

# Wayward Youth: Trans-Beringian Movement and Differential Southward Migration by Juvenile Sharp-tailed Sandpipers

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(Received 9 September 2009; accepted in revised form 22 December 2009)

**ABSTRACT.** The sharp-tailed sandpiper (*Calidris acuminata*) is a long-distance migrant that travels each year from breeding grounds in the Russian Arctic to nonbreeding areas in Australasia. Most adults migrate rapidly from breeding grounds along a largely inland route through Asia. Here we report on the highly unusual migratory strategy of this species in which some juveniles, but virtually no adults, take a pronounced detour to western Alaska before proceeding on southward migration. We analyzed data from our own studies in this region and published and unpublished observations and specimen records of sharp-tailed sandpipers from the entire Pacific Basin. Each autumn, sharp-tailed sandpipers began arriving on coastal graminoid meadows and intertidal habitats throughout western Alaska during the last half of August and the last sandpipers departed from southwestern Alaska during October and November. Body mass of birds banded or collected across multiple years and sites in western Alaska ( $n = 330$ ) increased by an average of  $0.57 \pm 0.06$  g per day between mid-August and late October. Records suggest a small, regular movement of juveniles (and a very few adults) along the Asiatic coast, but we estimate from surveys that a few tens of thousands of juveniles stage in western Alaska each autumn. The distribution of sight and specimen records from the Pacific Basin during autumn suggests strongly age-segregated migration routes, with the principal migration of juveniles crossing central and western Oceania in a possible nonstop trans-Pacific flight from Alaska. This is only the second well-documented case of differential migration among birds that involves different routes for adults and juveniles, and it raises intriguing questions about how and why this system has evolved.

**Key words:** sharp-tailed sandpiper, *Calidris acuminata*, Alaska, Beringia, Oceania, differential migration, autumn, body mass, fueling, staging, timing, shorebirds

**RÉSUMÉ.** Le bécasseau à queue pointue (*Calidris acuminata*) est un migrant de longue distance qui se déplace chaque année depuis les zones de reproduction de l'Arctique russe jusqu'aux zones de non-reproduction de l'Australasie. La plupart des adultes migrent rapidement à partir des zones de reproduction le long d'un corridor largement situé à l'intérieur qui traverse l'Asie. Ici, nous faisons état de la stratégie migratoire grandement inhabituelle de cette espèce dans le cadre de laquelle certains juvéniles, mais quasiment aucun adulte, font une déviation prononcée vers l'ouest de l'Alaska avant de migrer vers le Sud. Nous avons analysé les données dérivées de nos propres études dans la région de même que des observations publiées et inédites et des enregistrements de spécimens de bécasseaux à queue pointue de tout le bassin du Pacifique. Chaque automne, les bécasseaux à queue pointue commençaient à arriver sur les prés côtiers de graminoides et dans les habitats intertidaux de l'ouest de l'Alaska pendant la deuxième moitié du mois d'août. Les derniers bécasseaux quittaient le sud-ouest de l'Alaska aux mois d'octobre et de novembre. La masse corporelle des oiseaux en bandes ou recueillis au cours de plusieurs années et à plusieurs emplacements de l'ouest de l'Alaska ( $n = 330$ ) a augmenté en moyenne de  $0,57 \pm 0,06$  g par jour entre la mi-août et la fin octobre. Les données laissent voir la présence d'un petit mouvement régulier de juvéniles (et très peu d'adultes) le long de la côte asiatique, mais nous avons estimé d'après les dénombrements que quelques dizaines de milliers de juvéniles passent un certain temps dans l'ouest de l'Alaska chaque automne. La répartition d'enregistrements d'observations et de spécimens du bassin du Pacifique à l'automne laisse entrevoir des routes migratoires fortement ségréguées en fonction de l'âge et que la migration principale de juvéniles traversant le centre et l'ouest de l'Océanie dans le cadre d'un vol transpacifique est susceptible d'être sans escale depuis l'Alaska. Il s'agit seulement du deuxième cas bien répertorié de migration différentielle d'oiseaux dont les trajets diffèrent chez les adultes et les juvéniles, et cela soulève des questions à savoir comment et pourquoi ce système a évolué.

**Mots clés :** bécasseau à queue pointue, *Calidris acuminata*, Alaska, Béringie, Océanie, migration différentielle, automne, masse corporelle, avitaillement, préparation, répartition, oiseaux de rivage

Traduit pour la revue *Arctic* par Nicole Giguère.

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**РЕЗЮМЕ.** Острохвостый песочник (*Calidris acuminata*) – дальний мигрант, который каждый год пролетает из области размножения в Российской Арктике на зимовки в Австралии. Большинство взрослых птиц летит быстро из мест гнездования, главным образом, внутриматериковым азиатским путём. В этой статье мы сообщаем о крайне необычной стратегии миграций данного вида, при которой некоторые молодые птицы, но фактически без взрослых, используют явно окольный путь на Западную Аляску перед тем, как совершить перелёт на юг. Мы проанализировали данные собственных исследований в этом регионе, а также опубликованные и неопубликованные наблюдения и добытые экземпляры острохвостых песочников со всего тихоокеанского бассейна. Каждую осень острохвостые песочники начинают появляться на приморских злаковых лугах и в местообитаниях приливо-отливной зоны по всей Западной Аляске в течение второй половины августа, а последние песочники улетают с юго-западной Аляски в октябре и ноябре. Масса тела птиц, окольцованных или добытых в разные годы на Западной Аляске ( $n = 330$ ), увеличивалась в среднем на  $0,57 \pm 0,06$  г в день с середины августа по конец октября. Регистрации птиц указывают на существование слабого, но регулярного пролёта молодых (а также крайне малого числа взрослых) острохвостых песочников вдоль азиатского побережья, но, основываясь на обследованиях, мы оцениваем численность молодых птиц, ежегодно останавливающихся на Западной Аляске, в несколько десятков тысяч птиц. Размещение пунктов осенних визуальных встреч и добычи птиц в Тихом океане указывает на ярко выраженное разделение пролётных путей в зависимости от возраста птиц, при этом большинство молодых песочников пересекает Центральную и Западную Океанию, возможно, безостановочно в транстихоокеанском броске с Аляски. Это только второй хорошо документированный случай дифференциальной миграции среди птиц, при которой пути пролёта взрослых и молодых птиц различаются, и это ставит интригующий вопрос о том, как и почему выработалась такая система.

**Ключевые слова:** острохвостый песочник, *Calidris acuminata*, Аляска, Берингия, Океания, дифференциальная миграция, осень, масса тела, накопление резервов, остановки, сроки, кулики

## INTRODUCTION

It is easily understood why most birds breeding in the Arctic migrate to more hospitable regions following the brief and productive northern summer. What has stimulated much interest, however, is why and how birds travel in quite varied and sometimes complex patterns to their nonbreeding areas. Migrations to and from a given breeding area vary routinely across both time and space not only among species, but also within species. This latter phenomenon, termed differential migration, occurs when distinguishable groups of individuals (e.g., different age or sex classes) migrate differently from one another with respect to timing, distance, or both (Gauthreaux, 1982; Terrill and Able, 1988). In almost all species with differential migration, the different classes follow the same migration route during a given season, but do so in such a way that their movements are temporally staggered or the groups end up spatially segregated along a latitudinal gradient on the nonbreeding grounds.

Several hypotheses have been advanced to explain why individuals of different classes migrate different distances and become spatially segregated. These involve advantages accrued by increasing reproductive success (e.g., through early arrival on breeding territories; Ketterson and Nolan, 1979) or increasing survival (e.g., by reducing migration costs, reducing risk of predation, or improving foraging; Gauthreaux, 1978; Nebel, 2005, 2007; Nebel et al., 2005; see Cristol et al., 1999, for review). No single hypothesis has explained the diversity of migration patterns found among different species or even, in many cases, the patterns found among classes within a given species. Because individuals within a population often face different environmental and

biological conditions during their migrations, the optimal solutions to these challenges, in terms of effects on fitness, can also be expected to vary (Cristol et al., 1999; Farmer and Wiens, 1999; Hedenström, 2008).

Shorebirds breeding in Beringia, the region between the Russian Far East and Alaska, migrate to all continents except Antarctica and display a broad array of migration patterns (Pitelka, 1979; Gill et al., 1994). Within this group, the duration of parental care by males and females varies greatly among species (Pitelka et al., 1974), and there are both sex- and age-related differences within populations in the timing of southward migration (Connors et al., 1979; Gill and Handel, 1990). The sharp-tailed sandpiper (*Calidris acuminata*) is an endemic Beringian species that appears to have a highly unusual differential migration pattern southward from the breeding grounds. This sandpiper nests along a restricted area of Arctic coastal tundra in Yakutia, Russia (Flint and Tomkovich, 1978), and spends the nonbreeding season in Australasia (Higgins and Davies, 1996). The main southward migration of adults begins in early July and occurs along an interior continental route through Asia, with males preceding females (Tomkovich, 1982; Higgins and Davies, 1996). Juveniles do not migrate until the last half of August, and the only records from Asia occur along the Pacific Coast, far from the inland migration route that most adults follow (Tomkovich, 1982; Higgins and Davies, 1996). Each autumn the sharp-tailed sandpiper also occurs as a rare to locally common migrant in western Alaska (Gabrielson and Lincoln, 1959; Keith, 1967; Kessel and Gibson, 1978; Gill and Handel, 1981; Kessel, 1989; Gill, 1996; Gibson and Byrd, 2007), having traveled 1200–3000 km almost due east from the breeding grounds. What has intrigued us and other biologists for decades is

that this flight appears to be composed almost exclusively of juveniles. To our knowledge, only one other species of bird, the honey buzzard (*Pernis apivorus*) in Europe (Hake et al., 2003), has an age-differential migration that involves a different migration route. Here we summarize data on the timing and magnitude of the migration of juvenile sharp-tailed sandpipers in western Alaska and examine seasonal changes in body mass on staging areas in the region. We further explore the likelihood that a segment of the juvenile population reaches the nonbreeding grounds in Australasia via a trans-Pacific flight similar to that made by other, much larger shorebird species (Gill et al., 2005, 2009). Finally, we raise questions about what ecological factors may be driving this extraordinary annual event.

## STUDY AREAS AND METHODS

We studied sharp-tailed sandpipers at three principal sites in Alaska (Fig. 1): on the central Yukon-Kuskokwim Delta (hereafter Y-K Delta) from a camp on the Tutakoke River (61.2353° N, 165.6297° W) and on the Alaska Peninsula from camps at Ugashik Bay (57.4938° N, 157.5600° W) and Cinder Lagoon (57.2827° N, 158.2622° W). The Tutakoke and Alaska Peninsula study areas have been described by Handel and Gill (1992a) and Gill et al. (1997), respectively. Detailed descriptions of habitats are available for both the central Y-K Delta (Tande and Jennings, 1986; Kincheloe and Stehn, 1991; Person et al., 2003) and the Alaska Peninsula (Ducks Unlimited, Inc., 2007). All three study areas are typified by coastal mesic to dry sedge and grass meadows with numerous ponds, depressions, and tidal distributaries, which facilitate partial or complete inundation during extreme high tides. Dominant vegetation at all sites includes *Carex ramenskii*, *Puccinellia phryganodes*, *Hippuris tetraphylla*, and *Calamagrostis* spp.

### Use of Staging Areas in Alaska

We compiled all records of sharp-tailed sandpipers that we had observed during field studies throughout western Alaska from 1976 to 2008. We obtained historical records for Alaska from Gabrielson and Lincoln (1959), Kessel and Gibson (1978), and the repository of ornithological field notes maintained at the University of Alaska Museum of the North. We also included Alaskan records from other sources, including more recent publications (Gill et al., 1981; Tomkovich, 1982; Gill and Handel, 1990; Petersen et al., 1991; Lehman, 2005; Gibson and Byrd, 2007), reports of studies from the Outer Continental Environmental Assessment Program (e.g., Connors and Risebrough, 1978; Schamel et al., 1979; Shields and Peyton, 1979), and unpublished notes of local ornithologists (see Acknowledgements). We mapped all locations in Alaska where sharp-tailed sandpipers had been observed during the post-breeding period to compare with previously documented geographic distribution. For 18 sites at which earliest arrival dates had been



FIG. 1. Locations in northern and western Alaska where timing of southward migration of sharp-tailed sandpipers has been documented. Symbols show sites where arrival time was recorded (see Fig. 2).

recorded for one to six years, we tested whether arrival date was negatively correlated with latitude of the site (i.e., whether there was a southward progression of arrival dates suggesting southward movement through western Alaska). We treated each site-year combination as an independent data point to incorporate interannual variability in timing of arrival along the linearly distributed coastal sites. We also documented the dates or periods in these studies during which peak numbers of birds were recorded each year, as well as the last date the species was seen, although some sandpipers were often still present when researchers left the study areas. Such opportunistic data did not allow analysis for any possible long-term trends in seasonal timing over the years. To examine the timing of departure relative to the normal onset of freezing conditions across the region, we plotted by latitude the earliest autumn dates on which the average minimum temperature fell below 0°C for 21 National Weather Service Cooperative Observer (COOP) stations with long-term (1971–2000) archived data available (Western Regional Climate Center, 2009).

To assess the general magnitude of the sharp-tailed sandpiper migration into western Alaska, we recorded numbers of sharp-tailed sandpipers using coastal meadows during September and early October near our field camps at the Tutakoke River (2400 ha), Ugashik Bay (640 ha), and Cinder Lagoon (1340 ha). We recorded all sharp-tailed sandpipers observed during 17 hikes across 11 different routes (2.8–7.2 km; one surveyed 7 times) near Tutakoke (1978–80, 2006) and during 4 different hikes (1.6–4.1 km) near Ugashik Bay (1985). We counted all birds observed out to an unlimited distance and recorded whether they were on, flushed from, or flying across the meadows; we did not attempt to measure detectability. We also obtained estimates of minimum densities on 10 randomly selected strip transects, six at

Cinder Lagoon in 1986 and four at Tutakoke in 2006. Cinder Lagoon transects (0.7–2.0 km long, 200 m wide) were surveyed by two observers, each counting half-strips, and Tutakoke transects (1.6–2.6 km long, 50 m wide) by one or two observers. One Tutakoke transect was surveyed three times during the season.

For the unlimited-distance surveys at Tutakoke and Ugashik Bay, we plotted lineal densities of birds (total number seen per km) by date to examine seasonal occurrence on the study areas. For the fixed-width transects at Tutakoke and Cinder Lagoon, we calculated mean areal densities (number per ha) of birds on or flushed from the meadows, acknowledging that we likely missed birds, especially on the outer edges of the 200-m-wide transects at Cinder Lagoon. To avoid pseudoreplication when estimating the overall mean, we used the mean of the counts for the transect at Tutakoke that was surveyed three times. We used ArcMap 9.1 (Environmental Systems Research Institute, 1992–2005) to plot the transects across land cover maps available for the central Y-K Delta (75 600 ha around Tutakoke; Tande and Jennings, 1986) and the area encompassing Cinder Lagoon (4200 ha; Ducks Unlimited, Inc., 2007) to identify the predominant vegetation types occurring within the transects. We then calculated the area of the key types on each land cover map to estimate grossly the average number of sharp-tailed sandpipers present in those vegetation types during the survey periods; this estimate assumed that densities in the same vegetation on the surrounding mapped areas were similar to those on our smaller surveyed areas.

For another measure of seasonal occurrence at the Tutakoke study area, we counted the number of sharp-tailed sandpipers occurring along the banks of the Kashunuk and Tutakoke rivers each time we traveled by boat to resupply our field camp or conduct other investigations. To aid in navigation, we usually boated during mid-tide (rising or falling), when extensive sections of non-vegetated mudflats were exposed and regularly used by sandpipers. Complete surveys extended 8.5 km up the Tutakoke ( $n = 5$ ) and 41 km up the larger Kashunuk ( $n = 10$ ) from their mouths. One partial survey extended 3.2 km up the Tutakoke River. Partial surveys of the Kashunuk ( $n = 16$ ) extended 10.6–32.2 km; most of these were along the lower stretch of the river, where sharp-tailed sandpipers were more concentrated. Because of uneven spatial distribution of sandpipers along the rivers, lineal densities from complete and partial counts were not comparable; instead, partial counts were interpreted as the minimum number present along the river.

#### *Body Mass Gain on Staging Areas in Alaska*

We examined patterns of body mass gain of juvenile sharp-tailed sandpipers between mid August and late October in western Alaska to assess the relative importance of various regions of western Alaska to staging birds and to gain insights into potential migration strategies used by birds on southward migration. We included the following

records from our field studies: 197 banded and 63 collected birds near the Tutakoke River on the central Y-K Delta (1978–1980, 2006) and 25 banded and 27 collected along the north-central Alaska Peninsula. The Peninsula sites were Nelson Lagoon (56.0° N, 161.2° W; 2 collected 1976), Cinder Lagoon (8 collected 1986), and Ugashik Bay (4 collected 1985; 13 collected and 25 banded 2006). We augmented these data with mass data from 18 museum specimens collected between 1967 and 2004 from other sites in Alaska (Cape Krusenstern, 67.0° N, 162.9° W; Middleton Island, 59.4° N, 146.3° W; St. Paul Island, 57.2° N, 170.3° W; Nanvak Bay, 58.6° N, 161.7° W; Izembek Lagoon, 55.3° N, 162.9° W; Adak Island, 51.8° N, 176.5° W; Amchitka Island, 51.5° N, 179.1° E; and Attu Island, 52.9° N, 173.0° E; see Acknowledgements).

We used least-squares regression to fit a general linear model of body mass as a function of date, pooling birds across all years and geographic areas of Alaska and both sexes. Although important temporal and spatial patterns likely existed, we could not analyze for these because our visits to different locations were clustered during discrete, mostly non-overlapping seasonal periods. Sharp-tailed sandpipers are sexually dimorphic in body size (Rogers, 1995; Higgins and Davies, 1996), but fewer than half of the birds in our samples were of known gender. Gender had been determined by gonadal inspection for 74 specimens collected at various sites (1967–2004) and by molecular methods using blood samples (Griffiths et al., 1998; Sonsthagen et al., 2004) for 38 birds from Ugashik Bay (2006). To preclude potential bias in seasonal trend of body mass due to gender-related differences, we first used a binomial test to test for departure from an equal sex ratio among the subsample of individuals of known gender. We used a chi-square goodness-of-fit test to see if gender composition varied by time of season (< 15 September, 16–30 September, > 30 September). We then included date, sex, and a date•sex interaction term in a general linear model to test if the rate of change in mass differed by sex among birds of known gender. Finally, we used the full sample of sexed and unsexed birds to determine the overall rate of change in body mass across the season. We used SAS 9.1 (SAS Institute Inc., 1989) and Minitab 14.20.0.0 statistical packages to conduct analyses; means are given  $\pm$  standard errors.

#### *Timing and Routes of Southward Migration*

We searched a variety of sources for records of adult and juvenile sharp-tailed sandpipers occurring throughout the Pacific Basin to (1) assess the relative magnitude and timing of movements to and from Alaska, and (2) delineate potential southward migration routes. We limited our search to regions outside of the principal nonbreeding grounds in Australia and New Zealand and minor nonbreeding areas in New Guinea (Higgins and Davies, 1996). We focused on Alaska and the Russian Far East, the central and western Pacific, the eastern mainland of central and southeast Asia, and Indonesia. We focused less on the Pacific coast of North

America south of Alaska since many observational records documenting the sharp-tailed sandpiper's status there as a regular but rare migrant had already been compiled by Mlodinow (2001) and Hamilton et al. (2007).

To assess southward migration of the species in general, we relied primarily on known-age specimens from numerous ornithological collections throughout the world (see Acknowledgements). We considered southward migration to encompass the period between July and November (Higgins and Davies, 1996) and thus restricted our analyses to include only birds collected during that period. We then plotted these birds according to region (Alaska, Asia, Oceania, and the Pacific coast of North America south of Alaska), age (adult or juvenile), and abundance class (1, 2–5, 6–10, > 10 individuals per site). If birds were collected from multiple years at the same site, the abundance class reflected the total numbers collected there. Numbers collected are not measures of actual abundance, but they likely reflect relative abundance at the sites visited.

Adults and juveniles are readily distinguishable by plumage during southward migration (Hayman et al., 1986), but observers often fail to report the age of the birds seen. Several studies, however, have confirmed that the large majority of sharp-tailed sandpipers migrating between September and November are juveniles (Tomkovich, 1982; Higgins and Davies, 1996; Ge et al., 2006; this study). Thus, to further assess the migration routes of juveniles, we examined published and online records of observations from these months only. These sources included bibliographies (Byrne, 1979; Heather and Sheehan, 1990); the Shorebird Census in Japan (WWF Japan, n.d.); references in serial publications such as *Atoll Research Bulletin*, *Micronesica*, *'Elepaio*, *Pacific Science*, and *Sea Swallow*, and unpublished databases compiled by D. Watling (Fiji) and the late R. Pyle (Hawaiian Archipelago). Quite useful information was obtained from several online sites that post trip reports and species lists (searched through 2008) from birding tour groups throughout the world (e.g., *travelingbirder.com*, *surfbirds.com*, and *worldtwitch.com*). We also searched the extensive collections of birds (see above) and field notes from the Whitney South Seas Expedition and the Pacific Ocean Biological Survey Program (including notes of R. Clapp), which are maintained at the American Museum of Natural History and the U.S. National Museum, respectively. These records were derived mostly from field efforts, which are not evenly distributed on either a temporal or a spatial scale, so to avoid potential biases we used the records only to provide a general pattern of occurrence. Also, several sites were visited more than once each month in a given year. To avoid pseudoreplication, we selected the high monthly count at any given site in any given year. The resulting 235 records were then categorized by region (see above), categorized by abundance (0, 1–9, 10–99,  $\geq 100$  birds), and plotted on an orthographic projection. We also mapped the general extent of numerous scattered records along the Pacific coast of North America south of Alaska (Mlodinow, 2001; Hamilton et al., 2007).

A robust and uniform source of migration data across the central Pacific is contained in the Hawaiian Archipelago bird record database compiled for 1954–2004 by the late R. Pyle (unpubl. data). If sandpipers do migrate across the Pacific, the Hawaiian Archipelago is the first land birds would encounter south of Alaska and also very near a great-circle route between Alaska and the species' principal non-breeding grounds. We summarized the Hawaiian records on a semi-monthly basis and, for each location, recorded the presence or absence and the maximum number of birds reported during each semi-monthly period during any given year. We then summed the number of records and number of birds for each semi-monthly period across all years and locations in the Hawaiian Archipelago.

## RESULTS

### *Distribution and Timing in Alaska*

Juvenile sharp-tailed sandpipers were first noted in northern and western Alaska during the last 10 days of August and then progressively later at sites along the Alaska Peninsula and Aleutian Islands, although timing of arrival at the more southern sites showed greater interannual variability (Fig. 2A;  $r = -0.55$ ,  $p = 0.0002$ ,  $n = 40$  arrival dates at 18 sites). Numbers tended to peak during mid-September on the Y-K Delta, during late September and early October on the Alaska Peninsula, and slightly later in the Aleutian Islands, although peaks were sometimes difficult to define because of timing of departure of investigators from study sites (Table 1). Juveniles were last reported at sites in northern Alaska during late September, at sites along the Alaska Peninsula during late October or early November, and in the Aleutian Islands during mid-November (Table 1). The timing of movement out of these areas coincided with the long-term average onset of freezing conditions, which occurs progressively later in the season at more southern sites in the region (Fig. 2B;  $r = -0.91$ ,  $p < 0.0001$ ). The only adult sharp-tailed sandpiper observed in autumn during any of these studies in western Alaska was a single bird that was feeding with a group of seven juveniles on a coastal meadow in the Tutakoke River study area on 16 September 1980 (C.M. Handel and R.E. Gill, pers. obs.).

### *Seasonal Abundance in Western Alaska*

During boat trips up the Tutakoke and Kashunuk rivers, we observed an increase in the numbers of sandpipers using the intertidally exposed mud banks during early to mid September, although counts were highly variable (Fig. 3A). Numbers recorded during partial surveys were almost equal to those recorded during the full surveys, reflecting the birds' tendency to concentrate along the lower stretches of the rivers. Although many sandpipers were scattered along the shorelines in small groups of fewer than 10 birds, flocks of 50–150 birds were not uncommon along these

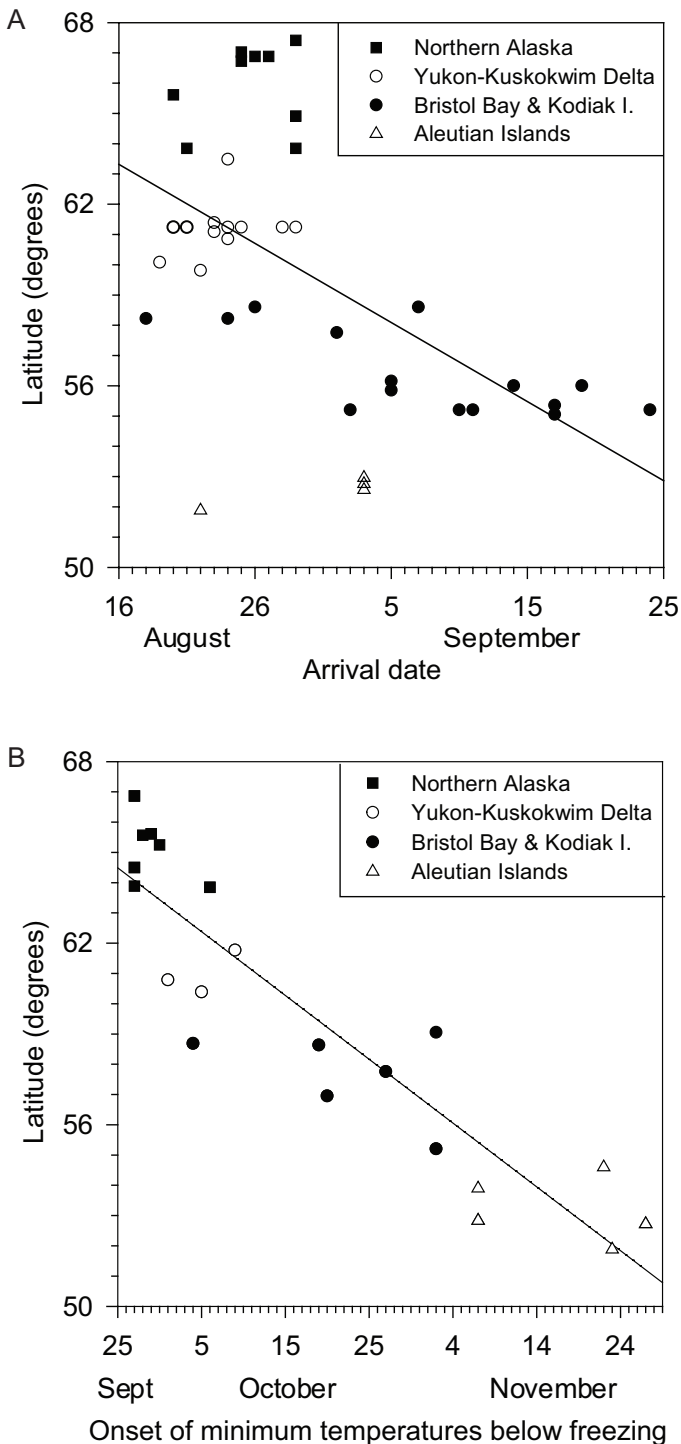


FIG. 2. (A) Timing of earliest arrivals of juveniles, by latitude of study site. Each symbol represents a different site-year combination (40 records from 18 sites shown in Fig. 1). For clarity, symbols are staggered slightly for cases in which first arrivals occurred on the same dates in multiple years. Line shows negative relationship between date of earliest arrival and latitude of study site ( $r = -0.55$ ,  $p = 0.0002$ ). (B) Earliest autumn date on which the long-term (1971–2000) average minimum daily temperature fell below 0°C at each of 21 coastal National Weather Service COOP stations in the study area. Line shows negative relationship between date and latitude of station ( $r = -0.91$ ,  $p < 0.0001$ ).

littoral habitats, especially on the depositional sides of the channels.

Birds were also commonly seen on adjacent wetland habitats. We recorded an average of  $25 \pm 7$  sharp-tailed sandpipers per lineal km during 17 hikes on 11 routes across coastal meadows of the Tutakoke study area on the central Y-K Delta from early to mid September (Fig. 3B). Densities were highly variable among routes, and we found no difference ( $p = 0.47$ , Kruskal-Wallis  $H = 0.53$ ,  $df = 1$ ) between the mean density estimated in 1978–80 ( $17 \pm 5$ ;  $n = 6$ ) and that estimated in 2006 ( $35 \pm 14$ ,  $n = 5$ ). There was no seasonal trend in densities recorded on the single route surveyed seven times in 2006 (Fig. 3B). Lineal densities during similar hikes at Ugashik Bay on the Alaska Peninsula during October 1985 averaged  $13 \pm 3$  ( $n = 4$ ). During all surveys, most sandpipers occurred as single birds or in small flocks ( $< 10$ ), but occasionally we encountered flocks of 30–50 birds feeding on or flying across the meadows, leading to the high variability in densities.

On the basis of the fixed-width transects across coastal meadows, we estimated areal densities to be  $0.7 \pm 0.2$  birds  $ha^{-1}$  ( $n = 4$ ) at Tutakoke in 2006 and  $0.5 \pm 0.2$  birds  $ha^{-1}$  ( $n = 6$ ) at Cinder Lagoon in 1986; these estimates excluded birds flying across the transects. At Tutakoke, sandpipers were observed using predominantly moist, graminoid meadows, which occurred across 7454 ha (~10%) of the encompassing area classified to vegetation type (Tande and Jennings, 1986). At Cinder Lagoon, sandpipers were most frequently observed on mesic/dry sedge and mesic/dry grass meadows, which occupied 627 ha (~15%) of that study area (Ducks Unlimited, Inc., 2007). Using these habitat associations, we projected mean population sizes of  $5000 \pm 1200$  sharp-tailed sandpipers on the Tutakoke study area and  $300 \pm 100$  birds at Cinder Lagoon during the autumn staging periods sampled.

#### Changes in Body Mass

The ratio of males (56%) to females (44%) among juvenile sharp-tailed sandpipers of known sex ( $n = 122$ ) banded or collected in western Alaska did not differ significantly from an equal sex ratio (binomial test,  $p = 0.24$ ), and gender composition did not vary across the early, middle, and late parts of the autumn staging period ( $p = 0.16$ ,  $\chi^2 = 3.65$ ,  $df = 2$ ). Within the sexed subsample, the rate of change in body mass did not differ between males and females ( $p = 0.47$ , partial  $F_{1,118} = 0.53$ ), so we pooled all birds of known and unknown gender into a single analysis to increase sample size. Among all birds across western Alaska (Fig. 4), there was a significant increase in body mass of  $0.57 \pm 0.06$  g per day throughout the autumn staging period ( $p < 0.0001$ ,  $F_{1,328} = 78.18$ ). Patterns of mass gain were less clear within subregions because data were not available across the entire season for any given study area. Beginning in mid-September, however, variability in mass increased dramatically, with some individuals on the Y-K Delta (120–145 g) reaching more than double the average mass of birds during late August, when sandpipers had just arrived (~62 g; Fig. 4). Birds on the Alaska Peninsula, which were measured

TABLE 1. Peak period and latest seasonal occurrence of sharp-tailed sandpipers at sites in northern and western Alaska.

Site <sup>1</sup>	Latitude	Year	Peak Period <sup>2</sup>	Last Seen <sup>2</sup>	Peak Number <sup>3</sup>	Source <sup>4</sup>
<b>Northern Alaska</b>						
Noatak River	67.0	1991		20 September		1
Wales	65.7	1978		≥ 11 September*		2
E. Norton Sound	64.8	1977	1 September	18 September	93	3
St. Lawrence I.	63.8	2001		29 September		4
		2003	25 August		34	4
		2004	3 September		30	4
<b>Yukon–Kuskokwim Delta</b>						
Kashunuk R. area	61.4	1978		≥ 12 September*	127	5
		1979		≥ 19 September*	280	5
		1980	6–16 September	≥ 22 September*	251	5
		2005		≥ 19 September*		5
		2006	29 August–20 September	≥ 20 September*	109	5
<b>Bristol Bay/Alaska Peninsula</b>						
Nanvak Bay	58.6	1973		24 September		6
		1996	13 September	21 September	38	7
Ugashik Bay	57.5	1985	1–5 October	≥ 18 October*	75	5
		1986	1–10 October	≥ 18 October*	14	5
		1987	1–20 October	≥ 30 October*	25	5
Cinder Lagoon	57.3	1986	26 September–5 October	≥ 20 October*	58	5
		1987	27 September–13 October	≥ 28 October*	30	5
		1988	3–11 October	≥ 16 October*	9	5
Nelson Lagoon	56.0	1976	22 September	≥ 8 October*	21	8
		1978	5 October**	≥ 16 October*	63	8
Izembek Lagoon	55.0	1986		31 October		9
		1987		2 November		9
		1988		14 November		9
		1993		17 October		9
<b>Aleutian Islands</b>						
Unalaska	54.0	1978	13 October		9	10
Attu	52.8	1983	19 October		19	11
Shemya	52.7	1978	9 October		45	11
		1984	19 September		19	11
Adak	51.7	1972	6 October		25	11
		1973		21 November		11
		1974		9 November		11
		1978		18 November		11
		1986		21 November		11
		1990		12 November		11
		2001		29 October		11
Amchitka	51.5	1965		7 November		11
		1972	8 October		30	11

<sup>1</sup> See Figure 1 for locations.

<sup>2</sup> Date or period during study when greatest number of birds was recorded. \*Personnel departed when birds were still present. \*\*Personnel did not arrive until 26 September.

<sup>3</sup> Greatest number recorded on a given date or during a series of replicated surveys.

<sup>4</sup> Source: 1 = R. Uhl, unpubl. data; 2 = P. Connors, pers. comm. 1979; 3 = Shields and Peyton, 1979; 4 = Lehman, 2005; 5 = this study; 6 = Petersen et al., 1991; 7 = T. Burke, unpubl. data; 8 = Gill et al., 1981; 9 = T.L. Tibbitts, pers. comm. 1993; 10 = R. Scher, unpubl. data; 11 = Gibson and Byrd, 2007.

primarily during late September and early October, also varied much more greatly in mass than birds measured elsewhere during August, although none had reached the extremely high masses recorded on the Y-K Delta.

#### *Southward Migration*

The southward migration of both adult and juvenile sharp-tailed sandpipers throughout the entire Pacific Basin was assessed through a combination of 349 specimens and, for juveniles, from observations of more than 3000 individuals from 198 different sites at which the presence or absence of birds had been recorded (Fig. 5). Plotting the distribution

of specimens collected between July and November revealed pronounced age-related pathways from the breeding grounds. Adults were primarily found along a continental route south through east central Asia with relatively few along the coast of Asia north of the Yellow Sea (Fig. 5A). In contrast, juveniles were found primarily in Oceania along a corridor between western Alaska and the central Pacific, with much smaller numbers recorded along the coast of Asia. When we partitioned these records by geographic region, a similar pattern emerged. Among adults ( $n = 67$ ), 78% were collected from mainland Asia while only 12% came from Oceania and 10% from Alaska. Among juveniles ( $n = 282$ ), comparatively few specimens were found from Asia (12%)

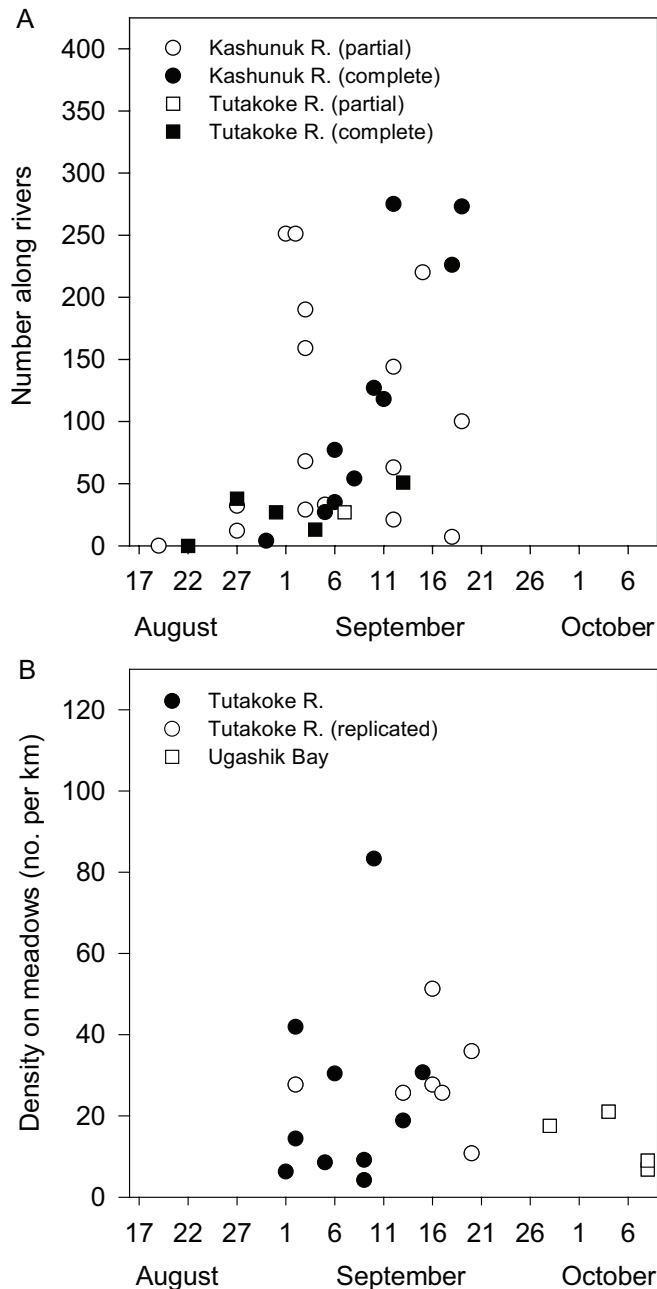


FIG. 3. Temporal abundance of juvenile sharp-tailed sandpipers in western Alaska. (A) Number observed along intertidally exposed mud banks during boat trips up the Kashunuk (circles) and Tutakoke (squares) rivers on the central Yukon-Kuskokwim Delta (1978–80, 2006). Complete surveys (filled symbols) encompassed 41 km from the mouth of the Kashunuk and 8.5 km from the mouth of the Tutakoke. Partial surveys (open symbols) covered the lower 10.6–32.2 km of the Kashunuk River and the lower 3.2 km of the Tutakoke River, where the sandpipers tended to concentrate. Numbers increased rapidly beginning in late August and early September. (B) Lineal densities of sharp-tailed sandpipers (birds per km) recorded during hikes across coastal meadows near the Tutakoke River (circles) on the central Yukon-Kuskokwim Delta (1978–80, 2006) and near Ugashik Bay (squares) on the Alaska Peninsula (1985). Routes varied from 2.8 to 7.2 km at Tutakoke and from 1.6 to 4.1 km at Ugashik. Densities varied markedly both among routes and seasonally within the single route at Tutakoke that was surveyed seven times (open circles).

or Oceania (23%); most (61%) were collected in Alaska, and only a few (4%) were collected from farther south along the Pacific Coast of North America.

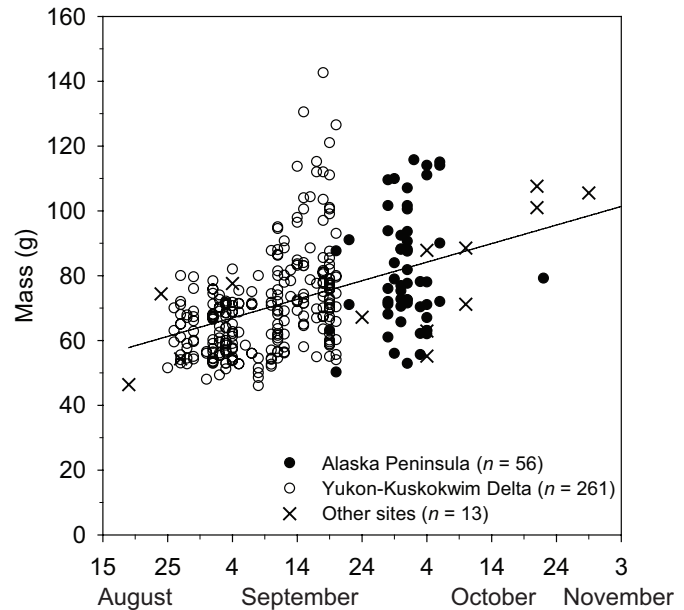


FIG. 4. Body mass of juvenile sharp-tailed sandpipers banded ( $n = 222$ ) or collected ( $n = 108$ ) across multiple years at various sites in western Alaska. Least-squares regression line shows average increase of  $0.57 \pm 0.06$  g per day during the autumn staging period.

When we plotted the distribution of sightings of birds during the September–November migration period of juveniles, the importance of central Oceania as a migration corridor was even more pronounced (Fig. 5B). Among the 161 records of single or flocks of sharp-tailed sandpipers, 85 (53%) were in Oceania, 61 (38%) were in Alaska, and only 15 (9%) were along the mainland of Asia (Table 2). Using the number of large groups observed as a measure of the intensity of passage through a particular region, we found that juveniles were recorded in groups of 100 or more birds on 14 occasions in Alaska, but only twice in Asia (Table 2). Among groups of 10–99 birds, only 3 were found in Asia while 32 were seen in Alaska and 17 were documented in Oceania (Table 2).

Observations from the Hawaiian Archipelago bird records database also strongly suggest a major southward flight by juvenile sharp-tailed sandpipers across Oceania. The number of birds and number of sightings recorded clearly depicts a major and regular occurrence within the archipelago during autumn (Fig. 6). The seasonal timing of these records indicates a peak occurrence between mid-October and early November, mirroring the equally late occurrence at sites in western Alaska (Table 1). Alaska and Oceania are the only regions throughout the Pacific Basin reporting such late occurrence of sharp-tailed sandpipers.

## DISCUSSION

Our study clearly demonstrates that large numbers of juvenile sharp-tailed sandpipers—but virtually no adults—detour east from Russian Arctic breeding grounds each autumn to stage on coastal meadows and riverine intertidal



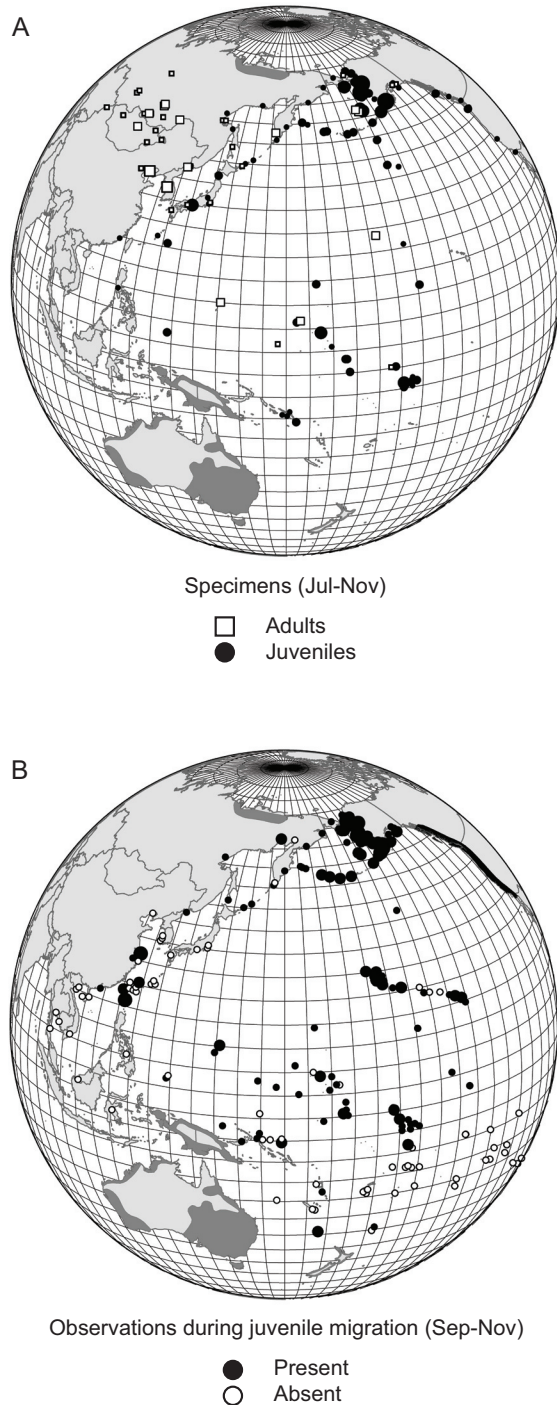


FIG. 5. Specimen and sight records of sharp-tailed sandpipers during the southward migration period. (A) Specimens collected between July and November ( $n = 349$ ), with adults depicted by open squares and juveniles by filled circles. The sizes of symbols from smallest to largest denote 1, 2–5, and 6–10 individuals per location for adults, and 1, 2–5, 6–10, and more than 10 individuals for juveniles. Numbers collected provide a general index of relative abundance at the sites visited. (B) Visual observations during September–November ( $n = 235$ ), when the vast majority of migrating sharp-tailed sandpipers are juveniles. Open circles depict locations where observers were present but no sandpipers were seen; filled circles (from smallest to largest) denote records of 1–9, 10–99, and 100 or more individuals, respectively. The breeding range in Arctic coastal Russia and the nonbreeding range in Australasia are shaded. Numerous scattered sight records exist for North America, particularly along Pacific coast states and provinces south of Alaska (Mlodinow, 2001). The extent of these records along the Pacific coast is depicted by a thick dark line. Data are plotted on orthographic projections.

TABLE 2. Number of records of sharp-tailed sandpiper observations, classified by group size, within different geographic regions of the Pacific Basin during September–November, the primary period of southward migration of juveniles.

Region <sup>1</sup>	Group Size			Total
	1–9	10–99	≥ 100	
Alaska	15	32	14	61 (38%)
Oceania	67	17	1	85 (53%)
Asia	10	3	2	15 (9%)
Total	92 (57%)	52 (32%)	17 (11%)	161 (100%)

<sup>1</sup> Alaska excludes southeast Alaska; Oceania excludes New Zealand and Australia; Asia includes Indonesia and the eastern mainland and archipelagoes from Thailand north to Chukotka, Russia. Records from mainland North America excluded from this analysis. See methods for sources of data.

habitats of western Alaska before migrating south. When we began to assess the significance of this unusual juvenile movement, several questions emerged. For example, do juveniles stage elsewhere in the Russian Far East, or is Alaska their principal staging area? We found comparatively few studies from coastal Russia that were conducted during the September–November migration period of juveniles, but those available—despite generally being from areas farther south and earlier in the season—gave no indication that juveniles are anything but a rare to uncommon transient in coastal Russia during southward migration (e.g., Nechaev, 1998; Antonov, 2003; Tomkovich, 2003; Gerasimov, 2004, 2005; Gerasimov and Huettmann, 2006; Bamford et al., 2008). Indeed, the species is seldom recorded after late August at the northernmost site reported by Gerasimov and Huettmann (2006), in the Magadan Region (59° N, 153° E, about the same latitude as the Y-K Delta). Sharp-tailed sandpipers are considered a scarce autumn migrant on Sakhalin Island (47° N, 153° E), just north of Hokkaido, Japan, where flocks of up to 100 birds, including adults and juveniles in unknown proportions, have been reported during August, and the last single young have been seen in early November (Nechaev, 1998). Still, we cannot rule out the possibility that some juveniles stage in Alaska and then late in the season return to Asia and follow a more coastal southward migration route (but see below).

Another question that emerged was what proportion of the juvenile cohort occurs in Alaska each autumn. The most recent assessment of the size of the entire sharp-tailed sandpiper population is about 160 000 birds (Bamford et al., 2008). The proportion of juveniles in the population—as assessed through capture data on the nonbreeding grounds, primarily in SE Australia (November–February; Minton et al., 2007)—varied between 8% and 42% over a 9-year period, with a 26-year median of 11.1%. Despite several potential biases in using juvenile proportion data to infer population size and status (Clark et al., 2004; Harrington, 2004; Rogers et al., 2004; McCaffery et al., 2006), we feel an estimate of 10–20% average annual recruitment is not

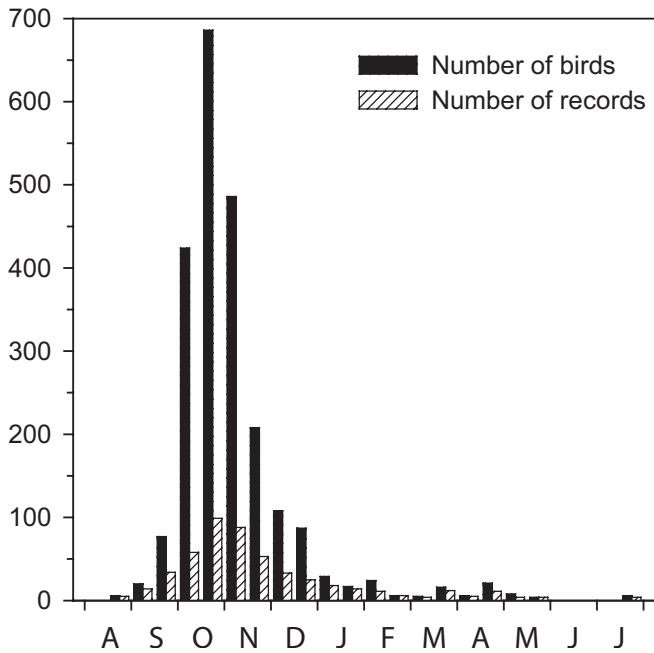


FIG. 6. Semi-monthly distribution of records and numbers of sharp-tailed sandpipers recorded from the Hawaiian Islands Archipelago. Each bar represents the maximum number of individuals (solid) or sightings (hatched) reported per semi-monthly period each year, summed across all years (1954–2004) and all sites in the Archipelago (R. Pyle, pers. comm. 2003, 2005).

unreasonable for this shorebird. Thus, the annual cohort of juveniles that survive the southward flight may average about 16 000–32 000 birds. Our transect data, when projected to one specific habitat type over our relatively small study area on the central Y-K Delta, accounted for about 5000 birds. We know, however, that during September these sandpipers occur much more extensively across wetland habitats elsewhere on the Y-K Delta, at St. Michael to the north, Tern Mountain to the south, and 15–25 km inland of the small area we sampled (B.J. McCaffery, unpubl. data; R.E. Gill and C.M. Handel, pers. obs.). Thus, it is not unreasonable to surmise that a few tens of thousands of juvenile sharp-tailed sandpipers occur annually on the Y-K Delta, likely comprising a large majority of the juvenile cohort.

The seasonal progression of occurrence suggests there may be some southward movement through western Alaska, but we had no marked birds to confirm this. Most sandpipers likely depart from more northern areas before the onset of freezing conditions, when thermoregulatory costs increase and foraging conditions deteriorate. High body masses of some individuals on the Y-K Delta suggest that a few may be ready to embark on migration in mid-September. Others certainly require more time to acquire the necessary fuel, and temperatures on the Y-K Delta generally remain hospitable to do so until early October. Although we estimated that only about 300 sandpipers were present on average at Cinder Lagoon, similar wetland habitats occur broadly across the north side of the Alaska Peninsula, and birds occur commonly at such sites (e.g., Gill et al., 1981; T.L. Tibbitts, pers. comm. 1993; this study). It is likely that several thousands of sandpipers occur annually on the

Alaska Peninsula into October, but concurrent regional studies of marked birds are needed to determine the extent of any southward movement to the Alaska Peninsula and Aleutian Islands.

The principal southward migration of juvenile sharp-tailed sandpipers from staging areas in western Alaska, as assessed through the distribution of specimens and sight records, clearly involves crossing central and western Oceania to reach their principal nonbreeding grounds. This passage begins during late September and peaks during mid-October to early November. Prolonged trans-Pacific flights by several shorebird species are now recognized (Williams and Williams, 1999; McCaffery, 2008; Gill et al., 2009), including nonstop flights from Alaska by individual bar-tailed godwits (*Limosa lapponica baueri*) that exceed 11 000 km (Gill et al., 2009). We do not know if the flight capabilities of sharp-tailed sandpipers match those of the much larger godwits (see Thompson, 1973; Davidson and Gill, 2008), but the timing and duration of their staging period, the amount of fuel carried (~doubling of lean body mass, cf. Gill et al., 2005; Å. Lindström, pers. comm. 2009), and the largely sympatric nonbreeding range of the two species suggest that some sharp-tailed sandpipers are fully capable of nonstop flights from Alaska at least to sites in Micronesia or Papua New Guinea (Bishop, 2006), a distance of between 5500 and 8500 km. The occurrence of sharp-tailed sandpipers along the coast of Asia in autumn, though encompassing many fewer sites and numbers (e.g., Carey et al., 2001; Barter, 2002; Ge et al., 2006; Moores, 2006; Zheng et al., 2006) than recorded throughout Oceania (Fig. 5), suggests that individuals following this route are also capable of very long flights. We interpret the cluster of records south from Taiwan and along the coast of the South China Sea (Fig. 5B) to represent birds that probably flew nonstop from Alaska or Chukotka—a distance of between 6000 and 7000 km.

It is quite surprising that the primary transoceanic route and the apparent secondary coastal Asiatic route that juveniles use during their first southward migration both differ from the more direct continental corridor used by almost all adults. Among most age-differential migrants, juveniles travel the same migratory routes as adults but migrate at different times during the season (Gauthreaux, 1982). The only species of bird documented in which adults and juveniles follow completely different routes is the honey buzzard in Europe (Hake et al., 2003). Among buzzards, however, juveniles follow the more direct route, and it is the adults that make a large-scale detour, ostensibly following a more favorable route that is learned from other experienced adults (Hake et al., 2003). During their first migration, birds are generally thought to be guided by innate information; in some species, the routes that juveniles follow unaided by adults can be quite complex, with distinct segments requiring changes in orientation (Wiltschko and Wiltschko, 2003).

To our knowledge, Keith (1967) was the first to raise the intriguing question as to why some sharp-tailed sandpipers, known to breed only in Asia, should cross over to North

TABLE 3. Potential advantages (+) and disadvantages (–) of southward migration of sharp-tailed sandpipers following a continental route across Asia or a trans-Pacific route via western Alaska during the periods when most adults (July–August) and juveniles (September–November) migrate. Effects of some factors are thought to be neutral (o) and others are unknown (?).

Factor	Continental across Asia		Trans-Pacific via Alaska	
	July–August	September–November	July–August	September–November
Shorter distance	+	+	–	–
Wind assistance	o	o	o/–	+
Lower predation risk	?	?	–	+
Lower pathogen risk	–	–	+	+
Increased food	?	?	?	+
Earlier arrival on nonbreeding areas	+	–	+	–
Reduced competition	+	–	–	+

America during autumn migration instead of following others down the coast of Asia. However, it is now known that the sharp-tailed sandpiper is but one of several shorebird species that migrate from Russian breeding grounds through western Alaska en route to nonbreeding grounds in Asia, Oceania, or the Americas (Thompson, 1973; Flint and Tomkovich, 1978, 1982; Holmes and Pitelka, 1998; Gill et al., 2002; Tomkovich, 2003). Multiple migratory flyways emanate from this region, and after the brief breeding season, many species of birds regularly cross between Asia and North America (Alerstam and Gudmundsson, 1999; Alerstam et al., 2007; Hedenström et al., 2009).

Alaska and the Russian Far East share a rich and unique Beringian avifauna, the composition of which has been strongly influenced by the complex glacial history of the region (e.g., Mayr, 1946; Hopkins et al., 1982; Avise and Walker, 1998). Flint and Tomkovich (1978, 1982) proposed that the ancestral form of the sharp-tailed sandpiper and its closely related congener the pectoral sandpiper (*Calidris melanotos*) bred along the Arctic coastal plain from northeast Asia to northern North America, and that the two species evolved in parallel after the continents separated in Beringia. During post-glaciation, the pectoral sandpiper likely reinvaded northeastern Russia, where it now nests sympatrically with the sharp-tailed sandpiper, with differences in breeding behavior acting as isolating mechanisms (Flint and Tomkovich, 1978, 1982). Pectoral sandpipers reach their primary nonbreeding areas in South America mainly along a continental route through interior North America and stage in relatively small numbers in western Alaska (Holmes and Pitelka, 1998; R. Gill, unpubl. data). Given the breeding sympatry and evolutionary history of these two species, it is not surprising that small numbers of each species are regularly found along migratory routes and on nonbreeding areas of the other (Higgins and Davies, 1996; Mlodinow, 2001).

Several species of shorebirds have both breeding and nonbreeding distributions that overlap those of the sharp-tailed sandpiper, but none exhibits similar age-segregation in southward migration routes (Higgins and Davies, 1996). Some adult and juvenile red-necked stints (*Calidris ruficollis*) follow a continental route through Russia and China, while others migrate along the Asiatic coast (Higgins and Davies, 1996; Gerasimov and Gerasimov, 1998; Bamford

et al., 2008). Their small body size (~27 g) may preclude the long trans-Pacific flight. Similar-sized North American semipalmated sandpipers (*Calidris pusilla*) are thought to undertake trans-Atlantic flights of only up to 4300 km after almost doubling their body mass on staging areas (Hicklin, 1987; Gratto-Trevor, 1992). Larger-bodied (~120 g) ruddy turnstones (*Arenaria interpres interpres*) have been documented staging on food-rich habitats on the Pribilof Islands in western Alaska before making trans-Pacific flights to nonbreeding areas throughout Oceania and Australasia (Thompson, 1973). Coastal meadows and extensive intertidal habitats on the Y-K Delta and north Alaska Peninsula provide extremely abundant food resources for shorebirds that are fueling for southward migration (Gill and Jorgenson, 1979; Handel and Dau, 1988; Gill and Handel, 1990; Handel and Gill, 1992b; T. Piersma and A. Dekinga, unpubl. data), and no analogous autumn shorebird staging areas are found in Russia along the western coast of the Bering Sea (Bamford et al., 2008).

Thus, the question of particular interest is not why do sharp-tailed sandpipers detour to western Alaska during their first southward migration, but rather why do they not continue to do so as adults? The timing of migration among sharp-tailed sandpipers, staggered by both age and sex, is related to their polygynous or promiscuous mating system, in which adult males do not incubate eggs or care for young (Flint and Tomkovich, 1978, 1982). Adult males depart breeding grounds rapidly during early July and most females depart during late July, usually well before juveniles (Flint and Tomkovich, 1978, 1982; Higgins and Davies, 1996). The differential migration of sharp-tailed sandpipers suggests that, as in the case of the honey buzzards, the alternative migration routes may have inherent differences in conditions during the periods when adults and juveniles are migrating. While juveniles still follow what is likely the more ancestral route, naive breeding adults may learn their route by following older adults southward.

Virtually nothing is known about conditions along the continental migration route used by most adult sharp-tailed sandpipers, including what habitats are used, what foods are eaten, or even how many stopovers are typically used en route, so we can only suggest some factors that might influence selection for age-differential migration in this species (Table 3). The continental route traveled by adults through

Asia is only 100–1600 km longer than great-circle routes (both 10 200 km) to either western Australia (Broome) or northeastern Australia (Queensland), where sandpipers first return during late August or early September (Higgins and Davies, 1996). Flights taken by juveniles from the breeding grounds to the Y-K Delta, Alaska, and then across the Pacific Ocean to eastern or western Australia would entail much longer total distances of 12 400 km or 13 100 km, respectively. If juveniles were to return to the Asiatic coast after a detour to Alaska, their journeys would be at least 1500 km longer than a transoceanic route. Thus, in terms of distance traveled, the continental route across Asia would be more advantageous for both age groups than any route detouring via Alaska (Table 3).

Minimizing time in migration, energy used, or risk of mortality (Alerstam and Lindström, 1990) might better explain the age-differential migration in this species. For example, a cursory examination of wind patterns across continental Asia using the NCEP/NCAR 40-year reanalysis project (Kalnay et al., 1996) suggests that migrants using that route would be neither assisted nor hindered by winds. In contrast, favorable winds could confer considerable savings in time and energy for transoceanic migrants departing from Alaska, especially later in the migration period, as they do for bar-tailed godwits (Gill et al., 2009). Furthermore, the transoceanic corridor would be essentially devoid of predators and likely of pathogens and parasites as well (Gill et al., 2009). We have no measure of predation or pathogen risk along the Asiatic continental route, but predation risk in western Alaska appears to decline later in the season as parasitic jaegers (*Stercorarius parasiticus*) and other potential avian predators depart (Gill et al., 2009; R.E. Gill and C.M. Handel, pers. obs.).

The rapid departure of adult sandpipers from the breeding grounds suggests that they may be time-minimizing migrants, which can benefit from arriving at their destination earlier than competitors (Alerstam and Lindström, 1990). Long-distance migrants breeding at northerly latitudes face severe time pressures, with concomitant selective pressures for the maximum possible migration speed (Hedenström, 2008). Molt, breeding, and migration are costly major events in a bird's annual cycle and are generally timed so as not to overlap (Payne, 1972; Buehler and Piersma, 2008). Both adult and juvenile sharp-tailed sandpipers delay onset of molt until their arrival on nonbreeding grounds, and these events are similarly staggered by age (Higgins and Davies, 1996). Northward migration is also staggered by age, and it is unknown how many sandpipers breed or even migrate all the way to breeding grounds during their first year (Higgins and Davies, 1996), although there have been a few confirmed cases of a one-year-old female breeding (P.S. Tomkovich, pers. comm. 2009). Feathers that are grown more slowly tend to be of higher quality (Dawson et al., 2000; Serra, 2001), and durable primaries may be particularly important for the survival of long-distance migrants (Serra et al., 1999; Serra, 2001). Thus, there may be an important trade-off in time spent

migrating (including fueling time) and time allotted to molt (De la Hera et al., 2009). Adult sharp-tailed sandpipers may benefit from early onset of molt or other advantages from early arrival on nonbreeding areas that increase their probability of surviving to the next breeding season. Juveniles, particularly if they delay breeding for a year, as many long-distance migrant shorebirds do (Higgins and Davies, 1996), may not face the same time constraints as adults. Differential age migration may also reduce competition between juveniles and more dominant adults for food resources (e.g., Townshend, 1985; Wichmann et al., 2004). An interesting question raised by Thomas Alerstam (pers. comm. 2009) is whether spatial age-segregation continues to occur within Australia, with adults and juveniles minimizing migration distances and arriving in the western and eastern parts of the continent, respectively.

Optimization models suggest that the temporal and spatial distributions of food have the greatest influence in determining how major events are organized in a bird's annual cycle (Barta et al., 2008). We currently know very little about the seasonal abundance of food along the two migratory routes, or about other factors that might influence survival. How conditions vary throughout the entire annual cycle should be compared for adults and juveniles, particularly in light of any different time constraints for the two age groups. The sharp-tailed sandpiper, with its unusual age-differential, long-distance migration system, provides an ideal opportunity to use powerful comparative analyses (cf. Piersma, 2007) to develop and test predictions about optimal migration theory and life history strategy.

#### ACKNOWLEDGEMENTS

This contribution was rooted in conversations with several colleagues in the late 1970s, in particular Peter Connors and Sasha Kistchinski. Over the ensuing 30 years many others have shared their insights about the phenomenon, including Mark Barter, Vern Byrd, Jessie Conklin, Chris Dau, Dan Gibson, Martin Green, Sarah Jamieson, Marcel Klaassen, Richard Lanctot, Åke Lindström, Brian McCaffery, David Melville, Theunis Piersma, Adrian Riegen, Danny Rogers, Dan Ruthrauff, Max Thompson, Lee Tibbitts, Thede Tobish, Pavel Tomkovich, and Nils Warnock. Thomas Alerstam, Åke Lindström, Dan Ruthrauff, and two anonymous reviewers shared helpful comments on this manuscript. Pavel Tomkovich kindly provided a Russian translation of the abstract. We thank them all. The late Robert Pyle generously shared his database of bird observations from the Hawaiian Archipelago. C.Y. Chiang provided records from Taiwan. Geoff Carey, Paul Holt, Zhijun Ma, and David Melville shared records and references from China. Nial Moores provided a summary of the occurrence of sharp-tailed sandpipers in Korea. We thank all curators of the following collections, which were searched for specimens: Academy of Natural Sciences, Philadelphia; Australia Museum; Bernice Bishop Museum, Honolulu; Burke Museum, University of Washington; California Academy of Sciences, San Francisco; Field Museum of Natural History, Chicago;

Museum of Vertebrate Zoology, Berkeley; Museum of Zoology, University of Michigan; National Museum of Natural History; Natural History Museum, Tring; Peabody Museum of Natural History, Yale University; Royal Ontario Museum; University of Alaska Museum, Fairbanks; University of Kansas Natural History Museum; University of Michigan Museum of Zoology; Yamashina Institute, Japan. Takeshi Yamasaki and Nigel Clark are especially thanked for their help in obtaining information from the Yamashina Institute and the Natural History Museum at Tring, respectively. Unpublished notes from numerous sites in Alaska were graciously shared by Toby Burke, Chris Dau, Craig Ely, Steve Heintz, Paul Lehman, Karen Kincheloe, Rich MacIntosh, Brian McCaffery, Lee Tibbitts, Thede Tobish, and Robert Uhl. We thank Philip Martin for estimating areas of wetland habitats and John Terenzi for helping to prepare distribution maps. The Swedish Academy of Science expedition to Beringia in 2005 was the impetus for renewed work on the species, especially by Åke Lindström and Marcel Klaassen. The U.S. Fish and Wildlife Service and the U.S. Geological Survey funded the work. Logistical support, in part, was provided by the Yukon Delta National Wildlife Refuge. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

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