrines involves a short, sharp, spring peak in late April and early May, which coincides with the northward passage of western sandpipers through the site. After a near-complete absence during May, June and early July, peregrine sightings increase in late July. Peregrine abundance rises steeply through August, peaking in October. The sightings through the winter represent winter residents, rather than migrants. Peregrine presence in the Wadden Sea, the major site in northwest Europe for migrating shorebirds, shows a similar annual pattern (Busche et al. 1998).

We now examine how danger management by sandpipers in the predator landscape may help us understand the adaptive value of aspects of the sandpiper migration strategies outlined above. As examples, we consider the three most numerous and best-studied species of nearctic shorebirds: the western sandpiper (*Calidris mauri*), the semipalmated sandpiper (*C. pusilla*), and dunlin, specifically Pacific dunlin (*C. alpina pacifica*). These small shorebirds are among the 24 species in the Calidridinae, all of which breed in high temperate or Arctic regions, and most of which migrate to temperate, tropical, or even southern hemisphere non-breeding grounds. Western sandpipers (ca. 25 g) breed in a relatively restricted range in western Alaska and on the Chutotski Peninsula (Fig. 4). The similarly sized semipalmated sandpiper breeds in a broad band of mid- to lower arctic all across North America. These two species are by far the most abundant shorebirds in North America, with populations in excess of 3 million, thus each accounts for ca. to 30% of all calidrids (Morrison et al. 2000). Pacific dunlin, a larger calidrid (ca. 50 g), breeds in the southern part of the western sandpiper's Alaska breeding range, and spends the boreal winter primarily along the west coast of the U.S., with smaller numbers in northwestern México and along the Pacific coast of Canada.

Timing of southward migration

Life history strategies focus on trade-offs between current and future reproductive effort. In sandpipers, one intriguing potential example of this is limited brood attendance and subsequent early migration by adults, which move southward up to a month prior to their young. This pattern is widespread among migratory calidrids, but not universal (e.g., Gill and Handel 1990: Fig. 4). The early departure by adults has been interpreted primarily with respect to competition for, or disappearance of, food on breeding grounds or at migratory stopovers (e.g. Pitelka 1959; Holmes 1971a, 1972; Pitelka et al. 1974; Ashkenazie and Safriel 1979; Schneider and Harrington 1981). Several authors have emphasised the importance of considering the interconnectedness of conditions at different stages of the annual cycle when attempting to interpret such phenomena (e.g. Myers 1981, Weber et al. 1998). We will review and compare details of the breeding and southward migration of these three calidrids, and consider potential ecological regimes that may favour migration strategies and differences in strategies between species and populations.

Western sandpipers

Western sandpipers arrive on breeding grounds in western Alaska in mid-May (Holmes 1972, Sandercock 1997). Territorial males display on and over the tundra (Lanctot et al. 2000), and

paired females lay clutches of four eggs as the snow recedes. Mean nest initiation dates range from 20–24 May near Nome (1993–1996: Sandercock et al. 1999, 2000), 25 May to 5 June in the central Yukon Kuskokwim Delta (1966–1969: Holmes 1972; 1999–2000: Ruthrauff 2002), 8–10 June at Cape Espenberg, at the northern tip of the Seward Peninsula (1976–1979 and 1994 – 1998, Schamel and Tracy, pers. comm.), and ca. 10–15 June on the Chukchi Peninsula in Siberia (1978–1980: Tomkovitch and Morozov 1983). Both parents usually incubate for 20–22 days and eggs hatch in mid-late June.

Miller (1985: p.1599) states as a generalisation that “In the Scolopacidae it is normal for at least one parent to attend the chicks until they are past the age at which they can make sustained flights”, and cites appropriate literature. For western sandpipers, this is more the case for earlier than later hatching clutches. The duration of parental attendance by both parents declines over the season (westerns: Neville 2002, Ruthrauff 2002). Male westerns typically accompany broods for up to three weeks, for early hatching nests, but only 10 days for those hatching at the end of the season, leaving unfledged young on their own. Females typically accompany broods for up to 10 days at the start of the season, but leave late broods within a few days of hatch. This suggests that the benefits to chicks of care and biparental care decrease later in the season, and/or that the costs to parents increase.

Why do parents migrate early, and what apparent deadline causes later breeders to further truncate parental attendance of pre-fledged young? We have examined the birds’ behaviour at subsequent stages of their southward migration in search of potential answers. Following departure from the breeding grounds, western sandpipers move to marine migratory staging periods in coastal southwestern Alaska (Gill and Handel 1990). From there, they appear to make a direct flight to temperate latitudes (Fig. 4, Butler et al. 1996, see below). The first migrants from Alaska, all adults, arrive in southwestern British Columbia in late June, followed a 3–4 weeks later by juveniles, which persist in significant numbers through mid-late August (Figs. 2, 3). We have studied migrants intensively at Sidney Island, a small stopover site off of southeastern Vancouver Island (Butler et al. 1987). The site has excellent feeding conditions, as assessed by circulating triglyceride levels, which index fattening rates (Williams et al. 1999), and measured directly by comparing invertebrate levels in mud samples with those of alternative sites (Wolf 2001). However, birds using the site are lightweight (Lissimore et al. 1999, Ydenberg et al. 2002), and the mean lengths of stay are short, ranging from 3–6 days through the season, with no difference between age classes (Butler et al. 1987, B. Smith, capture-recapture analysis of unpublished data collected 1992–2001). Although males stay with broods 5–10 days longer than females on the breeding grounds, there is only 1–2 day difference in the passage times of the sexes in southern B.C. (A. Neihaus et al., unpublished data). Thus males “catch up” with females. Western sandpipers continue southward and take up residency on non-breeding grounds. On arrival, adults undergo a rapid wing moult, which is completed by the start of October (Fig. 1, Watts 2001, O’Hara et al. 2002). Juveniles first arrive in Panama in mid-September, but retain their first set of flight feathers, grown on the breeding grounds, for over a year.

Semipalmated sandpipers

Semipalmated sandpipers arrive on the southern parts of their extensive breeding grounds in mid-May, and on northern areas in early June (Gratto and Cooke 1987) (Fig 4). Males establish territories, and females lay clutches of 4 eggs as the snow recedes. Mean laying dates were 17–18 June near Churchill, Manitoba, 1980–1983, and 17–18 June at Barrow during the late 1960–

early 1970s. Near Nome, mean nest initiation dates were 25–29 May, ca. 5–8 days later than western sandpipers breeding on exactly the same study site (1993–1996: Sandercock et al. 1999, 2000). Across their entire range, semipalmated sandpipers are thus starting to breed a week to 10 days later than westerns.

Both parents incubate for 20–22 days, and eggs hatch in late June and early July. As with western sandpipers, the duration of biparental care decreases for later hatched nests, with females usually abandoning the brood first (Gratto-Trevor 1991). Adults leave the tundra, shift to feeding on beaches or mudflats, and begin southward migration in mid-July (Fig. 2). Many adults from central and western Canada stage along the shores of James Bay in the last half of July, before proceeding to stopover sites further south. Adult females precede males by about five days on average in southern Canada (McNeil and Cadieux 1972, Morrison 1984), in contrast to westerns, where the sexes become more synchronous. Juveniles migrate later, with peak passage in temperate North America falling between late August and early September (Fig. 2).

Lank (1983) studied the temperate-zone behavioural ecology of southward migrant semipalmated sandpipers at a mid-continental inland staging site (Sibley Lake, North Dakota, in 1978), and an eastern coastal site (Kent Island, Bay of Fundy, in 1977 ; Fig. 4). The inland and coastal sites fall on quite different migratory routes. Birds arrived at Sibley Lake from Alaska and the western Canadian arctic, and continued their migration southeasterly across the continent towards Florida and the West Indies, with many en route stopover possibilities (Lank 1979). Birds arrived at Kent Island principally from the central and eastern Canadian arctic, and after staging, they initiated a non-stop trans-Atlantic flight to the West Indies or South America (McNeil and Cadieux 1972, McNeil and Burton 1977; Richardson 1979, Stoddard et al. 1983).

Despite substantial differences in feeding ecology, migration routes, and seasonal timing, the stopover residency periods at the two sites show an intriguing similarity. At both sites, birds arriving early in the season have lengthy residency periods, while those arriving later in the season move on more rapidly. Such lengthy residency periods of semipalmated sandpipers have puzzled a generation of researchers (Page and Middleton 1972, Lank 1983, Morrison 1984, Dunn et al. 1988, Pfister et al. 1998). Early migrants had mean minimum stopover periods as long as 25 d, compared to 5–10 days late in the season. Potential fattening rates, estimated at over 1.3 g/day, indicate that the mean stopover periods early in the season at both sites were substantially longer than necessary simply to fatten up as quickly as possible for the next flight, even the trans-oceanic flight from the coast, which requires ca. 25–30 g. of fat (Pfister et al. 1998, but see Kvist et al. 2001). Dunn et al. (1988) and Pfister et al. (1998) found similar seasonal decreases in residency times for semipalmated sandpipers, on the coast of Maine and Massachusetts, respectively, and also argued that early migrants were staying longer than necessary simply to prepare for and depart on their next migratory flight. The lack of movement cannot be attributed to waiting for favourable weather conditions, because these occur regularly throughout this time of year (Lank 1983). The shortening of the residency period primarily affects juveniles, which predominate towards the end of the season. However, it appears to apply even more strongly for the few adults still present at the end of the season. At Kent Island, the mean residency period of daily cohorts was shorter for adults than young during five of the six periods when both were present the end of the season.

The lengthy residency periods of semipalmated sandpipers, which would be even longer if estimated with capture-recapture techniques, instead of being the intervals between capture and last sighting, stand in sharp contrast to the 3–6 day stopovers of western sandpipers at the

same latitude. They also extend the migration season of semipalmated sandpipers 2–5 weeks beyond that of western sandpipers at comparable latitudes (Fig. 2).

Predation danger and the timing of migration

We propose that the migratory timing of these species, including differences between them, are adaptations to avoid encounters with migratory falcons. The broadest pattern is that the southward migrations of both species occur in spatial and temporal “windows of safety” at migratory stopover sites, well ahead of the concentrations of post-breeding falcons and their young along migration corridors (Figs. 1, 2, 3, 5). Western sandpipers appear to have a narrower time window than do semipalmated sandpipers, and their movement through at least one temperate zone migration stopover site is rapid. Although semipalmated sandpipers commence breeding ca. one week later than western sandpipers, the difference in migration timing extends 2 weeks to a month or more later for semipalmated sandpipers at a given latitude, particularly for juveniles further east (Fig. 2). Thus their later migration does not simply follow from their later start. Semipalmated sandpipers also may travel farther to reach temperate zone staging areas (Fig. 3), which would add time to their migration, but the key phenomenon of interest is their overly lengthy staging periods, which is a different matter. The lengthening of the sandpiper migration seasons from west to east may be related to the longer time window of safety created by the later falcon migration at mid-continental and eastern areas (Fig. 2). The eventual shortening of stopover times in central and eastern areas (Fig. 5) may be anticipate the eventual arrival of migrant falcons or other raptors.

The broad hypothesis that migrations are occurring within low-predation windows fails to mesh with a more detailed consideration of adult migration timing by both species of sandpipers. Adults are leaving their broods and migrating substantially earlier than needed simply to migrate within lower predation danger windows. They could readily remain and provide an additional week or more of care, even at the end of the season, and still move south ahead of most falcons. They could also remain longer at staging sites, particularly adult western sandpipers, which appear to be moving rapidly southward. We propose that adults are facing an additional “deadline”, after which their personal survivorship costs will outweigh the fitness benefits they might obtain earlier in the season by continuing to warn their pre-fledged young of predators, or assist them in finding suitable foraging areas. Figure 1 diagrams a possible explanation for this, with data from western sandpipers. Immediately on arriving at non-breeding grounds, adults moult their flight feathers. To speed this process, western sandpipers in Panama drop up to 5 inner primaries simultaneously (Watts 2001), becoming nearly flightless as they do so. This allows them to have completed their wing moult by the beginning of October, when migrant peregrines arrive in large numbers (Watts, pers. comm., Ridgely 1976).

Adult western sandpipers thus both migrate and undergo flight feather moult with minimal exposure to migratory falcons. They thereby undergo both these process, which compromise their flight performance, in relatively safe environments. We propose that this survivorship advantage is a fundamental selective force promoting in the early departure of adult sandpipers, and that this may provide a deadline responsible for the seasonal truncation of parental care on the breeding grounds by adults of many species of shorebirds.

Juveniles cannot initiate migration as early as do adults, but they do not fact a period of greater intrinsic vulnerability upon arrival on non-breeding grounds, since they retain the flight feathers they grew in the arctic until the following spring. At Kent Island, where both juveniles and adults overlap at the end of the season, the latest migrant adults have even shorter periods

than contemporaneous juveniles, as predicted if they obtain a greater benefit from reaching the non-breeding grounds in time to moult prior to the arrival of migrant falcons. However, whether adult semipalmated sandpiper moult and falcon arrival time frames on non-breeding grounds mesh as well as those of western sandpipers remains to be determined.

In support of the hypothesis that an early moult is advantageous, O'Hara et al. (2002) showed that the moult timing of flight feathers by western sandpipers that remain in Panama between April and July, rather than migrating, is advanced. Summer residents initiate moult in July, and many have completed it by the time the first migrants return. On the assumption that oversummer residents are better able to moult at the most propitious time, O'Hara et al. suggested that the absence of migratory falcons favoured moult at that time, and became increasingly disadvantageous as the season progresses.

Pacific dunlin: an alternative strategy?

We have argued that the basic strategy of western and semipalmated sandpipers is to migrate south ahead of concentrations of post-breeding falcons. An alternative strategy would be to migrate after migrant falcons had already moved through an area. This would be most advantageous for species whose non-breeding range was largely north of the non-breeding ranges of the falcons, thereby completely avoiding exposure to all falcons moving farther south. This may explain the moult and migration pattern of adult and young Pacific dunlin, which contrasts strongly with that of both western and semipalmated sandpipers. *C. a. pacifica's* breeding season begins at approximately the same time as that of western sandpipers (Holmes 1971b), but dunlin remain in Alaska more than two months longer than their congeners (Fig. 1). Following the breeding season, adults move to coastal areas and complete a wing moult prior to flying farther south at the end of October. When studied at roosting sites in August and early September of 1979 and 1980, these pre-migratory dunlin were disturbed by predators only once every 3 hours on average, and never by a falcon (Handel and Gill 1992). In 250 hours of observation time, Handel and Gill observed no predation events except one bird swallowed by a Glaucous-winged gull (*Larus hyperboreus*). Both facts suggest that the location is relatively safe for small sandpipers; many of their major predators have already departed southward. The dunlin arrive on temperate non-breeding grounds in mid-October, after passage by the major wave of migratory falcons. The young, which need not moult wing feathers, actually precede adults. We know that the mortality rates of Pacific dunlin to falcons can be substantial during the winter (Page and Whitacre 1975, Kus et al. 1984), and Dunlin may remain in Alaska to moult in an exceptionally safe place and lessen their period of vulnerability at coastal sites farther south. Finally, remaining further north makes the non-breeding grounds they eventually occupy less attractive for winter settlement by migrant falcons.

Further predictions

The predation-danger hypothesis for early migration by adults makes two predictions we are currently unable to test. The relative truncation of parental care during the season should be inversely related to the advantages to adults of earlier departure. We have argued that adult western sandpipers are on a tight time schedule, whereas adult semipalmated sandpipers have considerable leisure. We would expect this also to be true of dunlin, which make relatively short post-breeding movements. The slope of truncation of parental care should be steeper for western sandpipers (Neville 2002, Ruthrauff 2002) than that of semipalmated sandpipers (Gratto-Trevor 1991), or of dunlin, where detailed data on this relationship have not yet been published.

Unfortunately, the published data for western and semipalmated are not presented in formats that would allow us to test this prediction. Dunlin provide an excellent species to test further predictions about the importance of safety on migratory strategies. The 5 or more subspecies of this circumpolar species differ substantially in their migration and moult strategies, with some moulting following migration, similar to western and semipalmated sandpipers.

Alternative hypotheses

The major hypotheses previously suggested to account for the earlier departure of adult sandpipers center on seasonal patterns of food availability. These are not mutually exclusive with the predation hypotheses we have presented, but we don't feel that they are sufficiently well developed, or supported by adequate data, to account for the patterns we are considering.

Pitelka (1959, Pitelka et al. 1974) suggested that one parent often left the brood early to decrease competition with its chicks for food, and this hypothesis could be extended to early parental departures in general. Holmes (1966, 1969) measured a sharp decline in prey availability on the tundra in mid-July, but it is not clear that the departure of adults would significantly increase the prospects for juvenile growth. Dietary overlap is limited when the chicks are young. Moreover, broods of most calidrids typically do not remain on natal territories after hatch, and commonly change habitats once mobile (e.g. Miller 1983; *C. mauri* Ruthrauff and Neville, personal communication). Holmes (1972; p. 488), referring to western sandpipers, states that "With the decline in availability of insect larvae near the breeding areas, adult sandpipers and their fledged young move quickly, soon after breeding is completed, to feeding sites along the rivers and sloughs, and finally to the coast ..." where they fatten prior to southward migration (Gill and Jorgenson 1979). Finally, we question whether this mechanism can account for the widespread distribution of early departures over the range of species in which it occurs, which differ in foraging habitats and specializations. In some shorebird species, females cease laying eggs prior to a date after which their young would have difficulty finding food (Lank et al. 1985), and sandpipers would be unusual indeed if their timing of breeding was not such that the young had excellent prospects of finding sufficient food.

A second food-based hypothesis is that the earlier departure of adult sandpipers evolved to take advantage of a large and declining or a temporally-restricted abundance of prey at stopover locations along migratory routes. Schneider and Harrington (1981) documented a late summer decline in the major prey taxa of semipalmated sandpipers at a large staging area, and suggested that earlier arrival offered substantially higher food availability for migrants.

Few additional studies have measured comparable seasonal indices of invertebrate availability. We measured the seasonal pattern of potential prey abundance at Sidney Island during the southward migration period of 1992. In both July and August, we took 25 core samples along each of four 100 m transects, spaced over the mudflat (Table 1). Within the migration season, there was an almost two-fold increase, from about 10000 to 17000 potential prey items per core in total, due primarily to a large increase in *Corophium*, a major prey species of western sandpiper (Wolf 2001). There was no substantial decline within any of the major taxa. The food base at this site thus increased throughout the southward migration period. More studies of seasonal dynamics will be needed to further evaluate the generality of seasonal patterns and assess the potential effect of migrants in competition for a resource base (see also Piersma et al. 1994). Under the simplest hypothesis that food was being substantially depleted over the season at these sites (Schneider and Harrington 1981), we might expect later migrants to remain longer to accumulate sufficient fuel stores for the overwater flight, rather than moving

through more rapidly, assuming that individuals achieved similar masses prior to departure, rather than seeking alternative feeding areas. If alternative areas are available, however, the strength of the food limitation argument is lessened.

A further extension of a food-based hypothesis might consider the difference in moult patterns of adult and juvenile sandpipers after arrival on non-breeding grounds. Since rapid moult by adults may be energetically stressful, adults may gain more than juveniles by utilising food rich areas immediately following migration. However, there is little evidence in general for substantial depletion of relevant foraging resources for small shorebirds in sub-tropical or tropical wintering habitats (e.g. Schneider 1985, Kalejta 1993, Piersma et al. 1993; van der Meer et al. 2001, Zharikov 2002).

In summary, although the data are few, we see little evidence that changes in food abundance on breeding, stopover, or wintering grounds are a major general selective agent favouring earlier departures of adults and seasonal decreases in the duration of parental care. Any theory accounting for the early departure of adults will have to be quite general, since the pattern is so widespread across shorebirds, despite a range of feeding habits and migration distances, through both freshwater and marine sites. Within semipalmated sandpipers, for example, birds migrating through North Dakota foraged in and along shallow fresh and saline lakes, while those passing through the Bay of Fundy foraged on intertidal mudflats. While the database is regrettably scanty, we conclude that seasonal changes in food availability are unlikely to account for these phenomena.

Pacific dunlin and western sandpipers co-occupy intertidal areas of Alaska in July and early August, after which the western sandpiper leave and dunlin remain, while adults moult. Holmes (1971a) suggested that the dunlin's longer bills provide them with greater efficiency in harvesting marine resources, and also that the species' shorter migration distance facilitated remaining longer in the north, which we also believe, but possibly for a different reason. The dunlin's larger size might also provide it with a relative metabolic advantage in remaining longer at a more arctic site. Adults stay and take time to moult, utilising abundant resources (Alerstam and Högstedt 1982), and juveniles also persist for some time. However, a food-based hypothesis would have to demonstrate that comparable resources are not available in areas the birds do migrate to, and where studied, this does not appear to be the case, at least later in the winter (Kelly 2000). We suggest that remaining in a relatively predator-free zone, a shorter migration distance, and avoiding the southward wave of predators provide a cogent explanation for this difference in pattern.

Northward versus southward migration strategies

Semipalmated sandpipers

Many species of birds have different flight strategies on northward versus southward migration. Those of semipalmated sandpipers are particularly well documented. Following the breeding season, over a million semipalmated sandpipers move southeastward from their breeding grounds to the Maritime provinces on the Atlantic coast of Canada, and to New England (Fig. 4). After nearly doubling their body masses during coastal stopovers (McNeil and Cadieux 1972, McNeil and Burton 1977, Lank 1983, Dunn et al. 1988, Pfister et al. 1998), they depart, when weather systems provide favourable northeasterly tailwinds (Richardson 1979, Lank 1983), on courses that would take them to Africa if continued throughout the 2-3 day flight. However, their tracks shift southward over the mid-Atlantic, where cyclonic flow will often provide

northerly tail winds (Stoddard et al. 1983). Finally, the birds shift to a south or southwesterly track, flying in the northeasterly trade winds (Richardson 1976, Williams et al. 1977), making landfall in the West Indies or northern coast of South America (McNeil and Cadieux 1972, McNeil and Burton 1977). Many semipalmated sandpipers breeding in Alaska, or the far western Canadian arctic, take diagonal transcontinental flights rather than following the transoceanic route (Fig. 4; Harrington and Morrison 1979, Lank 1979, 1983; Morrison 1984).

On northward migration, semipalmated sandpipers follow the Atlantic coast or fly along inland routes, rather than attempting the reverse trans-Atlantic flights (Harrington and Morrison 1979, Morrison 1984, Gratto-Trevor and Dickenson 1994, Lyons and Haig 1995). The fat levels of northward migrants in Venezuela are substantially lower than those of southward migrants from the North Atlantic (McNeil and Cadieux 1972). The difference in migratory strategy difference has been attributed to seasonal variation in food availability (Harrington and Morrison 1979, Morrison 1984, Gratto-Trevor and Dickenson 1994) and prevailing wind conditions (Gauthreaux 1980). Clearly, flying the trans-Atlantic route in reverse would be exceedingly energetically challenging, starting with flights into the tradewinds, and encountering unpredictable conditions over the central Atlantic. It seems quite sensible that the birds instead move northwestward towards the southeastern U.S., and progress farther north overland.

We accept this basic argument, but also suggest that predation considerations also have influenced the seasonal difference in semipalmated sandpiper migration strategies in three major ways. First, the minimal predation danger for adults at stopover sites during July and early August permits the accumulation of the large fuel loads needed to make long southward flights without excessive risk. Semipalmated sandpipers preparing for transoceanic flight are exceedingly vulnerable. Lank (1979) noted that herring gulls (*Larus argentatus*) captured sandpipers preparing for transoceanic flight, which indicates their increased vulnerability, but also noted that no attacks on migrant shorebirds from raptors were seen despite daily field work throughout July and August of 1977.

Second, many young eastern birds take a more southerly migration route, moving to Virginia or the Carolinas rather than the Canadian Maritimes (Morrison 1984). This shift accounts for the relatively small number and short duration of passage by juveniles in the Maritimes (c.f. upper and lower panels in Fig. 5; Dunn et al. 1988) compared with North Dakota, which shows a more even age distribution. This shift from the route taken by most adults could be an attempt both to lessen the fuel load needed, since the overwater flight is shorter from more southerly sites, and to stay further ahead of migrant falcons.

Third, and more speculative, crossing the ocean may be safer than moving south along the coast. While transoceanic flights carry risks with respect to weather conditions and a lack of refuelling possibilities, they also completely avoid the possibility of being preyed upon at stopover sites along the coast.

Western sandpipers

Western sandpipers have a similar, if less dramatic, difference in northward and southward migration strategies, at least near the breeding grounds. In spring, hundreds of thousands of western sandpipers make a series of relatively short flights (e.g. 700–1000) km between several major stopover sites along the North Pacific coastline, up to the Copper River Delta of southern Alaska, prior to moving to the breeding grounds in western Alaska (Fig. 4, Senner et al. 1981, Iverson et al. 1996, Butler et al. 1997, Warnock and Bishop 1998, Bishop et al. 2000). After breeding, western sandpipers move to coastal staging areas in southwestern

Alaska, together with post-breeding dunlin (Gill and Jorgensen 1979, Gill and Handel 1990). Following a period of fattening, at a time when relatively few raptors are present (Handel and Gill 1992, see above), western sandpipers are next seen in large numbers in southwestern British Columbia and the coast of Washington, rather than on the estuaries of southeastern Alaska used so extensively in spring, even though these fall relatively close to the great circle routes from southern Alaska to the temperate-zone stopover sites. The birds thus apparently make a single direct flight of ca. 2400 km, rather than a series of short flights. This distance is not extreme for calidridine sandpipers, and birds presumably fly when tailwinds assist the flight (cf. Butler et al. 1997, Hedenström and Weber 1999, Kvist et al. 2001).

The western sandpiper pattern contrasts with seasonal differences in migration strategies of several species described by Gudmundsson et al. (1991), in which southward flights are made in a series of short flights, but birds overfly sites in spring. They suggest that this pattern occurs because food is likely to be better at successive sites as birds move southward, favouring shorter flights. The western sandpiper pattern also contrasts with a general pattern of having spring masses lower than those on autumn migration, at the same sites (Johnson 1985).

Butler et al. (1996) speculated that the seasonal difference in routes was due to favourable versus unfavourable wind conditions for direct flights across the Gulf of Alaska. We compared estimates of the time and energy costs of flying southward and northward between western Alaska and southwestern British Columbia, with and without stopovers, following the logic of “detour analysis” (Alerstam 2001). Distances were measured as great circle routes between Nome – Copper River – Stikine River – Fraser River estuaries (Butler et al. 1997) versus a direct great circle flight from Nome to the Fraser River. The occurrence of favourable winds and wind speed at about 1500 m altitude (Richardson 1979) were derived from Radiosonde data (Anonymous 1993) collected at Port Hardy, on northern Vancouver Island, British Columbia, and at Anchorage, Alaska, coded as the fraction of days when tailwinds would occur in a compass quadrant of the flight direction of the bird (Butler et al. 1997). We assumed that after accumulating the necessary fuel reserve, birds wait for a favourable wind before making a migratory flight. Flight time was estimated by dividing the distance by the sum of the assumed maximum range speed (38 kmh^{-1}), plus the mean following component of winds (northwesterly in July and August, southeasterly in spring). Flight costs were assumed to be 10.2 kJh^{-1} , and fat reserves to have an energy value of 39 kJ/g (Blem 1990). We assumed that reserves were built up at a rate of 0.34 gd^{-1} (Butler et al. 1987). This rate may be low; using a higher rate alters the magnitude of differences, but not the conclusions from, these analyses.

Our calculations are summarized in Table 2. For a bird of about 22.7 g lean mass (Butler et al. 1997) making a direct southward flight, the required departure mass in Alaska would be 31.5 g, a reasonable estimate for this species (B. K. Sandercock, pers. comm.). We calculate the direct southward trip as taking 28.9 days. This matches data from three western sandpipers fitted with radio transmitters near Nome, Alaska, after the breeding season, which were first detected in southern British Columbia 23–29 days later (Butler et al. 1996).

The distances of the direct and stopover strategies are similar because the stopover sites sit close to the great circle route between western Alaska and southern British Columbia. However, the lengthy waiting time associated with the probability of encountering favourable winds from each stopover site makes the stopover strategy much more time consuming: 46.2 vs. 28.9 days. The direct flight on southward migration appears clearly to be the more timely and economical strategy.

On northward migration, prevailing winds are often from the southeast. Our calculations suggest that a direct flight would again have an advantage in terms of less time (25.9 versus 30.4 d) and a similar energy expenditure. These simple calculations do not consider the higher transport costs of carrying a larger fuel load, but our conclusions remain when we incorporate these using Alerstam's (2001, see his eqn. 1a) method. Note that this conclusion does not depend on the flight-cost assumptions used in Table 3 (cf. Alerstam 2001). Western sandpipers could still save time and energy on northward migration by flying directly north, rather than stopping over en route. Why do they not do so?

The northward migration of western sandpipers in southern British Columbia coincides exactly with a sharp peak in the abundance of migrating peregrines (Fig. 3). In contrast to southward migration, when falcons are still tied to and dispersed on breeding territories, spring falcons may in fact track sandpiper movements northward. Assuming increasing mass-specific predation risk (Ydenberg and Burns 2002), individuals that built up larger reserves to make a direct flight would be both absolutely and relatively more vulnerable in British Columbia than those preparing for shorter flights along the coast. Several other aspects of migratory behaviour between seasons also indicate the anti-predator behaviour is more important in the spring. Western sandpipers migrate in much larger flocks on northbound compared to southbound migration, and stop over only on large and open estuarine sites. In contrast, when southbound they use diverse stopover habitats, including many small sites (O'Reilly and Wingfield 1995). In summary, a danger management strategy provides a coherent explanation for these route selections, if we include the assumption that sandpipers avoid long staging periods to accumulate large fat reserves when exposed to predators (see Houston, 1998).

General discussion and future directions

Alerstam and Lindström (1990) identified time, energy and safety as three major considerations governing avian migration strategies. We have shown that strategies for danger management have previously unappreciated explanatory power to resolve both general and specific aspects of the migration patterns of small sandpipers that are not adequately explained by time and energy considerations alone.

Mating, parental care, and migration systems

We have considered why adult sandpipers in general depart prior to their young. A related and long-standing conundrum in shorebird biology has been why parental care is male biased in so many socially biparental species, or why females often leave first (e.g., Currie et al. 2001, Gratto-Trevor 1991). For western and semipalmated sandpipers, Erckmann (1981) showed experimentally that single parent incubation was non-sustainable. Thus both parents remain with a breeding attempt through hatch. After hatch, however, females of both species, and of dunlin, typically abandon broods a week or more prior to the departure of males. In western sandpipers, but possibly not in the other two species, females also spend the non-breeding season farther south (Nebel et al. 2002), suggesting an association between migration distance and early departure. Furthermore, among calidridine sandpipers, species with longer migrations tend to show reduced parental care compared to short distance migrants, and have promiscuous or polygamous, rather than monogamous, social mating systems (Myers 1981, Reynolds and Székely 1995, see also Pitelka et al. 1974). Myers (1981) concluded that this co-varying pattern of mating, parental care and migration patterns is consistent with the hypothesis that "longer migration distances select for early departure, leading to the development of behavioural tactics

for single-parent care; this then facilitates the evolution of non-monogamous mating patterns." A major difficulty with this hypothesis has been identifying why early departure, a correlate of abandonment by one parent, need be associated with longer migration distances. Why might not parents leave at the same time, and the longer distance migrant simply arrive farther south at a later date? We believe that the spatial and temporal distribution of predation danger provides a potential mechanism favouring earlier departure, rather than later arrival, because it creates a general and widespread "deadline" for the arrival at non-breeding sites in ways that variation in food resources, for example, usually does not.

Our hypothesis is that southbound sandpiper migrants are able to gain a safety advantage either by migrating ahead of the wave of falcon migration (western and semipalmated sandpiper), or by delaying and moving south after it has passed (e.g. Pacific dunlin). Longer distance migrants advance departure from breeding areas because later departures would require them to fly past large numbers of falcons established along migratory routes and stopover areas. Short distance migrants in contrast, delay departure in order to avoid occupying their wintering area before large numbers of falcon have flown past. Extending parental care necessarily delays the earliest date at which departure could take place. We hypothesise that in long distance migrants, adults trade off the fitness gains of extended parental care against the fitness gains of increased survival gained by early departure. For species in which females spend the non-breeding season farther south, like western sandpipers, this could explain their earlier departure. An additional possibility is that females might be more vulnerable to predators, and thus alter their trade-off accordingly to migrate at an even safer time than do adult males.

Behavioural and evolutionary ecology of danger management

We have treated the distribution of predators as a static predator landscape, but in fact this may reflect a dynamic game in which both predators and prey adjust their distributions in time and space. We studied the most abundant shorebird prey species, thus those to which specialised predators would be most likely to match distributions.

It is not yet clear to what extent the timing and routing of sandpiper migration can be adjusted by behavioural as opposed to evolutionary mechanisms, though we are inclined to the view that individuals of many migrant species are rather flexible (c.f. Fransson and Weber 1997). The hemisphere-wide recovery of raptor populations since the 1970s has undoubtedly brought with it a great increase in danger for many migratory species. As predicted by safety consideration, western sandpipers make less extensive use of more dangerous stopover sites than was the case 25 years ago. At Sidney Island, despite good feeding conditions, the usage by migrants has fallen, their stopover times have decreased, and the masses of those birds that are present has decreased, as predicted by a condition-dependent habitat choice mechanism trading off danger and feeding priorities (Ydenberg et al., 2002, Ydenberg et al. unpublished data). Parallel changes have happened for semipalmated sandpipers passing through Kent Island in the 1970s (Lank 1983) versus the 1990s, when merlins hunt throughout the migration season (O'Reilly, pers. comm). We suggest that a powerful way of testing the potential influence of safety consideration on migratory strategies may be to examine how migratory behaviour in other species has changed as predators have become more numerous in the shorebird landscape over the past 20 years.

Finally, the effects we suggest and document here should not be restricted to sandpipers and falcons, although it is plausible that these groups have relatively tight relationships. We

hope that the examples we have presented will stimulate others to consider how danger management may affect the systems and questions they study.

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Table 1. Total number (N) of major invertebrate taxa measured in 25 cores from each of four areas of the mudflat at Sidney Island, during July and August, 1992. Each core was 10 cm in diameter, and was inserted to a depth of 5 cm, beyond the maximum probing depth of western sandpipers. The cores were frozen and stored. After the field season they were thawed, sieved through a 500 µm mesh screen, and all invertebrates sorted. These were identified to family or genus using a reference collection, counted, and stored in 85% ethanol. All of the taxa recorded have been confirmed as prey of western sandpipers (Wolf, 2001).

		Polychaeta	Crustacea			Amphipoda	Bivalvia	
Month	N	Worms	Corophium	Sinelobus	Other	Gammarid	Bivalve	Other
July								
Area 1	4502	1396	347	1661	41	324	725	14
Area 2	1416	136	1102	62	1	75	1	37
Area 3	1154	269	309	329	17	160	52	17
Area 4	2705	1591	955	49	22	46	32	11
Total	9777	3392	2712	2101	81	604	810	79
Aug								
Area 1	4460	874	2301	544	13	638	89	0
Area 2	3770	547	3102	30	4	83	0	0
Area 3	5101	755	2423	1138	20	729	31	0
Area 4	4013	799	3174	4	0	28	0	4
Total	17344	2975	11000	1716	37	1478	120	4

Table 2. Comparison of the energetic and time costs of migrating directly from Nome, Alaska (great circle route) versus following a coastal route with stopovers between Alaska and southwestern British Columbia. Similar values are obtained if starting from the Yukon-Kuskokwim Delta. The coastal route is comprised of legs from Fraser – Stikine River (909 km), Stikine – Copper River (929 km), and Copper River – Nome (1050 km) (Butler et al. 1997). Calculations are described in the text.

	Southward		Northward	
	Direct	2 stopovers	Direct	2 Stopovers
Distance (km)	2852	2888	2852	2888
% wind favourable days	39.7	12.5	0.320 ¹	0.320 ¹
mean wind speed (kmh ⁻¹)	45.7	49.2	58.7 ¹	58.7 ¹
flight time (h)	33.9	32.9	29.3	29.7 ²
total fat required (g)	8.9	8.6	7.7	7.8
total fat loading time (d)	26.1	25.3	22.6	22.9
waiting time per stopover (d) ³	1.4	6.5	2.1	2.1
Total time (d) required	28.9	46.2	25.9	30.4

¹ Northward wind strengths and directions are given in Butler et al. (1997), coded in compass quadrants.

² Butler et al. (1997; see their Table 2) calculate each leg of the flight separately, and arrive at figures of 36.4 h flight time and 9.6 g fat required. The discrepancy arises because they use a smaller following wind speed of 41.8 kmh⁻¹ on the Fraser – Stikine River leg.

³ Calculated as the mean of the probability distribution that a favourable wind (and hence departure) first occurs on day 1,2,3, N

FIGURES

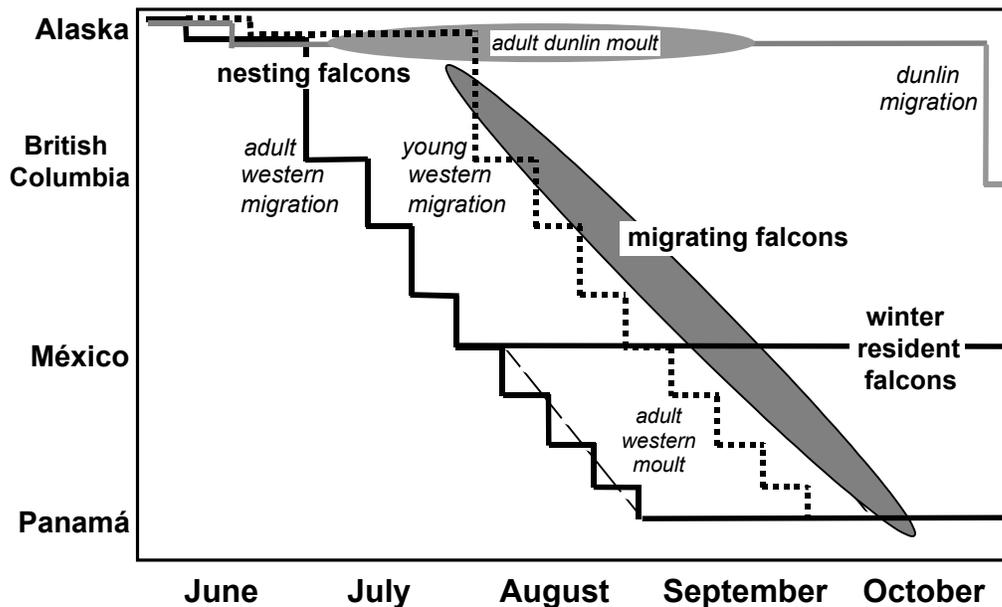


Fig. 1. A schematic representation showing the relationships between the "predator landscape" created by falcons, which disperse from arctic breeding areas and migrate through and occupy temperate and neotropical non-breeding area, and the southward migration timing of western sandpipers and dunlin. Crosshatched areas represent the spatial and temporal distribution of falcons. On arctic breeding grounds, falcons are widely dispersed at low local densities. The darker diagonal oval represents a concentrated southward-moving wave of post-breeding migrant adults falcons and their fledged young. The lighter area to the right of the wave represents a relatively low density of falcons that become resident for the non-breeding season, left behind as the main wave of raptors continues southward. The stair-shaped black lines represent the southward movement of peak western sandpiper migration, with solid lines for adults and broken lines for juveniles. Vertical steps represent migratory flights, and short horizontal segments are residence periods at stopover sites. The long horizontal lines indicate residence on non-breeding grounds, shown for one latitude in México and one in Panamá. The diagonally-shaded areas at non-breeding sites show the timing of adult wing moult at non-breeding sites. The grey line represents the timing of Pacific dunlin breeding, adult moult, and southward migration. Sources are given in the text.

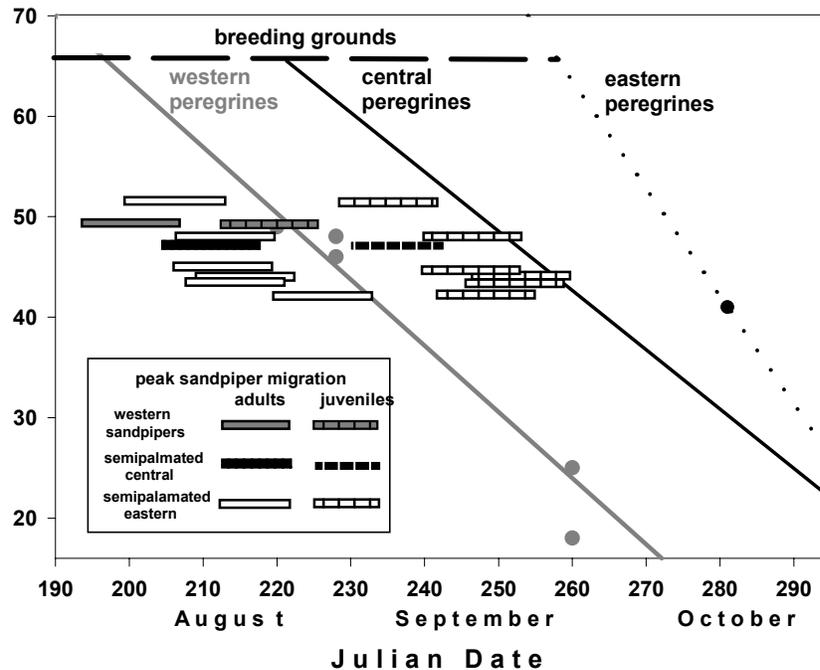
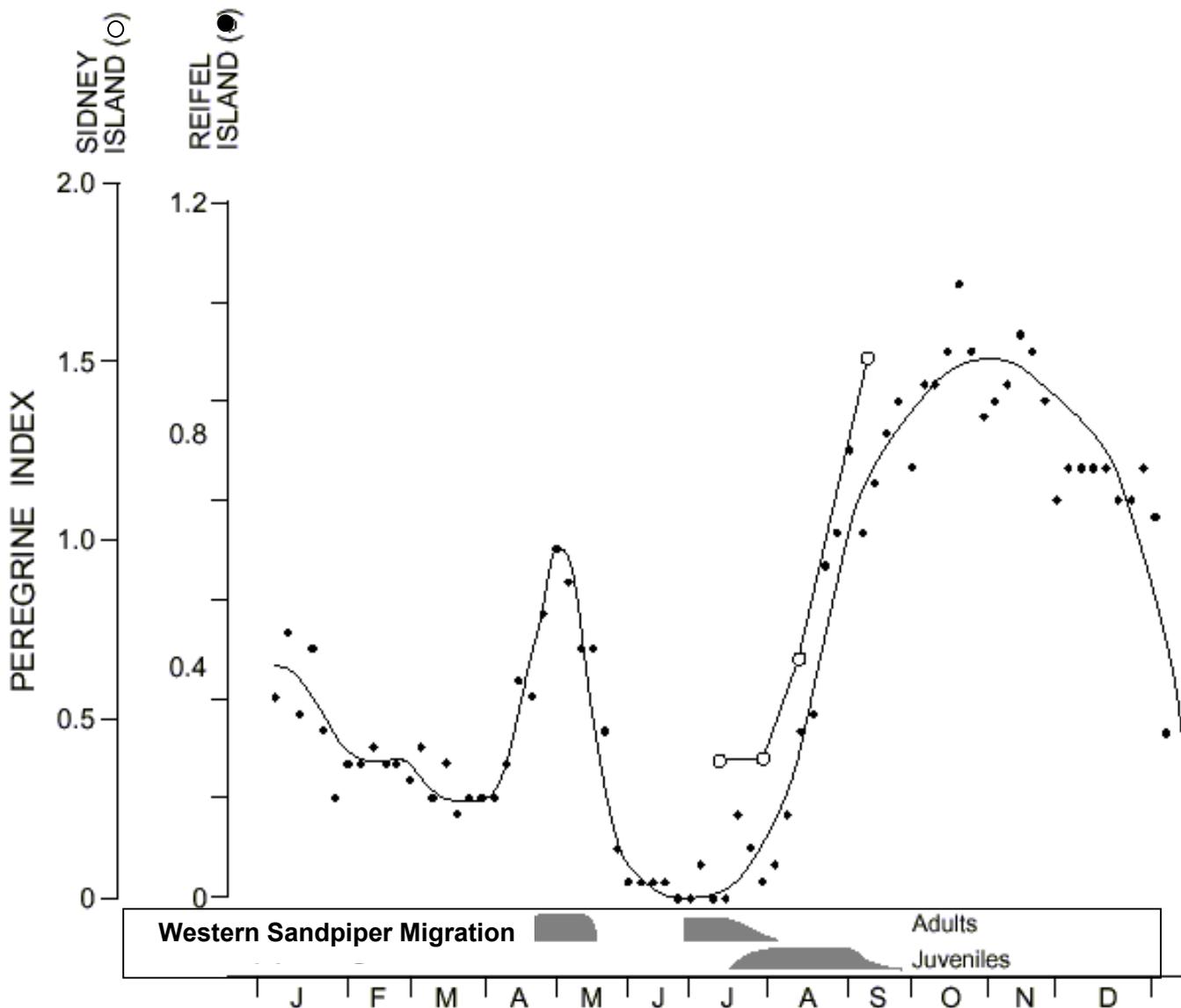


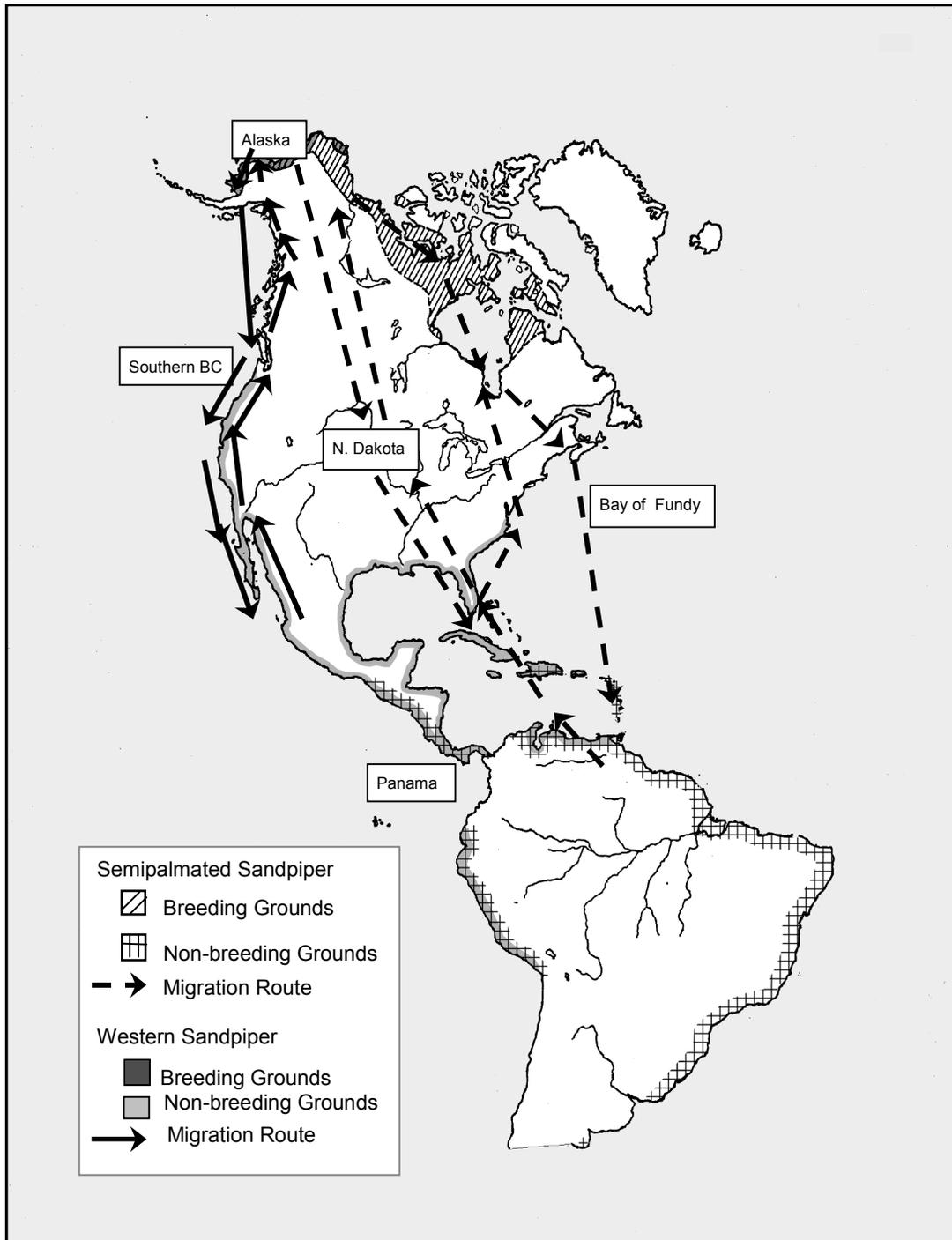
Fig. 2. The latitudinal progression of southward migration dates of peregrine falcons across North America, with respect to peak migration timing of western and semipalmated sandpipers. The dashed line at the top represents falcons on their breeding grounds. West coast data are depicted in grey, central mid-continental data are black, and open bars and the dotted line are eastern birds. The grey line for western peregrines is based on passage dates recorded in six regional field guides (Bent 1927, Jewett et al. 1953, Ridgely 1976, Campbell et al. 1990, Raffaele et al. 1998, Contieras 1998). The black line for passage down the central flyway is taken from Schmutz et al. (1991, their Fig. 3), based on recovery times of banded peregrines of the migratory races *anatum* and *tundrius*, marked predominantly in the Canadian arctic north of 60°. The dotted line of eastern passage is anchored at Hawk Mountain, Pennsylvania (Heintzelman 1975), with a rate of southward migration as measured by satellite-telemetry (172 km d^{-1} ; Fuller et al. 1998) from a sample of central and eastern migrants. The timings of migration by adult and juvenile sandpipers are depicted as bars of 14-day periods centred on reported peak abundances; methodologies varied among studies. Western sandpiper data are from 2789 birds captured in southern British Columbia between 1985-2001 (Canadian Wildlife Service and Centre for Wildlife Ecology). Semipalmated sandpiper data from the Central flyway are from Lank 1983, and data for the eastern flyway, from north to south, are from: Morrison 1984, McNeil and Cadieux 1972, Hicklin 1987, Dunn et al. 1988, Lank 1983, and Page and Bradstreet 1968.

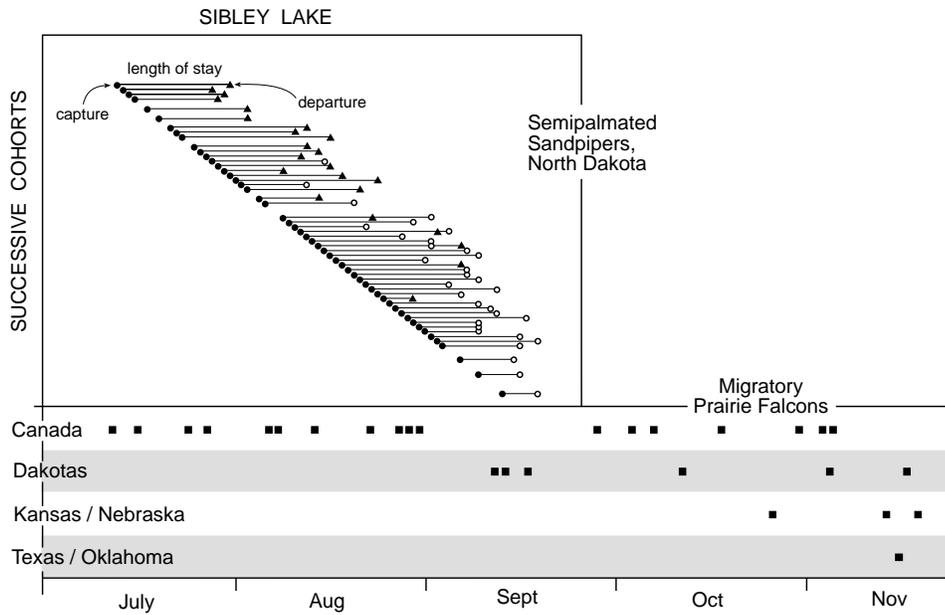
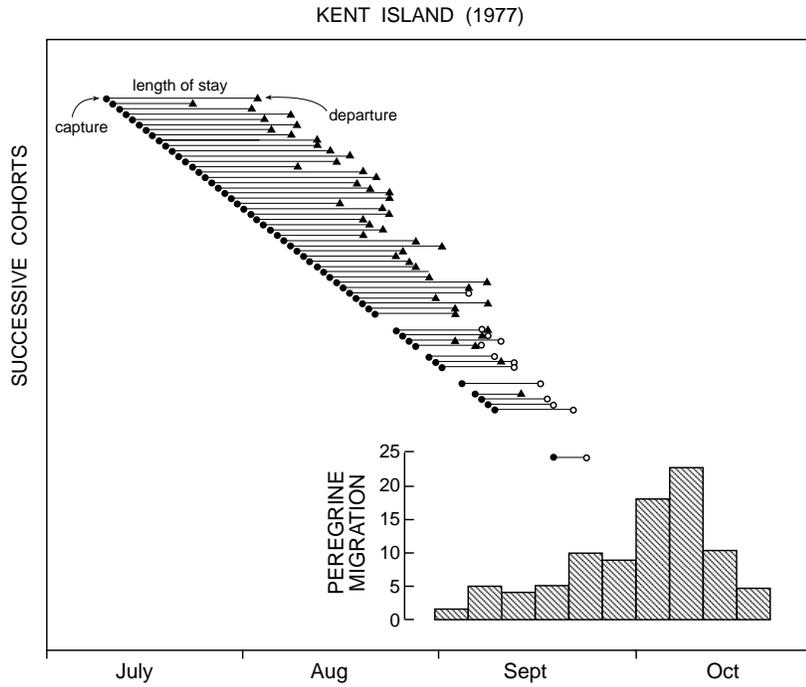
Fig. 3. An index of seasonal variation in peregrine abundance measured in the Strait of Georgia, British Columbia, and the passage timing of northward adult and juvenile migrant western sandpipers. Small solid dots: George C. Reifel Migratory Bird Sanctuary on the Fraser estuary; open dots: Sidney Island. See map in Lissimore et al. (1999) or Ydenberg et al. (2002) for locations. At Reifel, a near-daily 1h lunchtime watch has been mounted since 1986. The index reported here is the mean number of daily peregrine sightings, calculated over 5 d periods, and averaged over all years (1986–2000). The Sidney Island data show the number of peregrines sighted per party field hour during sandpiper mist-netting operations in July and August, averaged over 2 week periods. Both methods show a steep rise in the frequency of falcon sightings in late July.



Sandpiper migration

Fig. 4. Breeding, nonbreeding ranges, and northward and southward migration routes of the western and semipalmated sandpipers. Locations named in the text are labelled.





Sandpiper migration

Fig. 5. Stopover durations of semipalmated sandpipers at Sibley Lake, North Dakota (lower), and Kent Island, in the Bay of Fundy (upper), with respect to season, and the timing of migratory movements of falcons. At both sites, sandpipers were mist-netted daily throughout the migratory period, colour-marked, and censused daily to determine minimum stopover residency periods, defined as date captured through the date last seen (Lank 1983). Each horizontal bar shows the capture and mean date last seen of successive daily cohorts of marked sandpipers. The bottom of the lower panel plots the southward migratory progression of prairie falcons (from Fig. 1 in Schmutz et al. 1991). The bottom of the upper panel shows the cumulative passage of peregrines at Hawk Mountain, Pennsylvania (from Fig. 6 in Heintzelman 1975).