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Migration of two calidrid sandpiper species on the predator landscape: how stopover time and hence migration speed vary with geographical proximity to danger

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The effects of relative fuel load on migration speed and on vulnerability have been investigated, but the effects of seasonal variation in predation danger on the amount of fuel and duration of stopover have not been considered. We analyzed seasonal patterns of stopover residence times for western and semipalmated sandpipers *Calidris mauri* and *C. pusilla* on southward migration in relation to the passage of migratory peregrine falcons *Falco peregrinus*. We predicted that individuals on stopover far in advance of the seasonal arrival of falcons would adjust stopover length and hence relative fuel load to migrate slowly and cautiously. We predicted that individuals on stopover later in the season would increase migratory speed as the arrival of migratory falcons came closer, while individuals on stopover under or behind the passage of falcons would migrate slowly. Adult and juvenile semipalmated and adult western sandpipers migrated prior to seasonal increases in peregrine abundance, and as predicted, the seasonal patterns of their stopover durations are consistent with an increase in the speed of migration as the date of peregrine arrival approached. Juvenile western sandpipers, in contrast, migrating concurrently with falcons, slowed their speed of migration as predator abundance increased. Stopover patterns differ between species due to different relative fuel loads. The results fit predictions made based on a 'mortality-minimizing' migration strategy.

The tactics used in long distance avian migration are thought to have been selected for by time, energy, and safety considerations (Alerstam and Lindström 1990). Most early work focused on time and energy aspects (Lindström and Alerstam 1992, Hedenström and Alerstam 1997). More recently, the influence of predation danger has attracted theoretical and empirical attention (Dierschke 1998, Dierschke 2003, Lank et al. 2003, Ydenberg et al. 2004, 2007, Schmaljohann and Dierschke 2005, Lind and Cresswell 2006, Pomeroy 2006, Ydenberg et al. 2007, Bauer et al. 2010). Here we explore how minimizing the probability of mortality affects decisions made by migrants in the course of passage at a single stopover site.

Long distance migrants journey between breeding and non-breeding areas in successive flights between stopover sites at which fuel reserves are replenished. Most time during migration is spent at stopover sites (Hedenström and Alerstam 1997), and so the progression of migration is strongly influenced by the length of stopovers (Alerstam and Lindström 1990). Speed of migration and stopover length are related by the formula

$$S = \frac{c(1 - (1 + f)^{-0.5}}{t_e + f/k}$$

(from Alerstam and Lindström 1990, described in Alerstam and Hedenström 1998, and Houston 1998), where S is speed of migration (km d^{-1}), f is the relative fuel load (fuel load relative to lean body mass), c is a constant (km), k is the fuelling rate (rate of change in f; d^{-1}), and t_e the search/settling time (d).

The general form of this relationship is shown in Fig. 1, which illustrates that as migrants feed and load fuel at a stopover site, the potential flight range increases, but at a decelerating rate due to the drag created by the fuel load. The achievable speed of migration (km d^{-1}, as measured over the entire migration) rises to a maximum and then falls as the fuel load is enlarged. Migrants with very large fuel loads are able to make very long flights, but the speed of migration is low because the necessary fueling time is disproportionately long. Migrants with small fuel loads can make only short flights, but due to the amount of 'upfront' time required to settle at each site and be able to begin loading fuel, the fueling time is long and the speed of migration slow. The fastest migration speeds are attained at intermediate fuel loads (Fig. 1). Note especially that below the maximum speed, increases in stopover time increase speed of migration, while above the maximum speed, decreases in stopover time increase speed of migration.

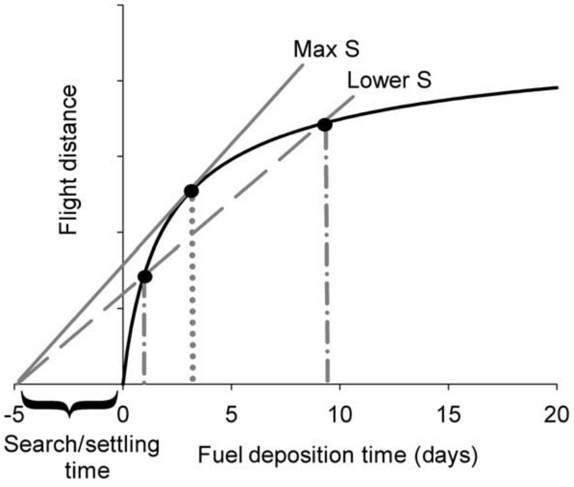

Figure 1. Flight distance as a decelerating function of the time (and hence the amount of fuel loaded) at a stopover site. The speed of migration (S) varies with stopover time, as shown by slopes of the diagonals. With a given fuel-loading rate (black curve), migrants maximize their speed of migration by departing with the stopover time corresponding to the steepest tangent line. Earlier or later departures (dashed grey line) slow migration speed. Short stopover times allow slow and cautious migration, while long stopover times permit great distances to be flown. Based on Alerstam and Lindström (1990).

Tactics that minimize the time or energy expended on migration have been identified. Time-minimizers are assumed to select the fuel load/stopover time providing the maximum speed of migration (Alerstam and Lindström 1990). 'Energy-minimizers' use tactics that minimize the energy expended while on migration, attained at the range-maximizing fuel load, which is smaller than that of time-minimizers (Pennycuick 1975).

Predictions concerning safety tactics for migrants are less well defined. We assume that safety demands select for tactics that minimize the cumulative probability of mortality from all sources ('mortality minimizers'). For example, if a migrant has a choice of strategy that results in no depredation, but increases starvation, mortality minimizers should accept increased predation danger if it reduces the overall mortality. Alerstam and Lindström (1990) reasoned that mortality-minimizers should minimize mortality per unit of distance travelled, and suggest that this results in a lower speed of migration than a migrant attempting to minimize time spent on migration. Their analysis takes into account the increased vulnerability that results from an increased fuel load. They do not explicitly consider seasonal changes in predation danger. Tactics that could be employed to reduce mortality include: migrating at times or along routes with reduced predator presence, even if the rate of migration is slowed; avoiding habitats or stopover sites with higher predation danger; increasing vigilance; and reducing the fuel load to decrease wing-loading, thereby increasing escape performance (Alerstam and Lindström 1990, Burns and Ydenberg 2002, Ydenberg et al. 2002, 2004, Lank et al. 2003, Pomeroy 2006, Pomeroy et al. 2006, Sansom et al. 2009, Bauer et al. 2010).

Raptors such as accipiters and falcons are also largely migratory (Heintzelman 1975, Bildstein and Zalles 2005). Worcester and Ydenberg (2008; see also Lank et al. 2003, Ydenberg et al. 2007) describe the southward progression of peregrine falcon *Falco peregrinus* migration in North America, showing that it occurs across a broad front with a measurable progression rate and a distinct geographical orientation. These raptors hunt actively each day on migration, and thus induce large changes in local predation danger as the wave of migrants passes over. Here we test the hypothesis that predictable seasonal changes in the stopover behavior of sandpipers will be observed at a stopover site throughout the course of southward migration as the predation danger induced by migratory peregrines changes. We assume that danger rises as the wave of migratory peregrines approaches.

The predation danger (sensu Lank and Ydenberg 2003) posed by peregrines is likely to affect the speed of migration. Migrations with many short stopovers and small fuel loads slow the overall speed of migration and hence extend the time required to complete a migration. However, the stay at each site is likely relatively safe because the small fuel loads compromise escape performance only slightly, and fuel can be accumulated carefully (e.g. with high vigilance, in safer places). These are tactics for a slow and cautious migration. Increasing the speed of the migration to the maximum possible (Fig. 1) requires longer stays and higher fuel loads, and thus the stay at each site is more dangerous. The large fuel load necessary for extremely long flight necessitates long stopovers, with accompanying highly compromised escape performance. This requires few, but relatively dangerous stopovers. We previously showed that western sandpipers *Calidris mauri* made a decade-long adjustment of migratory tactics as peregrine populations recovered after 1973 (when DDT was banned and the Endangered Species Act became law), shortening stopover times and reducing fuel loads at a more dangerous stopover site, while maintaining higher fuel loads at a less dangerous site (Ydenberg et al. 2004). Here we test whether analogous changes occur on a seasonal scale.

The earliest southbound sandpipers travel far ahead of the southward migrating wave of peregrines (hereafter 'falcon front'), and we predict that they are able to migrate relatively slowly. Their large headstart keeps them safe from migrating peregrines, and they can take extra time for caution to keep safe from other predators and hazards that will be encountered along the route. Somewhat later migrants have greater temporal proximity to the earliest migrant peregrines, and we predict that to maintain or increase their headstart distance on the falcon front they increase speed of migration. This would increase their vulnerability to other predators, but keeps to a minimum exposure to migratory falcons along the remainder of the migration. The latest migrants are directly under the falcon front, and we predict that they revert to more cautious behavior, and so slow the rate of migration. These predictions are depicted schematically in Fig. 2.

Methods

We captured, banded and resighted adult and juvenile western (*Calidris mauri*) or semipalmated (*Calidris pusilla*) sandpipers at three different sites on southward migration.

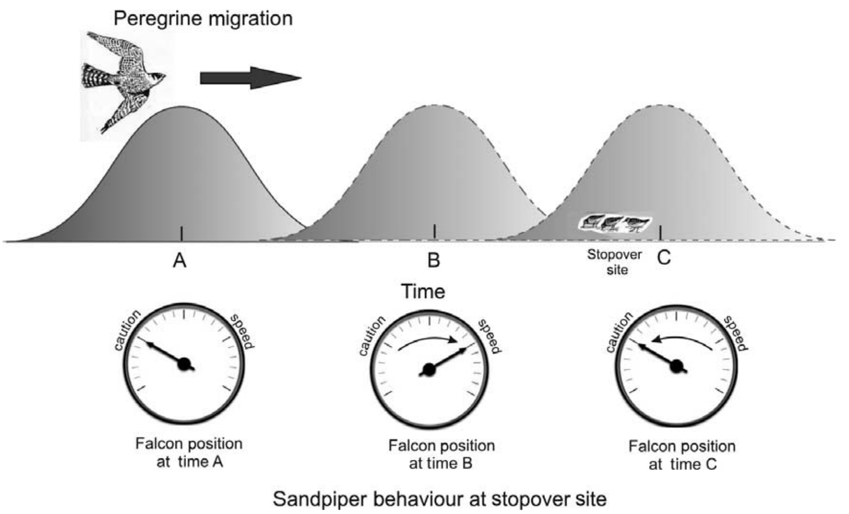

Figure 2. How migratory behaviour (speed vs caution; inset) of sandpipers at a stopover site is predicted to change with temporal proximity to migrating falcons. The wave (Fig. 3) of migratory falcons is represented far from (position A), approaching (position B) and passing over (position C) a stopover site where sandpipers load fuel. Sandpipers stopping over far in advance of falcon arrival (falcon wave at position A) are in little danger and can proceed slowly and cautiously, thus gaining extra safety from other predators that will be encountered along the migratory route. As the wave approaches (position B) sandpipers at the stopover site alter fueling behaviour to increase migration speed and thus retain distance on the falcon front. Sandpipers under or behind the wave (position C) must behave more cautiously.

Both species have temporally separated age-specific southward migrations, with adults migrating about a month before juveniles (Page and Middleton 1972, Butler et al. 1987; Fig. 3).

Western sandpipers were captured at Sidney Island, British Columbia (48°38′N, 123°20′W) during the 1990s. Western sandpipers use this site and others within the surrounding Strait of Georgia as the first stopover point after departing Alaska. Most continue south along the Pacific coast, although some head southeast towards wintering areas along the Gulf of Mexico and Caribbean (Butler et al. 1996). Adult passage is in July, and juvenile passage during August (Butler et al. 1987). Peregrine falcon arrival in the Strait of Georgia begins to rise steeply in late July (Lank et al. 2003). Adult western sandpipers therefore migrate ahead of the falcon front, while juvenile western sandpipers experience rapidly increasing predation danger throughout their migratory period (Lank et al. 2003, Niehaus and Ydenberg 2006).

Semipalmated sandpipers were captured at Sibley Lake, North Dakota (46°57′N, 99°43′W) during the late 1970s. Sibley Lake is a permanent saline lake on the western edge of the mid-continental semipalmated sandpiper flyway. Migrants stopping over here are making a transcontinental migration in a southeasterly direction, with adult passage in August, and juvenile passage during September (Lank 1983, 1989, Morrison 1984). Falcons arrive in mid- or late September (Lank et al. 2003, Worcester and Ydenberg

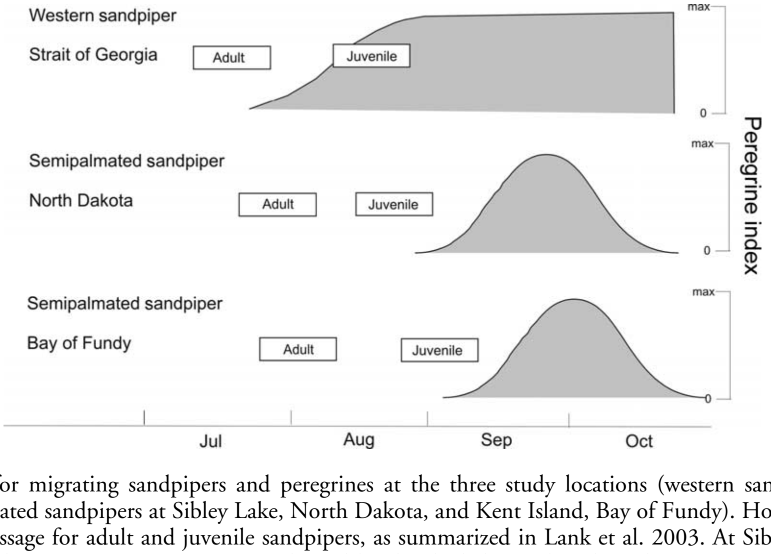

Figure 3. Passage timing for migrating sandpipers and peregrines at the three study locations (western sandpipers at Sidney Island, Strait of Georgia; semipalmated sandpipers at Sibley Lake, North Dakota, and Kent Island, Bay of Fundy). Horizontal bars give the 14 d period centered on peak passage for adult and juvenile sandpipers, as summarized in Lank et al. 2003. At Sibley Lake and Kent Island, peregrines are migrants, and passage occurs as a wave (indicated by the shaded area; based on data in Worcester and Ydenberg 2008). Peregrines are winter residents in the Strait of Georgia, with numbers accumulating from late July onward. Maximum peregrine numbers are scaled to 1.0.

2008). Adult and most juvenile semipalmated sandpipers at this site therefore migrate ahead of the falcon front. Semipalmated sandpipers were also captured at Kent Island, New Brunswick, in the Bay of Fundy (44°35′N, 60°27′W) during the late 1970s, a small stopover site similar in many respects to Sidney Island. Adult passage is in August, and juvenile passage during September, with most migrants preparing for a long transoceanic flight (McNeil and Cadieux 1972, Lank 1983, 1989). Falcons arrive in late September (Worcester and Ydenberg 2008). Both adult and juvenile semipalmated sandpipers at this site therefore migrate ahead of the falcon front.

At each of the sites migrants were caught, assigned an age class based on plumage characteristics, and colour banded (western sandpipers; n = 282 adults and 1021 juveniles) or marked with wing tags (semipalmated sandpipers; Sibley Lake, n = 636 adults and 800 juveniles; Kent Island, n = 1172 adults and 281 juveniles). At Sidney Island, marked birds were searched for almost daily from 3 July to 3 September, between 1992 and 2001. These data are described by Ydenberg et al. (2004), who analyzed the decade-long trend in sandpiper stopover residency time with respect to changes in falcon numbers. Capture, marking and resighting methods at Kent Island and Sibley Lake are described by Lank (1979). Trapping and resighting of semipalmated sandpipers occurred between 13 July and 27 September 1978 at Sibley Lake, and 11 July and 23 September 1977 at Kent Island. Stopovers and departures from these sites were analyzed by Lank (1983) with respect to weather patterns, and by Lank et al. (2003) with respect to falcon migration, but no detailed CMR analysis was undertaken.

We used Cormack–Jolly–Seber (CJS) mark–recapture methodology for western sandpipers, and program MARK for semipalmated sandpipers (Lebreton 1992, White and Burnham 1999, Ydenberg et al. 2004) to estimate the daily probability of departure from the stopover site. The daily residence probability estimates were converted into mean conditional residence times. A custom CJS analysis for western sandpipers was used to account for the variable recapture effort between years, which cannot be accomplished in program MARK. Program MARK allowed us to analyze simultaneously the patterns of adults and juveniles, giving greater strength to comparisons of stopover lengths between age groups in semipalmated sandpipers. The effects of week and year on the two age classes in western sandpipers, and the effects of 3-d intervals and 1st capture effect on the two age classes in semipalmated sandpipers (Brownie and Robson 1983), were combined to generate candidate model sets. There were insufficient captures of western sandpipers in each year to allow for a 3-d analysis. As we did not have a specific prediction of the shape of the trends in residence time, both linear and quadratic models were included for each variable. Previous analysis of semipalmated sandpiper residence time (Brownie and Robson 1983) has shown that there was a different probability of recapture in the first recapture session, when compared with subsequent recapture probabilities. This 'first capture effect' has not been shown in western sandpipers, and therefore we had no a priori reason to include it in our models.

Models were ranked based on Akaike's information criterion (AIC) (Burnham and Anderson 2002). Based on the AIC weights, weighted daily residence probability estimates were calculated. The daily residence probability estimates were converted into mean conditional residence times for each time-interval and age group ($-1/\ln$[daily local residence]). True survival was assumed to be 100% over the residency period.

Predictions

Our general hypothesis is that western and semipalmated sandpiper stopover times (and hence speeds of migration) are influenced by the temporal proximity to the approaching falcon front: the predation danger posed by peregrine falcons at a site increases as the front advances. Predictions about seasonal changes in stopover time differ between age groups and locations because the arrival of the falcon front occurs much earlier (early August) at Sidney Island than at the other sites (mid- or late September).

Age- and site-specific effects on migration speed of changes in relative fuel load were calculated from Alerstam and Lindström's (1990) formula, and are presented in Fig. 4. Western sandpipers at Sidney Island accumulate small fuel loads, below that which would maximize their speed of migration. Adults migrate in advance of peregrines. The early-August arrival of peregrines at Sidney Island means that juveniles migrate under much more dangerous conditions. We therefore predict that seasonal fuel loads and stopover times should increase in the course of adult passage (to increase speed of migration) and then decrease in the course of juvenile passage (to slow speed of migration).

Semipalmated sandpipers at both sites accumulate fuel loads well in excess of the speed of migration maximum (Alerstam and Lindström 1990), and both adults and juveniles migrate ahead of falcons. Both age-classes should increase migration speed as the falcon front approaches,

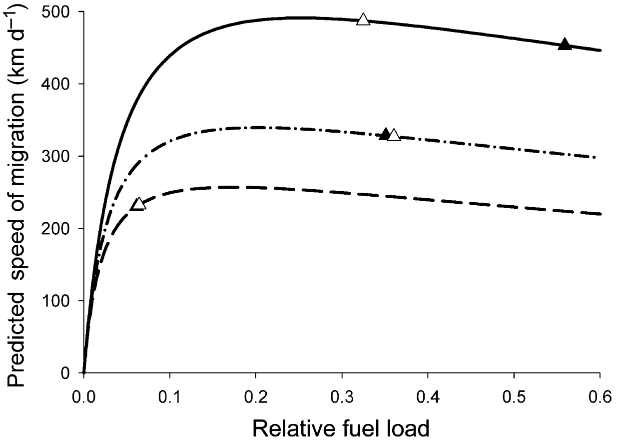

Figure 4. Calculated mean speed of migration for adult (solid triangles) and juvenile (open) western sandpipers and semipalmated sandpipers on their southward migration, using Alerstam and Lindström's (1990) formula. Parameter values are given in Table 1. The estimated fuel-loading rate is highest at Kent Island (2.0 g d^{-1}; solid line), followed by Sibley Lake (1.3 g d^{-1}; dot/dash), with Sidney Island (1.0 g d^{-1}; dashed), having the lowest rate (based on estimates summarized in Lank 1983, Ydenberg et al. 2002).

Table 1. Parameter values used to estimate speed of migrations in adult (A) and juvenile (J) western sandpipers (WESA) and semipalmated sandpipers (SESA) at Sidney Island (SI), Kent Island (KI) and Sibley Lake (SL).

Site	Species	Age	N	C (km)	Te (days)	Mean mass at capture (g)	Wet lean mass (g)	Rate of mass gain ($g\ d^{-1}$)
SI	WESA	A	515	15000	0.5	24.4^{A}	23.0^{C}	1.0^{A}
SI	WESA	J	1173	15000	0.5	24.5^{A}	23.0^{C}	1.0^{A}
KI	SESA	A	1176	15000	0.5	34.0^{B}	21.8^{D}	2.0^{B}
KI	SESA	H	281	15000	0.5	28.9^{B}	21.8^{D}	2.0^{B}
SL	SESA	A	641	15000	0.5	29.5^{B}	21.8^{D}	1.3^{B}
SL	SESA	I	832	15000	0.5	29.7^{B}	21.8^{D}	1.3^{B}

[A] Butler et al. (1987), Ydenberg et al. (2004).
[B] Lank (1983).
[C] Guglielmo and Williams (2003).
[D] Lyons and Haig (1995).

which requires a decrease in stopover time. These predictions are summarized in Table 2.

Results

The seasonal pattern of migration speeds, as inferred from mean conditional residence time, matches all the site- and age-group specific predictions summarized in Table 2. For western sandpipers at Sidney Island, the data provide strongest support for models in which the estimated stopover time increased throughout the adult and decreased through the juvenile passage period (Fig. 5). Models that did not include seasonal trends received little or no support. Support for the model with a linear trend in adult departure probability (hence increase in residence time) was stronger than that with a quadratic change ($\omega_i = 0.46$ vs 0.24), but in juveniles support for a model with a quadratic trend (i.e. initially more rapid decreasing residence time) was stronger ($\omega_i = 0.55$ vs 0.21). A complete model list and AIC results from all sites are supplied in the Supplimentary material Appendix 1.

In semipalmated sandpipers at both sites, an effect of first capture was supported (parameter likelihood = 1 at both sites) and was estimated separately from mean conditional residence times. The inclusion of mass at capture as a covariate did not improve model fit. At Sibley Lake, the estimated conditional residence time declined throughout the migratory period for both adults and juveniles (Fig. 6). Though residence time appears to increase slightly at the start of the juvenile migration period, support for this was no stronger than for a linear decline ($\omega_i = 0.33$ vs 0.28). Models without a seasonal trend received no support from the data ($\omega_i = 0$). The estimated residence time also decreased for both adults and juveniles at Kent Island (Fig. 7), and the decline was much more rapid for later-arriving juveniles. All models with $\omega_i > 0.08$ had linear trends in 3-d survival for both adults and juveniles.

Discussion

Our simple model of seasonal changes in speed of migration observed in the course of passage at a stopover site (Fig. 2) is based on the temporal proximity of the wave of southbound migratory peregrine falcons (the ‘falcon front’). Migrants are predicted to increase speed of migration as the front advances, while under and behind the front migrants become increasingly cautious and hence speed of migration is predicted to decrease. This model successfully predicted the seasonal changes in residence time (and hence migratory speed) of both adult and juvenile western and semipalmated sandpipers at three locations.

Semipalmated sandpipers, which were ahead of the falcon front at both Kent Island and Sibley Lake, carry fuel loads larger than that maximizing migration speed, and as predicted, they increased migratory speed (by shortening residence time) as the season progressed and the falcon front advanced. A likely consequence of this adjustment is that the total fuel load accumulated was reduced, which would in turn mean that later-migrating individuals have shorter range. If true, this suggests that later-migrating semipalmated sandpipers might fly a different route than early migrants, who make a very long (~4500 km) flight out over the Atlantic to South America.

Adult western sandpipers at Sidney Island migrate ahead of the falcon front, and increased migratory speed as the falcon front approached. In contrast to semipalmated sandpipers, however, they carry fuel loads smaller than that maximizing the speed of migration speed, and lengthened residence time to increase speed. But juvenile western sandpipers migrated behind the falcon front, and as the season advance slowed migration speed (by shortening

Table 2. Mortality minimizing predictions of age- and species-specific seasonal patterns in residence time, based on position relative to the falcon front.

Species	Age	Proximity to falcon front	Migration speed prediction	Fuel load relative to optimum	Residence time prediction	Residence time result
WESA	A	ahead	increasing	below	increasing	increasing
WESA	J	behind	decreasing	below	decreasing	decreasing
SESA	A	ahead	increasing	above	decreasing	decreasing
SESA	J	ahead	increasing	above	decreasing	decreasing

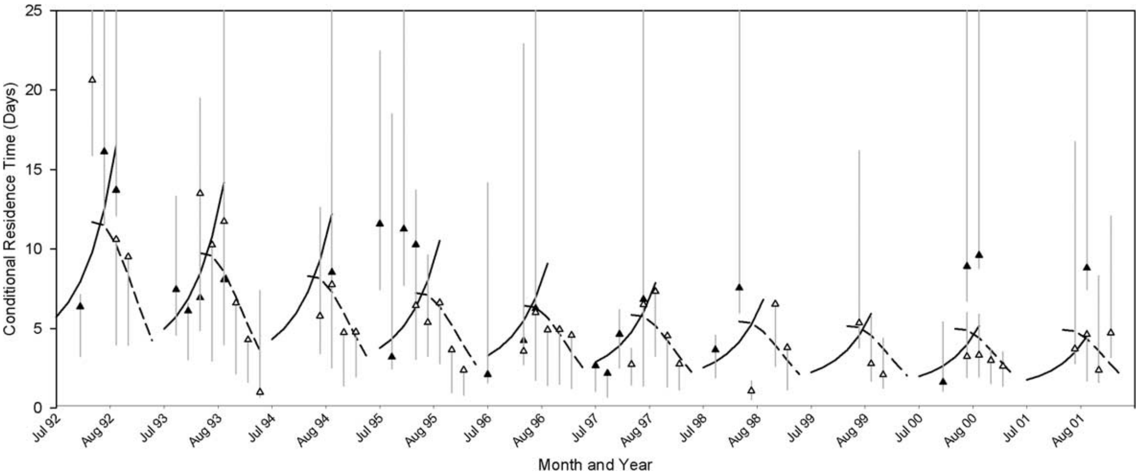

Figure 5. Estimates of conditional residence time in days for western sandpipers at Sidney Island, over each migratory season between 1992 and 2001. Adults (solid curves) and juvenile (dashed) models were based on predictions from QAIC model weights. Triangles (black filled adults; open juveniles) are year-week averages for residence time with associated 95% confidence intervals. Mean 50% falcon arrival date for the area (vertical dashed line) occurs around the end of the adult migration (8 August), though there is substantial variation between years (Niehaus and Ydenberg 2006).

residence time) to gain safety. These results support the hypothesis that western and semipalmated sandpiper residence times (and hence speeds of migration) are influenced by the temporal proximity to the falcon front, and support the notion that western and semipalmated sandpipers stopover decisions are made to minimize the probability of mortality on migration.

Time and energy have previously been highlighted as being important factors driving migratory decisions (Alerstam and Lindström 1990, Hedenström and Alerstam 1997, Farmer and Wiens 1999, Scheiffarth et al. 2002, Duijns et al. 2009), though seasonal variations in time- and energy-minimizing tactics have not been explored in detail. These models show that stopover duration is affected not only by fueling conditions at the current site, but by conditions at other stopovers. Hence, it is theoretically possible that the seasonal changes in stopover duration measured here are attributable to systematic changes in the food available at our study sites, or at other sites, or both. Unfortunately, there are few data available to investigate this factor. Food abundance increases, or at least does not decrease during southward migration at Sidney Island (Lank et al. 2003), which does not support any hypothesis for stopover duration based on local food availability. A seasonal decline in food abundance has been demonstrated at one location on the eastern flyway (Schneider and Harrington 1981), but occurred with only some prey species in some years and was not observed until mid-September, after all adult and some juvenile semipalmated sandpipers had passed through Kent Island. According to migration theory, if refuelling rate were lower for later migrants, it should take longer to reach the optimal

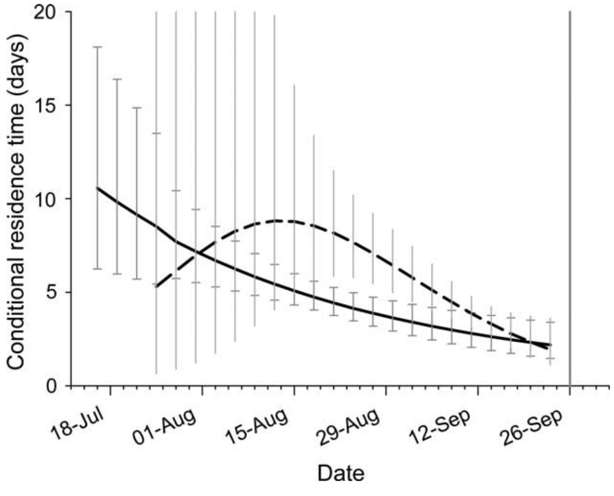

Figure 6. Estimates of conditional residence time in days for semipalmated sandpipers at Sibley Lake, North Dakota, 1977, with 95% confidence intervals for adult (solid) and juvenile (dashed) migrants. The estimated 50% falcon arrival date for Sibley Lake is shown (vertical grey line).

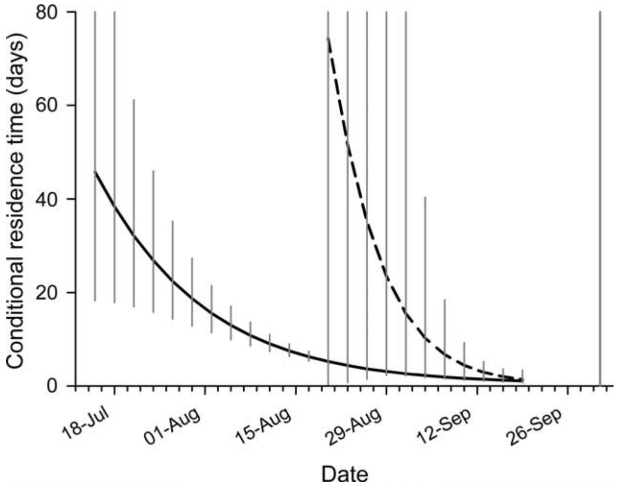

Figure 7. Estimates of conditional residence time in days for semipalmated sandpipers at Kent Island, Bay of Fundy, 1978, with 95% confidence intervals for adult (solid) and juvenile (dashed) migrants. The estimated 50% falcon arrival date for Kent Island is shown (vertical grey line).

departure fuel load and residence time should increase for time- and energy-minimizing migrants (Alerstam and Lindström 1990). Clearly, this was not observed at Kent Island or at Sibley Lake.

Changes in food availability at other sites also seem unlikely to provide much explanatory power for the seasonal changes in residence time that were measured here. If food abundance drops more quickly at northern stopovers, southbound time-minimizers at those sites are predicted to depart sooner, but the pattern for energy-minimizers is independent of food abundance relative to other sites. Without substantive information on temporal and spatial patterns of prey abundance, similar to that of the predator landscape, food abundance cannot be demonstrated to be influencing residence time patterns in migrating sandpipers.

Our residence time estimates are based on resightings made between initial capture and eventual departure date, as calculated by the models. These estimates assume that the daily departure probability prior to first capture is similar to that after capture (Schaub et al. 2001), and that captures are made at random. Violations of these assumptions may introduce biases. For example, if migrant numbers at the stopover site decline, departure probability might be underestimated (and hence residence time overestimated) if migrants with low departure probability are as a consequence overrepresented in the sample. At all three of our study sites, a more-or-less steady stream of migrants flows through the sites for six or eight weeks, making our reported residence time estimates are of course subject to error, making it very unlikely that our basic results (seasonal patterns of increase or decrease in residence time) result from such biases.

Ydenberg et al. (2004; see also Ydenberg et al. 2002) found that after the recovery of peregrine populations during the 1980s and 1990s, western sandpipers on stopover had lower weights at Sidney Island, but not at large, less dangerous sites on the Fraser estuary. The data for semipalmated sandpipers presented here were collected in the late 1970s (Lank 1983), before the continental recovery of peregrine populations, and stopover behaviour may now be different. Unpublished data (K. M. O'Reilly pers. comm.) collected in 1996 at Kent Island (a small site similar to Sidney Island, and assumed dangerous) and in 1999 at nearby Johnson's Mills (a large mudflat, assumed relatively safe) show that capture masses are now lower at Kent Island than in the 1970s, but are unchanged at Johnson's Mills. This pattern is reminiscent of that found with western sandpipers.

The importance of predator landscapes in shaping migratory strategies and tactics is beginning to be explored in shorebirds (Lank et al. 2003, Ydenberg et al. 2007, Duijns et al. 2009, Bauer et al. 2010). As raptor populations recover across the world, the influence of temporal and spatial changes in predation danger should become more apparent. Including predictions of reactions to changes predator abundance is important when considering migratory tactics. Time, energy and predation were initially described as the key factors influencing migration decisions, and while time and energy have been well analyzed, both future and current predation danger need to be also included in migratory tactic models.

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References

Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. – In: Gwinner, E. (ed.), Bird migration: the physiology and ecophysiology. Springer, pp. 331–351.

Alerstam, T. and Hedenström, A. 1998. The development of bird migration theory. – J. Avian Biol. 29: 343–369.

Bauer, S., Ens, B. J. and Klaassen, M. 2010. Many routes lead to Rome: potential causes for the multi-route migration system of red knots, *Calidris canutus islandica*. – Ecology 91: 1822–1831.

Bildstein, K. and Zalles, J. 2005. Old World versus New World long-distance migration in accipiters, buteos and falcons: the interplay of migration ability and global biogeography. – In: Greenberg, R. and Marra, P. P. (eds), Birds of two worlds: the ecology and evolution of migration. John Hopkins Univ. Press, pp. 154–167.

Brownie, C. and Robson, D. 1983. Estimation of time-specific survival rates from tag-resighting samples: a generalization of the Jolly–Seber model. – Biometrics 39: 437–453.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.

Burns, J. G. and 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., Kaiser, G. W. and Smith, G. E. 1987. Migration chronology, length of stay, sex-ratio, and weight of western sandpipers, (*Calidris mauri*) on the south coast of British-Columbia. – J. Field Ornithol. 58: 103–111.

Butler, R. W., Delgado, F. S., dela Cueva, H., Pulido, V. and Sandercock, B. K. 1996. Migration routes of the western sandpiper. – Wilson Bull. 108: 662–672.

Dierschke, V. 1998. High profit at high risk for juvenile dunlins *Calidris alpina* stopping over at Helgoland (German Bight). – Ardea 86: 59–69.

Dierschke, V. 2003. Predation hazard during migratory stopover: are light or heavy birds under risk? – J. Avian Biol. 34: 24–29.

Duijns, S., van Dijk, J. G. B., Spaans, B., Jukema, J., de Boer, W. F. and Piersma, T. 2009. Foraging site selection of two subspecies of bar-tailed godwit *Limosa lapponica*: time minimizers accept greater predation danger than energy minimizers. – Ardea 97: 9.

Farmer, A. H. and Wiens, J. A. 1999. Models and reality: time-energy trade-offs in pectoral sandpiper (*Calidris melanotos*) migration. – Ecology 80: 2566–2580.

Guglielmo, C. G. and Williams, T. D. 2003. Phenotypic flexibility of body composition in relation to migratory state, age, and sex in the western sandpiper (*Calidris mauri*). – Physiol. Biochem. Zool. 76: 84–98.

Hedenström, A. and Alerstam, T. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. – J. Theor. Biol. 189: 227–234.

Heintzelman, D. 1975. Autumn hawk flights: the migrations in eastern North America. – Rutgers Univ. Press.

Houston, A. I. 1998. Models of optimal avian migration: state, time and predation. – J Avian Biol. 29: 395–404.

Lank, D. B. 1979. Dispersal and predation rates of wing-tagged semipalmated sandpipers *Calidris pusilla* and an evaluation of the tag technique. – Wader Study Group Bull. 27: 41–46.

Lank, D. B. 1983. Migratory behavior of semipalmated sandpipers at inland and coastal staging areas. – Cornell Univ.

Lank, D. 1989. Why fly by night? Inferences from tidally-induced migratory departures of sandpipers. – J. Field Ornithol. 60: 154–161.

Lank, D. B. and Ydenberg, R. C. 2003. Death and danger at migratory stopovers: problems with 'predation risk'. – Avian Biol. 34: 225–228.

Lank, D. B., Butler, R. W., Ireland, J. and Ydenberg, R. C. 2003. Effects of predation danger on migration strategies of sandpipers. – Oikos 103: 303–319.

Lebreton, J. 1992. Modeling survival and testing biological hypotheses using marked animals – a unified approach with case-studies. – Ecol. Monogr. 62: 67–118.

Lind, J. and Cresswell, W. 2006. Anti-predation behaviour during bird migration; the benefit of studying multiple behavioural dimensions. – J. Ornithol. 147: 310–316.

Lindström, Å. and Alerstam, T. 1992. Optimal fat loads in migrating birds – a test of the time-minimization hypothesis. – Am. Nat. 140: 477–491.

Lyons, J. E. and Haig, S. M. 1995. Fat-content and stopover ecology of spring migrant semipalmated sandpipers in south carolina. – Condor 97: 427–437.

Mcneil, R. and Cadieux, F. 1972. Fat content and flight-range capabilities of some adult spring and fall migrant North American shorebirds in relation to migration routes on the Atlantic coast. – Nat. Can. 99: 589–605.

Morrison, R. 1984. Migration systems of some New World shorebirds. – In: Burger, J. and Olla, B. L. (eds), Shorebirds: migration and foraging behavior. Plenum Press, pp. 125–202.

Niehaus, A. C. and Ydenberg, R. C. 2006. Ecological factors associated with the breeding and migratory phenology of high-latitude breeding western sandpipers. – Polar. Biol. 30: 11–17.

Page, G. and Middleton, A. 1972. Fat deposition during autumn migration in semipalmated sandpiper. – Bird-Banding 43: 85–96.

Pennycuick, C. J. 1975. Mechanics of flight. – In: Farner, D. S. and King, J. R. (eds), Avian biology. Academic Press, pp. 1–75.

Supplementary material (Appendix J5347 at <www.oikosoffice.lu.se/appendix>). Appendix 1.

Pomeroy, A. C. 2006. Tradeoffs between food abundance and predation danger in spatial usage of a stopover site by western sandpipers, *Calidris mauri*. – Oikos 112: 629–637.

Pomeroy, A. C., Butler, R. W. and Ydenberg, R. C. 2006. Experimental evidence that migrants adjust usage at a stopover site to trade off food and danger. – Behav. Ecol. 17: 1041–1045.

Sansom, A., Lind, J. and Cresswell, W. 2009. Individual behavior and survival: the roles of predator avoidance, foraging success, and vigilance. – Behav. Ecol. 20: 1168–1174.

Schaub, M., Pradel, R., Jenni, L. and Lebreton, J.-D. 2001. Migrating birds stop over longer than usually thought: an improved capture–recapture analysis. – Ecology 82: 852–859.

Scheiffarth, G., Wahls, S., Ketzenberg, C. and Exo, K.-M. 2002. Spring migration strategies of two populations of bar-tailed godwits, *Limosa lapponica*, in the Wadden Sea: time minimizers or energy minimizers? – Oikos 96: 346–354.

Schmaljohann, H. and Dierschke, V. 2005. Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*. – J. Anim. Ecol. 74: 131–138.

Schneider, D. C. and Harrington, B. A. 1981. Timing of shorebird migration in relation to prey depletion. – Auk 98: 801–811.

White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – Bird Study (Suppl.) 46: 120–138.

Worcester, R. and Ydenberg, R. 2008. Cross-continental patterns in the timing of southward peregrine falcon migration in North America. – J. Raptor Res. 42: 13–19.

Ydenberg, R. C., Butler, R. W., Lank, D. B., Guglielmo, C. G., Lemon, M. and Wolf, N. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. – J. Avian Biol. 33: 47–55.

Ydenberg, R. C., Butler, R. W., Lank, D. B., Smith, B. D. and Ireland, J. 2004. Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. – Proc. R. Soc. B 271: 1263–1269.

Ydenberg, R. C., Butler, R. W. and Lank, D. B. 2007. Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. – J. Avian Biol. 38: 523–529.