A Puzzling Migratory Detour: Are Fueling Conditions in Alaska Driving the Movement of Juvenile Sharp-Tailed Sandpipers?

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INTRODUCTION

Many shorebirds breeding in the Arctic make spectacular migrations between breeding grounds on northern tundra and distant nonbreeding grounds in the Southern Hemisphere. Adults and juveniles of most migratory birds, including shorebirds, normally follow the same migration routes. Along these routes they rely on food-rich stopover sites for successful fueling (Alerstam 1990). In shorebirds, the timing of fall migration of the age classes often differs, adult birds migrating several weeks earlier than juveniles (Kolthoff 1896, Alerstam 1990, Ydenberg et al. 2004). Accordingly, most juveniles migrate without guidance from experienced conspecifics.

There is one striking exception to the rule that adult and juvenile arctic shorebirds follow the same migration route (Fig. 1). Adult Sharp-tailed Sandpipers (*Calidris acuminata*) migrate from their breeding grounds in northeast Russia on a course due south toward their wintering grounds in Australia (Higgins and Davies 1996, Handel and Gill 2010). A substantial proportion of the juveniles, however, including at least thousands and possibly tens of thousands of birds, first makes a detour east to western Alaska (Gill and Ha 6(e).7(r)-14.7(st 4TJT*-57-0.01 T20.4(6)1.6(d 6)-5]TJ6)-3.7()-10.44l64ah6((G6-15.4(i6-10.44l)

13–26 September, however, the slope of mass on date (linear regression) was 4.2 ± 0.3 g day^{-1} for males (n = 36, P < 0.001) and 3.2 ± 0.3 g day^{-1} for females (n = 17, P < 0.001). It should be noted that the period 13–26 September represents data from one year almost exclusively (for 13 September there are data for 2004 only; for 14–26 September all data are from 2005).

If we assume a lean body mass of 67 g for males and 56 g for females (the average mass of birds with fat scores 0–1, with a range of 61.4–76.0 g for males and 49.9–64.0 g for females), in early September (1–12) males added fuel at a rate of 0.6% lean body mass day^{-1}, females at 0.5% day^{-1}. In late Septem-

FLIGHT-RANGE ESTIMATES

The estimated distances of flight in still air were close to 7100 km for both males and females. With a body-drag coefficient of 0.05 (see Methods), the predicted capacity of flight in still air of both sexes of the Sharp-tailed Sandpiper is around 9800 km.

PREDATION DANGER

We observed eight species of potential avian predator during 2005 and 2006 (in decreasing frequency): the Parasitic Jaeger (*Stercorarius parasiticus*), Northern Harrier (*Circus cyaneus*), Peregrine Falcon (*Falco peregrinus*), Gyrfalcon (*F. rusticolus*), Glaucous Gull (*Larus hyperboreus*), Merlin (*F. columbarius*), Short-eared Owl (*Asio ammeus*), and Long-tailed Jaeger (*S. longicaudus*). Combined, they accounted for 61 observed interactions with shorebirds, 45 (74%) involving Parasitic Jaegers, 8 (13%) Northern Harriers, and 4 (7%) Peregrine Falcons. In 2006, the year we recorded observer effort, shorebirds and predators interacted at a rate of 0.07 hr^{-1}. Both values are roughly equal to one observed predator–prey interaction per day of field work. In 2006, shorebirds' resulting mortality rate was 0.02 hr^{-1}, roughly one shorebird killed every 3 days. We observed seven events that ended in mortality, five by Parasitic Jaegers and two by Glaucous Gulls. The Glaucous Gull is likely not a serious predator of small shorebirds during the autumn staging period. Both instances of predation by gulls involved gulls hunting along the shoreline, where they found Dunlins or Rock Sandpipers that were likely injured during our trapping. We identified four of the prey as Dunlins; none of the others could positively be identified as Sharp-tailed Sandpipers.

DISCUSSION

As outlined in the Introduction, there are several costs associated with migratory detours, related to time, energy, and orientation, suggesting that detours should be selected against. In the case of the detour made by juvenile Sharp-tailed Sandpipers there obviously must be benefits exceeding these costs.

FUEL DEPOSITION AND LENGTH OF STAY

The rate of fueling of free-living individual birds can be estimated in two ways, either by retrapping individual birds or by the average change in mass of the population as a whole (Lindström and Piersma 1993). Ideally, the latter method requires that the population be closed, that is, all of the members of a population at any given site arrive and depart at the same time. Because we retrapped too few birds to evaluate mass change by individuals, we derived a population-based estimate of fueling rates.

By deploying and detecting radio transmitters on a number of birds, we determined individuals' minimum length of stay. Plotting minimum length of stay against date of deployment (Fig. 3A) confirms the impression that most birds arrived within a small interval in early September and stayed in the area until the end of September. Assuming that the birds stayed in the area until they reached an average fuel load of 100% (the approximate fuel load of the birds we trapped late in September), we expected an average day of departure of 27 and 29 September for males and females, respectively, which is in agreement with the observations of apparent duration of staging with respect to date of deployment of the transmitter (Fig. 3).

Six of the 30 birds apparently left the area within 0–3 days of capture. At the average fueling rates we calculated, such short length of stay would not have provided those individuals time to achieve a mass sufficient for departure. One possibility is that these birds were transients that left our study area to accumulate their fat reserves elsewhere, that is, our population is not completely closed. We cannot exclude our methods as causes of the short apparent stays, for example, that some radios failed prematurely or birds left prematurely because of our handling. Overall, however, the transmitter data indicated that a sufficient proportion of the Sharp-tailed Sandpipers stayed long enough in our study area for us to use the birds' average mass change as an estimate of fuel-deposition rate (cf. Lindström and Piersma 1993).

Body mass increased over the whole period, as did the amount of visible fat, indicating that a large part of the mass increase was due to fat deposition. The increase in mass seemed to be divided into two periods. Until 12 September, the average mass increased only slowly (0.5–0.6% of lean body mass day^{-1}). The fuel-deposition rate increased sharply in the second half of September, averaging about 6% of lean body mass day^{-1}. According to Lindström's (2003) review of maximum rates of fuel deposition in migrating birds (based on field data), at the population level the rate expected for similar-sized migrants is 3.0–3.3% of lean body mass day^{-1}. Handel and Gill (2010) analyzed body-mass data on Sharp-tailed Sandpipers from the whole of southwestern Alaska and found an average of 1.0% of lean body mass day^{-1} from mid August to late October. The discrepancy between these findings may be a result of the heterogeneity in Handel and Gill's (2010) data set, which includes birds at multiple sites over multiple years, possibly leading to a less accurate estimate of mean fueling rates. It should be noted that Handel and Gill (2010) also found many birds with body masses   100 g, suggesting that the kind of fueling we recorded takes place at other sites in Alaska as well.

Among the ten species of shorebirds whose lean body mass ranges from 40 to 65 g and in which high fueling rates have been found, only the Dunlin (lean body mass 40 g) along the German coast of the North Sea was found to have a higher population fueling rate, 8.5% of lean body mass day^{-1} (Dierschke 1998, Lindström 2003). This rate is still lower, however, than the average of 9.6% of lean body mass day^{-1} found in 15 species of similar-sized shorebirds fed ad libitum in captivity during the fall migration season (Kvist and Lindström 2003). The latter value is probably close to the physiological maximum

rate achievable under ideal conditions. Nevertheless, the fuel-deposition rate achieved at our Alaskan study site, 6% of lean body mass day^{-1}, is among the highest found in a wild migratory shorebird.

Lindström et al. (2010) also found two apparent phases of fuel deposition in adult European Golden-Plovers (*Pluvialis apricaria*) on fall migration in Sweden, where the shift from slow to fast fueling coincided with the termination of primary molt. The juvenile Sharp-tailed Sandpipers were not molting. Whether internal processes, such as rebuilding organs involved in the digestion of food (Jehl 1997, Piersma and Lindström 1997), prevent fast fueling upon the birds' arrival in Alaska, or whether external factors such as temporal changes in food availability or predation danger are at play, awaits further investigations.

During fall migration, fuel loads deposited by shorebirds breeding in the Arctic vary by species, age class, and stage of migration. During the first stages of southward migration over the tundra, juveniles of several species rarely add more fuel than 10% of their lean body mass (Lindström 1998, Tulp et al.

around the coast of northern Norway, whereas adults migrate mainly through the Baltic basin.

Factors other than thermal flight dynamics must provide

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