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RESIDENCY PATTERNS OF MIGRATING SANDPIPERS AT A MIDCONTINENTAL STOPOVER[1]

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Abstract. Arctic-nesting shorebirds require several refueling stops during their long migrations between breeding grounds and Central and South American wintering areas. The protection of stopover habitats for transcontinental migrants depends on whether birds fly long distances between a few select sites or fly short distances and stop at several wetlands. Although the Great Plains historically provided a vast array of wetlands for use by migrants, wetland loss and conversion have reduced the availability of stopover sites in recent decades. In this study, we examined (1) residency periods, (2) fat dynamics, and (3) migration chronology of two shorebird species, the Semipalmated Sandpiper (*Calidris pusilla*) and White-rumped Sandpiper (*C. fuscicollis*) at Quivira National Wildlife Refuge (NWR), Kansas. Semipalmated Sandpipers had prolonged periods of species residency with overlapping arrivals and departures. Individual residency periods were highly variable and were unrelated to lipid reserves upon arrival. In contrast, White-rumped Sandpipers arrived and departed more synchronously. Birds that arrived in poor condition stayed longer than those with more body fat in 1991, but not in 1992. Wind direction did not influence patterns of departures of either species. We hypothesize that Semipalmated Sandpipers are ecologically eurytopic when migrating across the Great Plains in the spring. Highly variable patterns in arrival, residency, and lipid levels indicate that spring migration of this species is relaxed and opportunistic. White-rumped Sandpipers showed a pattern of reduced flexibility. Flight range estimates suggest that most birds require intermediate stopovers before reaching the breeding grounds. Interior wetlands appear to function as migration stopovers rather than staging areas for shorebirds.

Key words: Shorebirds; Calidris pusilla; Calidris fuscicollis; *migration; stopover; lipids; flight range estimates.*

INTRODUCTION

Many shorebird species migrate long distances, up to 12,000 km, between arctic and subarctic breeding grounds and Central and South American wintering areas. These journeys require several en route refueling stops. Coastal migrants are renowned for long flights over extensive bodies of water, preceded by long refueling stops (Myers et al. 1987, Helmers 1992, Gratto-Trevor 1992). A "jumping" strategy (Piersma 1987, Smit and Piersma 1989), characterized by long distance travel with few stops, is necessary if stopover sites are limited or if large expanses of water or unhospitable terrain must be crossed. Jumping can be risky because lack of food resources at stopover sites or unfavorable wind conditions can severely hinder progress (Piersma 1987).

An alternate migration strategy, "hopping" (Piersma 1987, Smit and Piersma 1989), is characterized by flying short distances between stops and by brief refueling periods. Hopping is energetically less costly than long "jumping" flights (Piersma 1987) and has reduced risk. In theory, the absence of available food at stopovers is not as critical to hoppers because they can move easily to the next suitable site.

Approaches to the protection of migration stopover habitats depend on whether birds jump to a few select sites or hop among several scattered wetlands. Historically, the Great Plains provided an array of wetlands, or series of stepping stones, for use by migrants (Skagen and Knopf 1993). In this landscape context, transcontinental migrants may have evolved hopping rather than jumping strategies. In recent decades, wetland loss and conversion has modified the face of the Great Plains (Tiner 1984, Dahl 1990) and has reduced the availability of suitable stopovers for hoppers.

The primary objectives of this study were to examine (1) residency periods, (2) fat dynamics, and (3) migration chronology of two abundant shorebird species at a midcontinental stopover, the Quivira National Wildlife Refuge in central Kansas. This information will provide clues to the nature of transcontinental migration by the

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two focal species. The Semipalmated Sandpiper (*Calidris pusilla*), one of the smallest sandpipers (21–32 g), migrates between breeding areas in the Canadian Arctic and its wintering range in northern South America (Harrington and Morrison 1979, Gratto-Trevor 1992). The larger White-rumped Sandpiper (*C. fuscicollis*; 40–60 g) also breeds in the Canadian Arctic, but travels to winter in the southern extremities of South America, making one of the longest animal migrations in the Western Hemisphere (Harrington et al. 1991, Parmelee 1992). Both species are highly dependent on stopover resources for refueling en route.

STUDY AREA AND METHODS

During April and May of 1991 and 1992, we counted migrating Semipalmated and White-rumped Sandpipers in and around the extensive mudflats, marshes, and managed water units at Quivira National Wildlife Refuge, Stafford County, Kansas (38°10′N, 98°40′W), an 8,830-ha refuge of the U.S. Fish and Wildlife Service.

Soon after the first arrivals of each species to the study site, we captured the sandpipers with mist nets and applied radio transmitters. Immediately upon capture, we measured the body mass (0.1 g, Ohaus Electronic Balance C305), tarsus length (0.1 mm), wing length (flattened, 1 mm), total head length (0.1 mm), and exposed culmen (0.1 mm) of each individual. In 1992, we also measured total body electrical conductivity (TOBEC) with an EM-SCAN SA-1 Small Animal Body Composition Analyzer (Skagen et al. 1993) on 75% of the birds. The TOBEC methodology required an additional handling time of three to four minutes per bird.

Before attaching the radio transmitters, we trimmed the body feathers from a small area (about 5 mm × 10 mm) between the scapula of the birds. We affixed transmitters (Model BD-2A, Holohil Systems, Ltd., Ontario, Canada; 0.75 g, dimensions 15 mm × 7 mm × 4 mm, battery life about 4 weeks) using a specially formulated epoxy (B. Scheuch, Titan Corporation, Lynnwood, WA). Radio transmitters weighed 3.5% and 2.0% of the average lean body mass and 2.9% and 1.6% of the average total body mass (including body fat) of Semipalmated and White-rumped Sandpipers, respectively (Skagen et al. 1993).

The time from capture to release of the birds was shorter when only one bird was processed (about 21 min) than when three or more birds were simultaneously processed (about 41 min). Total processing time averaged 31.8 ± 2.1 min ($n = 66$). Upon release, we observed the general behavior of subjects for several minutes when possible to assure that transmitters were not unduly affecting the birds.

We tracked birds 1–2 times daily, using a Wildlife Materials TRX-1000S receiver (164 MHz band), a truck-mounted 11 element dual beam Yogi antenna (5 m total height above ground), and a hand-held three element Yogi antenna. Signal range extended from one to two km, depending on weather conditions. We covered Quivira NWR thoroughly by searching for radio signals from several points. If subjects did not move between consecutive ground sightings, we walked up to birds to visually verify that the transmitters were intact on the birds. When birds departed, we also searched for radio signals at Cheyenne Bottoms Wildlife Management Area (WMA), Kansas, about 30 km north of Quivira NWR.

We tested the reliability of our daily surveys for transmittered birds. Following a morning search for all radio frequencies on 16 May and 20 May 1991, we conducted a relocation effort using aircraft. The aerial effort surveyed not only the Quivira NWR, but also surrounding wetlands that included the Cheyenne Bottoms WMA. We confirmed the presence of the birds equipped with transmitters (11 and 10 birds on 16 and 20 May, respectively). Most significantly, however, the aerial surveys confirmed that transmittered birds which were no longer being detected during ground surveys had, in fact, migrated from the study vicinity.

We acquired surface weather data recorded by the National Weather Service, National Oceanic and Atmospheric Administration, at Hutchinson, Kansas, 46 km east of Quivira NWR. Wind direction data recorded by NOAA were comparable to our daily log entries at the refuge. For three time periods daily (06:00–12:00, 12:00–18:00, and 18:00–24:00 CST [weather data was not generally recorded between 00:00 and 06:00]), we calculated average wind speed and wind direction in four primary quadrants where north, south, east and west formed the center of the quadrants. We used data on surface winds rather than for winds aloft because (1) surface winds would provide the proximate cues available to birds, (2) surface wind conditions are generally correlated with winds aloft (Richardson 1978), and (3) the data were readily available.

We assumed nocturnal migratory flights by the sandpipers (Lank 1989), with departures at sunset and arrivals at sunrise. Assuming these bounds, we calculated the observed Minimum Duration of Stay (MDS) for each individual, bounded by the dates of capture and last sighting.

We estimated lipid levels from body mass and morphological measurements using species-specific equations for Semipalmated Sandpipers and White-rumped Sandpipers captured in Kansas (Skagen et al. 1993). Because these equations have broad prediction intervals (Skagen et al. 1993), we also grouped fat estimates into 2-g fat classes for further data analyses. We determined criteria for sexing Semipalmated Sandpipers in Kansas based on morphological measurements of 24 birds (14 males and 10 females; see Skagen et al. 1993) for which we determined sex by dissection. We were able to correctly classify 23 of 24 (95.8%) birds using one measurement; total head length of males was less than 39 mm and of females greater than 39.2 mm. A sample of 11 male and 13 female White-rumped Sandpipers (see Skagen et al. 1993) revealed no apparent sexual dimorphism, so we did not develop sexing criteria for this species.

We performed statistical analyses, including Pearson correlations, analyses of variance, *t*-tests, median and chi-square tests, using SYSTAT 5.0. Means ± SE are reported unless otherwise specified.

RESULTS

DURATION OF STAY

We applied 13 and 11 transmitters in 1991 and 22 and 23 transmitters in 1992 to Semipalmated and White-rumped Sandpipers, respectively (Fig. 1), soon after the first arrivals of each species to the study area. We captured Semipalmated Sandpipers two days earlier in 1992 than in 1991 ($\chi^2 = 7.53$, df = 1, $P < 0.01$, median test). Semipalmated Sandpipers stayed at Quivira NWR an average minimum of 3.4 days (±3.7 days SD, $n = 13$) in 1991 and 9.7 days (±5.8 days SD, $n = 22$) in 1992. Their MDS ranged from 1 to 17 days and varied considerably within and between years (Table 1, Fig. 2). Both male and female Semipalmated Sandpipers stayed longer in the spring of 1992 than in 1991, even though lipid reserves at capture did not differ between years (Table 1). The residency period was influenced by the sex of the migrant (partial-$F = 3.869$, df = 4, 30, $P = 0.058$; Table 1) and year (partial-$F = 8.393$, df = 4, 30, $P < 0.01$). Date of arrival (capture) did not influence MDS (partial-$F = 2.161$, df = 4, 34, $P = 0.15$) of Semipalmated Sandpipers.

White-rumped Sandpipers became more abundant in early May of 1991 than in 1992 (Fig. 1), which resulted in birds being captured significantly earlier ($\chi^2 = 5.82$, df = 1, $P < 0.025$, median test). The median dates of capture and transmitter application were 14 May 1991 and 19 May 1992. White-rumped Sandpipers stayed an average of seven days (±3.7 days SD; range 2–16 days, $n = 34$). There was no significant difference in average MDS of White-rumped Sandpipers between years (Table 1). Date of capture had no effect on MDS in 1991 (partial-$F = 0.576$, df = 2, 8, $P = 0.81$) but did in 1992 (partial-$F = 29.692$, df = 1, 21, $P < 0.001$). In 1992, later-arriving birds had shorter stays than their earlier-arriving conspecifics.

We saw no evidence that processing time of a bird prolonged its duration of stay ($r = -0.214$, $P = 0.20$, $n = 35$ for Semipalmated Sandpipers; $r = 0.092$, $P = 0.61$, $n = 34$ for White-rumped Sandpipers). In 1992, processing with EM-SCAN did not alter residency periods of White-rumped Sandpipers ($t = 0.524$, df = 22, $P = 0.61$).

ANNUAL POPULATION VARIATION

Annual population patterns of Semipalmated Sandpipers differed markedly between years (Fig. 1). The first Semipalmated Sandpipers arrived in early April in both years. In 1991, numbers rose steadily, peaking at about 2,500 on 1 May, whereas in 1992, after an initial early peak of 1,000 on 13 April, numbers remained low until rising to about 3,300 on 9 May. Population curves suggest that in early May 1992, many late-arriving Semipalmated Sandpipers stayed at Quivira NWR only 3–5 days. Late-arriving Semipalmated Sandpipers departed the refuge gradually in 1991 and quickly in 1992. A few birds stayed on the refuge until late-May and early-June of both years.

White-rumped Sandpipers first arrived in late April of both years. In 1991, White-rumped Sandpipers appeared in large numbers (i.e., 500–

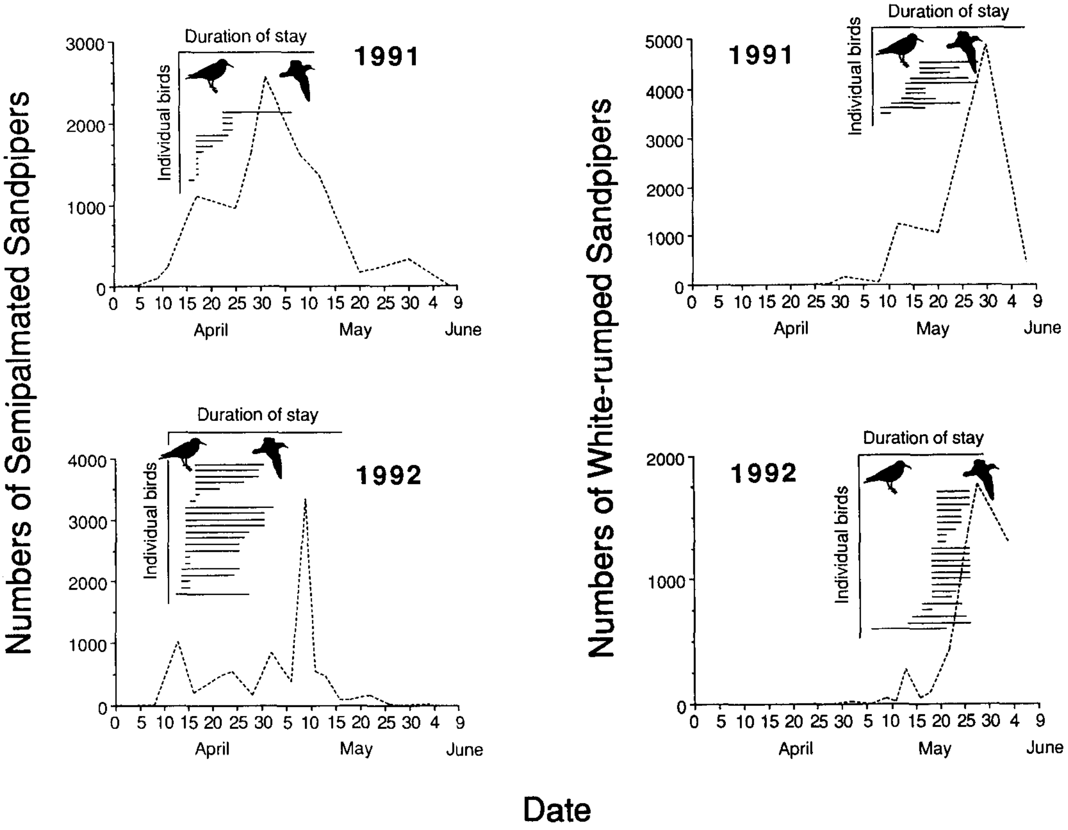

FIGURE 1. Annual population variation of Semipalmated Sandpipers and White-rumped Sandpipers at Quivira National Wildlife Refuge, Kansas, in spring 1991 and spring 1992. Duration of stay and departure patterns of individual birds equipped with radio transmitters overlay population curves.

1,000 birds) 12–13 days earlier than in 1992. Their peak numbers occurred at about the same time both years, but were lower in 1992 than in 1991. Departure patterns were similar in both years.

PATTERNS OF DEPARTURE

We found no distinctive patterns of departures of sandpipers relative to prevailing surface wind direction and speed. Semipalmated Sandpipers

TABLE 1. Minimum Duration of Stay (MDS, days) and estimated lipid reserves (g) [mean ± SE (*n*)] of Semipalmated Sandpipers and White-rumped Sandpipers at Quivira National Wildlife Refuge, Kansas, during spring migrations 1991 and 1992. *P* values from *t*-tests between years are reported.

Sandpipers	MDS (days) 1991	MDS (days) 1992	*P*	Lipid (g) 1991	Lipid (g) 1992	*P*
Semipalmated						
Males	2.9 ± 0.75 (9)	8.2 ± 1.69 (15)	$P = 0.03$	2.2 ± 1.32 (9)	1.3 ± 0.35 (15)	NS
Females	4.5 ± 3.18 (4)	12.9 ± 0.51 (7)	$P < 0.01$	1.0 ± 0.39 (4)	1.5 ± 0.62 (7)	NS
Total	3.4 ± 1.04 (13)	9.7 ± 1.24 (22)	$P < 0.01$	1.9 ± 0.33 (13)	1.3 ± 0.30 (22)	NS
White-rumped	8.5 ± 0.3 (11)	6.8 ± 0.7 (23)	NS	4.8 ± 0.66 (11)	4.3 ± 0.62 (23)	NS

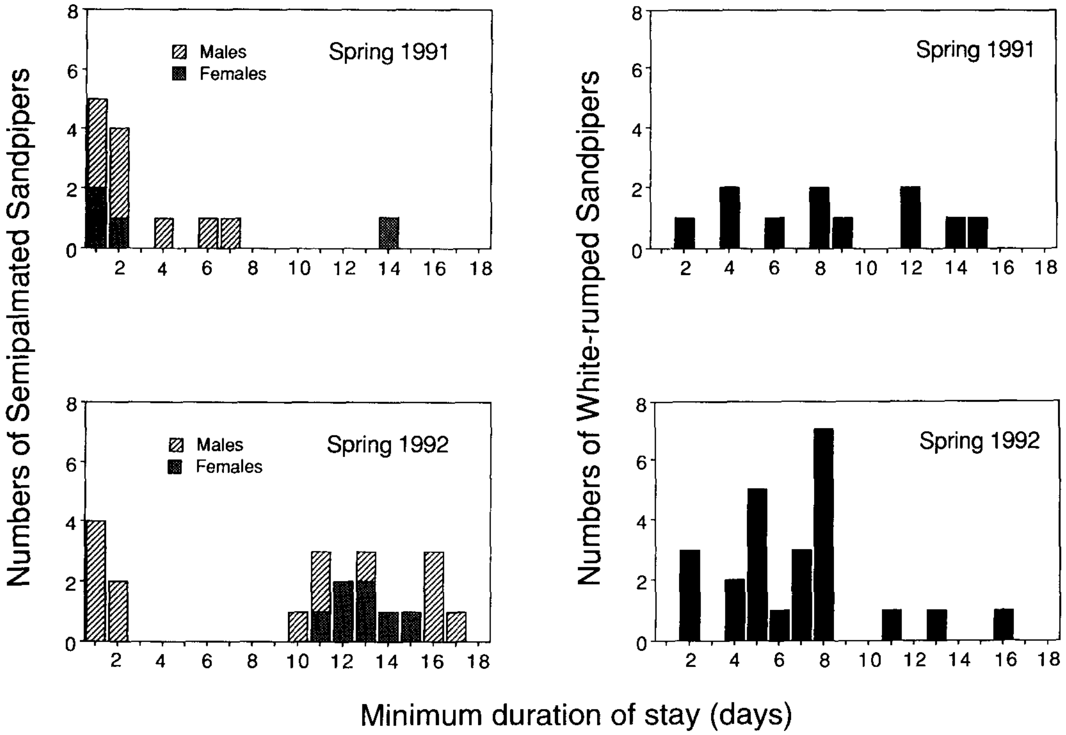

FIGURE 2. Minimum duration of stay (days) of male and female Semipalmated Sandpipers and White-rumped Sandpipers equipped with radio transmitters at Quivira National Wildlife Refuge, Kansas, in springs of 1991 and 1992.

were as likely to depart with prevailing southerly as northerly evening winds ($\chi^2 = 0.44$, df $= 1$, $P = 0.51$ for 1991; $\chi^2 = 0.842$, df $= 1$, $P = 0.36$ for 1992, where departure patterns are compared with the product of the number of birds with transmitters and evenings of north or south winds [bird-days]).

Similarly, White-rumped Sandpipers were as likely to depart with northerly as southerly winds in 1991 ($\chi^2 = 1.82$, df $= 1$, $P = 0.18$). However, in 1992, White-rumped Sandpipers left more often when the winds were northerly ($\chi^2 = 6.14$, df $= 1$, $P = 0.01$). There were more opportunities to leave with headwinds (more bird-days of north winds) in 1992 than in 1991 ($\chi^2 = 9.94$, df $= 1$, $P = 0.002$), especially late in the season when White-rumped Sandpipers were in the area. In fact, the last ten White-rumped Sandpipers to depart did so simultaneously on 26 May with a wind that had been northerly for four days.

The Semipalmated Sandpipers fitted with transmitters departed later ($\chi^2 = 13.79$, df $= 1$, $P < 0.001$, median test) in 1992 than in 1991 (median dates 25 April and 20 April, respectively). The median departure dates of White-rumped Sandpipers (22 May 1991 and 24 May 1992) did not differ between years ($\chi^2 = 1.25$, df $= 1$, $P > 0.25$, median test).

INFLUENCE OF BODY CONDITION

The estimated lipid reserves of Semipalmated Sandpipers at the time of capture were similar ($t = 0.672$, df $= 34$, $P = 0.51$) for both sexes and bore no relationship with the subsequent MDS (Table 1; partial-$F = 0.757$, df $= 4, 30$, $P = 0.39$). In contrast, the initial lipid reserves did significantly influence the MDS of White-rumped Sandpipers in 1991 ($F = 12.989$, df $= 1, 9$, $P = 0.006$; Fig. 3), but this pattern was not readily apparent in 1992 ($F = 2.462$, df $= 2, 20$, $P = 0.13$). When the latest departures (ten White-rumped Sandpipers that departed simultaneously on 26 May) were omitted from the 1992 analysis, an influence of lipid reserves was suggested (partial-$F = 3.834$, df $= 2, 10$, $P = 0.08$). The trends identified when using the 2-g fat classes

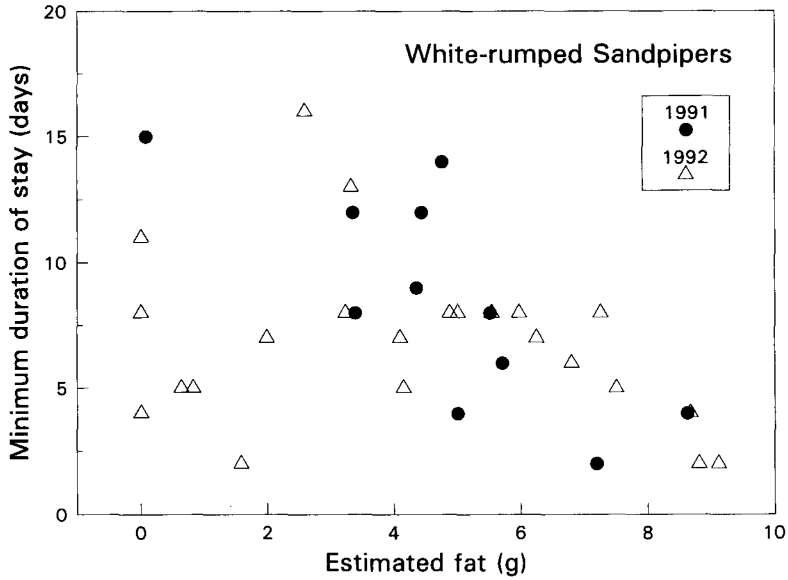

FIGURE 3. Relationship between estimated lipid reserves at capture and minimum duration of stay (MDS) of White-rumped Sandpipers at Quivira National Wildlife Refuge, Kansas, in springs of 1991 (closed circles) and 1992 (open triangles). $F = 12.989$, df $= 1, 9$, $P = 0.006$ in 1991; $F = 2.462$, df $= 2, 20$, $P = 0.13$ in 1992.

were virtually identical to those using the lipid estimates.

DISCUSSION

We sampled the earliest migrants of both species because we wanted to capture birds immediately upon their arrival to the refuge. We gleaned additional information on durations of stays of later-arriving birds from population curves. In 1992, the sudden population peak of Semipalmated Sandpipers in early May was short-lived, indicating a cohort of migrants with short stays. The precipitous declines in the White-rumped Sandpipers in late May and early June suggested some late migrants had fairly brief stays.

Residency periods at this midcontinental stopover were highly variable within and between years for Semipalmated Sandpipers and within years for White-rumped Sandpipers. Collectively, Semipalmated Sandpipers had a prolonged period of residency, with overlapping arrivals and departures spanning nearly two months. White-rumped Sandpipers arrived later and left fairly abruptly in late-May and early-June. We were unable to identify factors, either intrinsic (e.g., lipid reserves) or extrinsic (e.g., wind patterns or time of season) that explained the within-season variation in the durations of stay of Semipalmated Sandpipers. Duration of stay of White-rumped Sandpipers was correlated with estimated fat on arrival in one year.

The large variation among individuals of each population may be due to several contributing factors. Competition for food (implicated by the longer stays in April 1992 when the population of migrants was low, and by the prevalence of aggression during the stopovers [unpubl. data]), may result in varying rates of fattening among individuals. Other factors that we did not examine, e.g., age, foraging efficiency, social grouping, food availability, and additional aspects of weather (Morrison 1984), may also affect residency patterns in these species.

ON FLIGHT RANGE CALCULATIONS

To infer from our data that birds of a species are hopping between wetlands, it was necessary to estimate flight ranges based on fat loads at departure. We estimated fat reserves at arrival but were unable to recapture the birds to obtain departure estimates. We therefore made assumptions about spring fat deposition rates based on a review by Gudmundsson et al. (1991) encompassing three species and twelve studies. They report daily gains in mass relative to lean body mass ranging between 1.0 and 3.6%. For our calculations, we assumed a daily gain in mass of both 2% and 3% relative to lean mass (0.43 g/day and 0.65 g/day for Semipalmated Sandpipers and 0.70 g/day and 1.05 g/day for White-rumped Sandpipers, respectively).

Flight range calculations also require assumptions regarding flight conditions and flight speed, for which values are seldom known. We calculated flight ranges after Castro and Myers (1989), assuming still air conditions. Because flight ranges are directly proportional to the assumed flight speed, and because reported and assumed flight speeds are highly variable, we chose two flight speeds. For one analysis, we assumed a cruising speed of 40 km/hr (11 m/sec) for Semipalmated Sandpipers and of 45 km/hr (12 m/sec) for White-rumped Sandpipers, according to Pennycuick's (1969) calculations of the most economical cruising speed of birds based on body mass. These speeds are somewhat faster than the optimal speeds for birds in this range of body sizes (30 km/hr) as presented by Peters (1986). For a second analysis, we assumed a higher flight speed of 65 km/hr (18 m/sec), after Gudmundsson et al. (1991). Castro and Myers (1989), Harrington et al. (1991), and McNeil and Cadieux (1972) assumed flight speeds of 75, 80, and 81 km/hr, respectively. Speeds of 65–80 km/hr are considerably faster than speeds recommended by Pennycuick (1969) and approach a rough estimate of the maximum speed of flight for 1 kg birds (Peters 1986).

Assuming gains of 2% and 3%/day, respectively, the median percentage fat (fat/total body mass) at departure for Semipalmated Sandpipers was 18.0% and 22.4% and for White-rumped Sandpipers 22.6% and 26.1%. Estimates of percentage fat at departure ranged widely, from 2 to 40% for Semipalmated Sandpipers and from 7 to 36% for White-rumped Sandpipers. Semipalmated Sandpipers appeared to be considerably more variable in body condition at departure than White-rumped Sandpipers. We found no evidence that birds depart only after attaining a threshold mass (Harrington et al. 1991).

The calculated flight ranges of departing sandpipers were highly sensitive to our assumptions of fat deposition rates and flight speeds. Our most conservative model, which assumed a fattening rate of 2%/day and flight speeds of 40 km/hr for Semipalmated Sandpipers and 45 km/hr for White-rumped Sandpipers, predicted median flight ranges (rounded to the nearest 50 km) of 850 and 1,500 km, respectively (Fig. 4). Assuming a fattening rate of 3%/day increased the respective median distances to 1,150 and 1,700 km. Our most liberal model (3%/day fattening rate and 65 km/hr flight speed for both sandpipers) predicted median flight ranges of 1,850 and 2,450 km, respectively (Fig. 4).

It follows that flight range estimates can be increased dramatically by altering assumptions on fattening rates, flight speeds, and flight conditions. We therefore agree with Gudmundsson et al. (1991) that flight range estimates must be interpreted with caution and are most useful as relative measures to compare species or populations. Our shortest flight range estimates are probably most realistic; even they exceed predictions of maximum distance for nonstop migration for birds of this body size (Peters 1986) by more than 50%. Our calculations also assumed still air conditions during flight, even though we found no clear pattern to suggest that shorebirds waited for calm (or following) winds to resume northward migration. Although many migration studies have correlated peak migration with following winds, many birds do migrate with calm, side, or opposing winds (Richardson 1978).

MIGRATION STRATEGIES

Semipalmated Sandpipers are acclaimed for long transoceanic flights from the Bay of Fundy, eastern Canada, to South America (Lank 1983, Hicklin 1987, Gratto-Trevor 1992) in late summer. A fat load of 30–40% is probably required for this extensive flight across water (Dunn et al. 1988). The species refuels for about 15 days (range 5–22 days) at the Bay of Fundy and in the northeastern U.S. prior to this southward migration (Hicklin 1987, Dunn et al. 1988). Harrington et al. (1991) concluded that White-rumped Sandpipers departing Cheyenne Bottoms WMA, Kansas, were able to reach the breeding grounds in one long jump. This conclusion was based on ten birds with the greatest fat loads and the untested assumption that the fattest birds reflected the departure mass of the population in general. Our data suggest, however, that not all birds reach a threshold mass.

Our study suggests that, regardless of the assumptions on fattening rates and flight speeds, most Semipalmated Sandpipers and White-rumped Sandpipers departing our study site were not able to reach the breeding grounds in one long jump. We estimate that <40% of fat loads

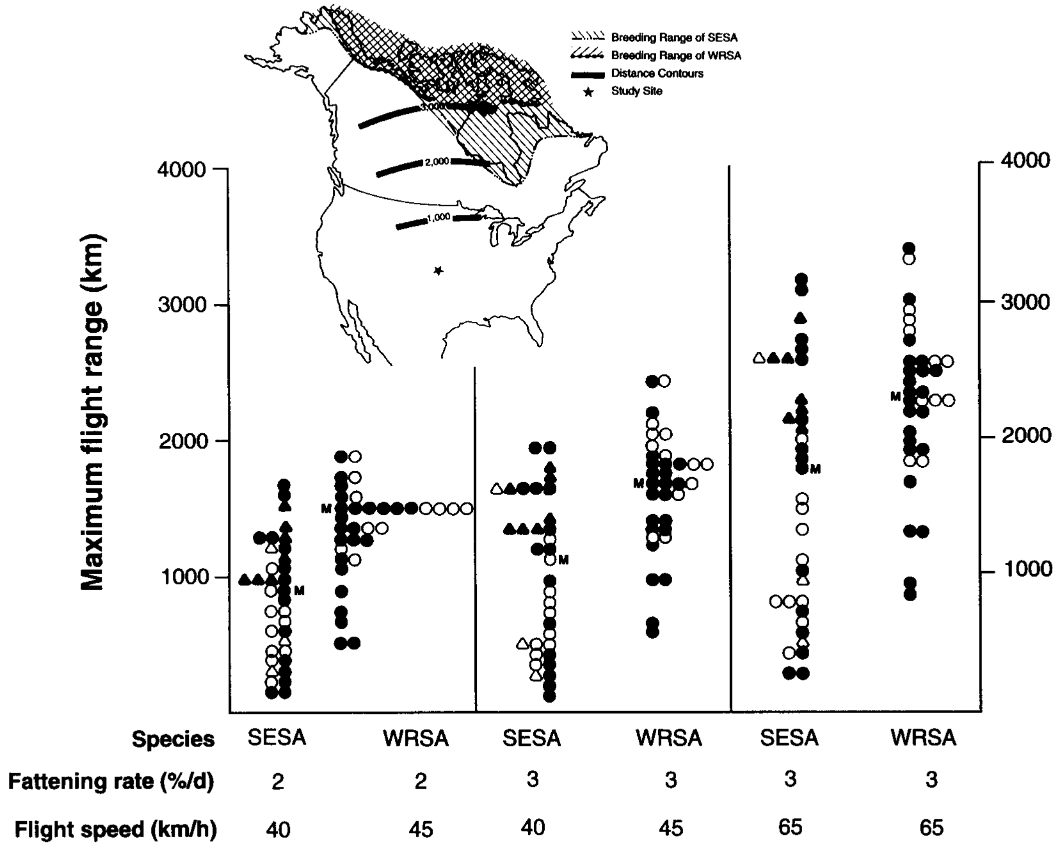

FIGURE 4. Estimated maximum flight ranges of Semipalmated Sandpipers (SESA) and White-rumped Sandpipers (WRSA) calculated according to Castro and Myers (1989), assuming still air conditions and three combinations of fattening rates (expressed as %/day relative to lean body mass) and flight speeds (km/hr). Open symbols represent birds equipped with radio transmitters in 1991 and closed symbols in 1992. For Semipalmated Sandpipers, triangles represent females and circles represent males. Circles represent both sexes of White-rumped Sandpipers. Breeding ranges (Hayman et al. 1986) and distance contours from the study site are designated.

at departure was present on the birds when they arrived. The remaining fat is obtained at the stopover site and is probably proportional to the residency period. The highly variable residency patterns, especially of Semipalmated Sandpipers, suggest that birds leave with greatly varying fat loads, and that many birds can make only short or medium length flights to the next stop.

We postulate that Semipalmated Sandpipers are ecologically eurytopic when crossing the Great Plains. Highly variable patterns in arrival, residency, and lipid levels suggest that spring migration of this species is relaxed and opportunistic across the plains. Similarly, Semipalmated Sandpipers migrating southward in late summer/fall from interior stopovers in Ontario (Page and Middleton 1972) and North Dakota (Lank 1983) are variably-provisioned, with some individuals capable only of short hops while others depart with ample reserves for extensive flights.

White-rumped Sandpipers migrating across the Great Plains showed a pattern of some flexibility, but to a lesser extent than their congener. Late-arriving 1992 migrants were influenced by time of the season as well as by lipid reserves, suggesting that White-rumped Sandpipers can no longer delay northward flights. In both years, all transmittered birds left the area by the end of May regardless of lipid levels or wind direction. In fact, the last ten departures of White-rumped Sandpipers fitted with transmitters in 1992 were simultaneous and coincident with north surface winds. The final exodus from Kansas of White-rumped Sandpipers, the latest shorebird species to migrate through the region, occurs only a few days before the average arrival times at the breeding grounds (Parmelee et al. 1968, Parmelee 1992). The higher fat loads at departure of White-rumped Sandpipers either enabled them to fly farther (Fig. 4) than Semipalmated Sandpipers, or provided more risk insurance for inclement conditions (i.e., headwinds) en route.

We present evidence that spring migrating Semipalmated Sandpipers and White-rumped Sandpipers require intermediate stopover sites between Kansas and their arctic breeding areas. For birds that are minimizing energy expenditure during migration (Alerstam and Lindstrom 1990), a "hopping" strategy may be preferred because it is energetically less costly than "jumping" (Piersma 1987) and because adequate sites are generally available across the plains to do so. Alternatively, interior sites may not have sufficient resources to allow all birds to refuel for longer jumps. Birds that are minimizing time spent on migration (Alerstam and Lindstrom 1990, Lindstrom and Alerstam 1992), may also choose to make shorter flights between stopovers, depending on resources.

CONSERVATION OF MIGRATING SHOREBIRDS ON THE GREAT PLAINS

Interior wetlands, with dynamic water regimes and unpredictable resources (Skagen and Knopf 1993, 1994), probably function as migration stopovers rather than staging areas for shorebirds. We do believe, however, that insufficient data exists to label wetlands in the midcontinent region as consistent shorebird staging areas rather than stopover sites. In shorebird systems, the term "staging areas" primarily refers to en route feeding stops during migration (Myers 1983, Harrington et al. 1991), and implies long stays and intensive fattening at sites with predictable and abundant food resources. The pattern of gradual immigration followed by abrupt departures at a threshold date is typical of coastal staging sites (Harrington et al. 1991). Cheyenne Bottoms WMA, Kansas, has been previously considered a major staging area (Harrington et al. 1991), however it does not consistently meet the accepted definition. Resource availability at Cheyenne Bottoms WMA is not predictable during migration (Castro et al. 1990, Skagen and Knopf 1994), shorebird departures appear gradual rather than simultaneous (Helmers 1991), and estimated fat reserves of shorebirds at Cheyenne Bottoms WMA do not indicate that intensive fattening occurs (Castro, pers. comm.). Rather, the significance of Cheyenne Bottoms to migrating shorebirds lies in its role as another major wetland in a complex that includes Quivira NWR and Salt Plains NWR, Oklahoma; that complex assures that some favorable wetland sites will exist to support migrating shorebirds every year in a region of highly variable precipitation and wetland dynamics. Effective conservation of shorebird habitat in the midcontinent region must reflect the need for intermediate stopping points between major stopover areas and breeding areas.

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