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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

David D. Hope, David B. Lank, Barry D. Smith and Ronald C. Ydenberg

D. D. Hope (dhope@alumni.sfu.ca), D. B. Lank, B. D. Smith and R. C. Ydenberg, Centre for Wildlife Ecology and Evolutionary an Behavioural Ecology Research Group, Simon Fraser Univ., Burnaby, BC V5A 1S6, Canada. BDS and RCY also at: Pacific Wildlife Res Centre, Canadian Wildlife Service, 5421 Robertson Road, Delta, BC V4K 3Y3, Canada.

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

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

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

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 which requires a decreasein stopover time.

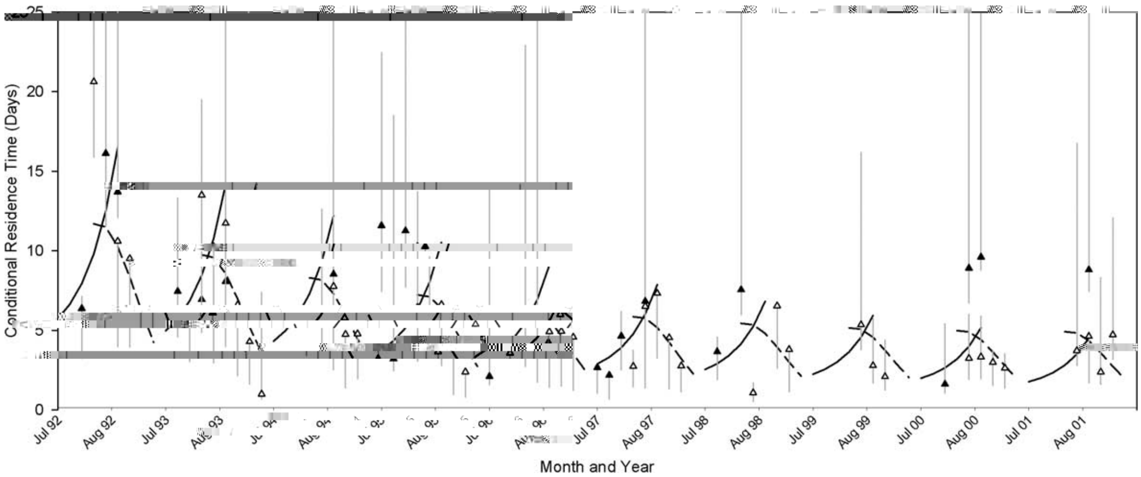

Figure 5. Estimates of conditional residence time in days for western sandpipers at Sidney Island, over each migratory season between

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 departure fuel load and residence time should increase for time- and energy-minimizing migrants (Alerstam and Lindströ

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