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Residency Times and Patterns of Movement of Postbreeding Dunlin on a Subarctic Staging Area in Alaska

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ABSTRACT. Understanding how individuals use key resources is critical for effective conservation of a population. The Yukon-Kuskokwim Delta (YKD) in western Alaska is the most important postbreeding staging area for shorebirds in the subarctic North Pacific, yet little is known about movements of shorebirds there during the postbreeding period. To address this information gap, we studied residency times and patterns of movement of 17 adult and 17 juvenile radio-marked Dunlin (*Calidris alpina*) on the YKD between early August and early October 2005. Throughout this postbreeding period, during which Dunlin were molting, most birds were relocated within a 130 km radius of their capture site on the YKD, but three birds were relocated more than 600 km to the south at estuaries along the Alaska Peninsula. On average, juvenile Dunlin were relocated farther away from the banding site (median relocation distance = 36.3 km) than adult Dunlin (median relocation distance = 8.8 km). Post-capture, minimum lengths of stay by Dunlin on the YKD were not significantly different between juveniles (median = 19 days) and adults (median = 23 days), with some birds staging for more than 50 days. Body mass at time of capture was the best single variable explaining length of stay on the YKD, with average length of stay decreasing by 2.5 days per additional gram of body mass at time of capture. Conservation efforts for postbreeding shorebirds should consider patterns of resource use that may differ not only by age cohort but also by individual condition.

Key words: Dunlin, *Calidris alpina*, Alaska, Bering Sea, migration, staging, shorebird

RÉSUMÉ. Pour donner lieu à la conservation efficace d'une population, il est essentiel de comprendre comment les individus se servent des ressources importantes. Le delta Yukon-Kuskokwim, dans l'ouest de l'Alaska, est l'escale de post-reproduction la plus importante des oiseaux de rivage du Pacifique Nord subarctique. Pourtant, on en sait peu sur les déplacements des oiseaux de rivage à cet endroit pendant la période de post-reproduction. Afin de combler ce manque d'information, nous avons étudié les durées de résidence et les habitudes de déplacement de 17 bécasseaux variables (*Calidris alpina*) adultes et de 17 bécasseaux variables juvéniles radio-marqués dans le delta Yukon-Kuskokwim du début août au début octobre 2005. Pendant la période de post-reproduction pendant laquelle les bécasseaux variables muaient, la plupart des oiseaux ont été déplacés dans un rayon de 130 km de leur lieu de capture dans le delta Yukon-Kuskokwim, mais trois oiseaux ont été relocalisés à plus de 600 km vers le sud, aux estuaires le long de la péninsule de l'Alaska. En moyenne, les bécasseaux variables juvéniles ont été déplacés plus loin du lieu de baguage (distance de déplacement médiane = 36,3 km) que les bécasseaux variables adultes (distance de déplacement médiane = 8,8 km). Par bécasseau variable, les durées de séjour minimales après la capture au delta Yukon-Kuskokwim ne différaient pas considérablement entre les juvéniles (médiane = 19 jours) et les adultes (médiane = 23 jours), certains oiseaux faisant escale pendant plus de 50 jours. La masse corporelle au moment de la capture était la meilleure et la seule variable expliquant la durée du séjour au delta Yukon-Kuskokwim, la durée moyenne du séjour diminuant de 2,5 jours par gramme supplémentaire de masse corporelle au moment de la capture. Les efforts de conservation des oiseaux de rivage en période de post-reproduction devraient tenir compte des modèles d'utilisation des ressources qui risquent de différer non seulement en fonction de la cohorte d'âge, mais également en fonction de l'état de l'individu.

Mots clés : Dunlin, *Calidris alpina*, Alaska, mer de Béring, migration, escale, oiseau de rivage

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INTRODUCTION

Backed by a rich theoretical framework (Alerstam and Lindström, 1990; Hedenström, 2008), many studies of shorebird migration have focused on the decisions birds make in choosing both sites at which to stop and how long to reside at a given site (e.g., Gudmundsson et al., 1991; Warnock and Bishop, 1998; Farmer and Wiens, 1999). Decisions about when and where to stop are shaped in part by time and energy constraints (Lyons and Haig, 1995; Farmer

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and Wiens, 1999) and in part by the risk of predation (Lank et al., 2003). Postbreeding shorebirds often concentrate in great numbers in specific areas for prolonged periods to accumulate fuel for long-distance, nonstop migratory flights, a phenomenon often referred to as staging (Mercier, 1985; Alerstam et al., 1986; Warnock, 2010). Although local movements by shorebirds on postbreeding staging areas have been described at the population level for some species (e.g., Handel and Gill, 1992), little attention has been paid to decisions individuals make regarding such movements while preparing for migration.

Alaska's Yukon-Kuskokwim Delta (YKD) is the most important postbreeding staging area for shorebirds in the subarctic North Pacific (Gill and Handel, 1981, 1990). Each summer and autumn, millions of adult and juvenile shorebirds congregate after the breeding season on extensive mudflats and coastal meadows of the YKD, where they molt and fatten prior to southward migration. Their migratory destinations range throughout the Pacific Basin as far south as Australia, New Zealand, and Chile. Although the broad outlines of these trans-hemispheric migrations are fairly well known (Gill et al., 2005, 2009; Handel and Gill, 2010; Battley et al., 2012), very little is known about residency times and patterns of movements of individual postbreeding shorebirds staging on the coastal YKD (but see Lindström et al., 2011).

In this study we focused on Dunlin, *Calidris alpina*, which undergo a complete prebasic molt over a two- to three-month period during autumn while staging along coastal areas of subarctic Alaska (Holmes, 1966b; Warnock and Gill, 1996). Two subspecies are known to stage on the YKD, *C. a. pacifica*, which breeds in western Alaska on the YKD, north to the Seward Peninsula, and south to the Alaska Peninsula, and *C. a. arcticola*, which breeds in northern Alaska (Warnock and Gill, 1996; Gill et al., 2013). Some postbreeding *C. a. arcticola* are thought to leave northern Alaska directly for nonbreeding areas in East Asia (MacLean and Holmes, 1971; Norton, 1971), but others continue south at least to the YKD, where they mix with *C. a. pacifica* between August and October before migrating to Asia (Gill and Handel, 1990; Taylor et al., 2011; Gill et al., 2013). After nesting, *C. a. pacifica* gradually move to coastal staging areas, particularly along the YKD and within estuaries on the Alaska Peninsula (Holmes, 1971; Gill and Jorgensen, 1979; Gill and Handel, 1990; Handel and Gill, 1992; Gill et al., 2013). The migration of *C. a. pacifica* from staging areas along the Alaska Peninsula appears to follow a direct route across the Gulf of Alaska to the Pacific Northwest and California (Gill and Jorgensen, 1979; Gill et al., 2013; R.E. Gill, unpubl. data), but previous work had not resolved whether Dunlin from the YKD moved to the Alaska Peninsula before migrating to wintering areas. Ascertaining the extent of connectivity among major staging areas in western Alaska is important for assessing the structure of the population and its consequent vulnerability to conservation threats.

Here we report on postbreeding movements of radio-marked adult and juvenile Dunlin in western Alaska prior to their southward departure to wintering areas. Studies of migrating radio-marked sandpipers elsewhere have shown that the length of stay at sites may be influenced by both date and age of the bird (Warnock and Bishop, 1998; Warnock et al., 2004). In addition, heavier birds are predicted to stay shorter periods of time than lighter birds (Alerstam and Lindström, 1990). By monitoring the movements of radio-marked Dunlin, we sought to determine (1) how long individuals stay on the YKD; (2) whether birds staging on the YKD maintain a sedentary residency in a single embayment or move southward along the coast during the autumn staging period; (3) whether birds move from the YKD to staging areas on the Alaska Peninsula before migrating to wintering areas; and (4) whether patterns of movement are dependent upon age, date of capture, or body mass. Understanding the ecological implications of how birds use different areas of their global landscape is an important step in protecting these migratory species (Webster et al., 2002; Newton, 2006).

METHODS

Study Area and Protocols

We studied birds at the mouth of the Tutakoke River in Angyoyaravak Bay on the YKD in western Alaska (Fig. 1). Between 4 and 13 August 2005, we captured 18 adult and 18 juvenile Dunlin at or near roost sites in the bay, using mist nets, walk-in traps, and a rocket net. We aged birds on the basis of differences in plumage (Prater et al., 1977), which were still quite evident at the time of capture. On average, *C. a. arcticola* are smaller in size and mass than *C. a. pacifica* (Todd, 1953), but males and females of the two subspecies overlap considerably in measurements (MacLean and Holmes, 1971; Browning, 1977; Greenwood, 1986), and we had no reliable criteria for determining subspecific status of individuals. We marked each bird with a metal U.S. Geological Survey band on the upper right leg and measured body mass to the nearest 0.5 g, exposed culmen to the nearest 0.1 mm, and flattened wing to the nearest 1 mm. We glued a 1.25 g VHF transmitter (BD-2, Holohil Systems Ltd., Woodlawn, Ontario, Canada) to the lower back following established methods (Warnock and Warnock, 1993; Warnock et al., 2004). Radios had an expected battery life of eight weeks and weighed less than 2% of the average bird's body mass when attached.

On 24 days between 9 August and 18 September 2005, we used handheld three-element Yagi antennae to ground-search for radio-marked Dunlin at high tide roost sites near where they were captured (Table 1). During some of these searches, we also traveled by boat around the bay, just offshore at high tide, to listen for birds at known roost sites within 5–10 km of the banding location. We also conducted

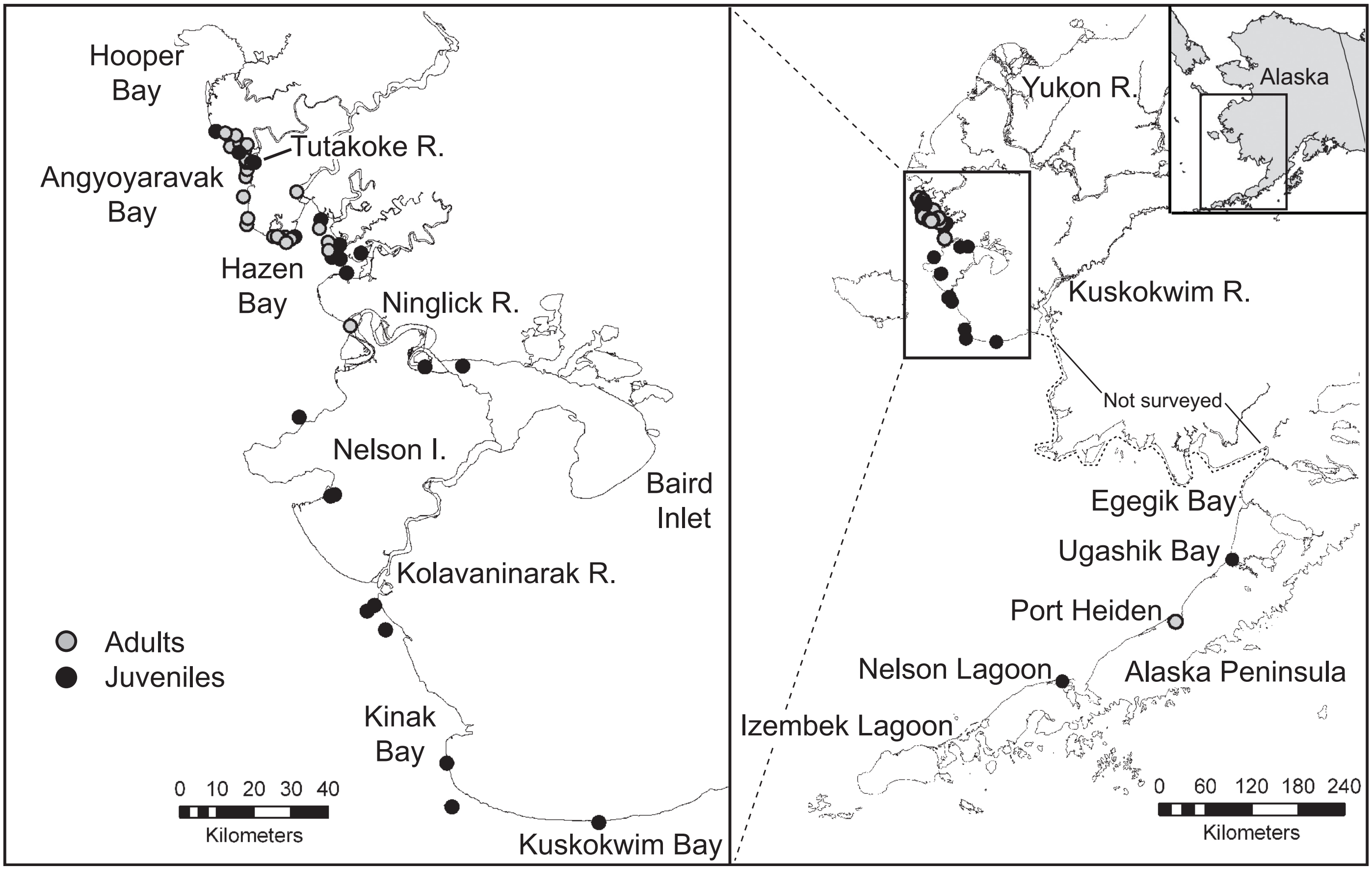

FIG. 1. Relocations (*n* = 109) of radio-marked adult (*n* = 17) and juvenile (*n* = 17) Dunlin in western Alaska between 9 August and 4 October 2005 (note that some dots are stacked in areas of high use such as Angyoyaravak Bay). See Methods and Table 1 for details.

TABLE 1. Search effort for radio-marked Dunlin in western Alaska between August and October 2005. Searches focused on coastal mud flats and barrier islands at low tide. Flight distances (mean ± SD km) are minimum estimates calculated from Google Earth along the coastline between the beginning and end points of each survey. See Fig. 1 for locations.

Method	Dates	Area covered
Ground	August 9–20, 25, 26, 28–30; September 1–4, 8, 9, 18 (*n* = 24 searches)	Coastal areas within 10 km radius of mouth of Tutakoke River
Aerial – YKD	August 26, 31; September 19, 30; October 4, 7 (*n* = 6 searches)	Flights of various lengths (262 ± 100 km) between south end of Hooper Bay and mouth of Kuskokwim River
Aerial – Alaska Peninsula	September 10, 21; October 3, 13, 18 (*n* = 5 searches)	Flights of various lengths (303 ± 180 km) along north side of Alaska Peninsula between Egegik Bay and Izembek Lagoon

aerial monitoring from planes equipped with exterior, dual-mounted antennae and used a test radio transmitter at camp as a beacon to check aerial telemetry equipment. Between 26 August and 7 October, we flew six telemetry flights along a stretch of YKD coastline roughly 300 km long from the south end of Hooper Bay to the mouth of the Kuskokwim River (Fig. 1, Table 1), although routes and directions varied because of weather and logistical constraints. Between 10 September and 18 October, we flew five telemetry flights along the north side of the Alaska Peninsula, from its base west to Izembek Lagoon (Fig. 1, Table 1).

Data Analysis

We considered all detections of radio-marked Dunlin after the day of banding as relocations. One adult that died a few days after banding and one juvenile that was not recorded after the day on which it was marked were excluded from our analysis. For each bird we calculated the straight-line distance between the banding site and its farthest relocation site. We defined the minimum length of stay on the YKD study area (the coastal area between Hooper Bay and the mouth of the Kuskokwim River) as the number of days between the day a bird was banded and the last day it was detected on the YKD, including the day of capture as the first day. We compared a series of general linear models to evaluate the potential effect of age, body mass, and date of capture on the minimum length of stay on the YKD. One juvenile whose mass and culmen were not measured was excluded from this analysis. We initially included wing and culmen in the models to control for variation in structural body size due to sex and subspecies. However, culmen and wing were correlated (Pearson r = 0.52, $p = 0.002$, $n = 32$), and culmen was a stronger explanatory variable in the models, so we dropped wing from further analysis. We examined variance inflation factors (VIF) for evidence of multicollinearity (Neter et al., 1990) and found no problems among the remaining independent variables (all VIF < 2).

To evaluate the effects of mass, culmen, age, and banding date on the minimum length of stay on the YKD, we followed an information-theoretic approach (Burnham and Anderson, 2002). We considered models with the lowest Akaike information criterion values corrected for small sample size (AIC_c) to be the most parsimonious. We calculated ΔAIC_c values by subtracting the AIC_c of the model of interest from the most parsimonious model in the candidate set. Models with ΔAIC_c values of 2 or less were considered to have substantial support and those with values of 10 or higher to have little or no support (Burnham and Anderson, 2002). We computed Akaike weights (w_i) for each of the models in the candidate set and then calculated the sum of the weights across all models in which each predictor variable occurred to estimate the variable's relative importance (Burnham and Anderson, 2002).

We used the Kruskal-Wallis test to evaluate whether adults and juveniles moved different distances from their site of banding because the distribution of distances moved could not be normalized through transformations. We used ANOVA to test whether culmen length or body mass at time of capture differed by age. Statistical analyses were performed with STATA (StataCorp, 2003) and SAS (SAS Institute Inc., 2002–08) software. Tests were two-tailed with significance set at $p < 0.05$. Statistics are presented as medians with interquartile ranges (IQR) or as means ± 1 SD.

RESULTS

From 36 Dunlin radio-marked on the YKD between 4 and 13 August 2005, we obtained a total of 109 relocations of 17 adults and 17 juveniles. Adults weighed 53.5 ± 4.4 g ($n = 17$) at time of capture; initial mass of juveniles (54.6 ± 2.3 g, $n = 17$) was similar ($F_{1,32} = 0.95$, $p = 0.34$). Average culmen length of juveniles (39.0 ± 1.9 mm, $n = 17$) did not differ significantly from that of adults (37.6 ± 2.4 mm, $n = 17$; $F_{1,32} = 3.61$, $p = 0.07$). We relocated each adult an average of 3.6 ± 1.5 times (range 2–7, $n = 17$) and each juvenile 2.7 ± 1.9 times (range 0–6, $n = 18$).

Marked birds were found on the YKD from Angyoyaravak Bay, where they were initially banded, southward to the mouth of the Kuskokwim River (Fig. 1). The last relocations on the YKD were found on 4 October 2005. Movements of adults and juveniles differed both spatially and temporally. Initially birds moved short distances between high-tide roost sites and low-tide foraging areas within central Angyoyaravak Bay, usually within 10 km of the banding site. During subsequent surveys on the YKD, numbers of relocations continued to decline, but adults were split about equally between Angyoyaravak Bay and Hazen Bay, whereas juveniles were more variable in their locations and directions of movement (Fig. 2). No birds were found during ground surveys of the Tutakoke study area that were not also relocated during aerial surveys.

No Dunlin were detected during our first survey of the Alaska Peninsula on 10 September, but on 21 September we found one adult at Port Heiden and one juvenile at Ugashik Bay, 628 and 607 km, respectively, from the banding site on the central YKD (Figs. 1, 2). On 3 October, we relocated another juvenile that had moved 640 km from the southern YKD to Nelson Lagoon (Fig. 2). We did not relocate any marked Dunlin during subsequent surveys of the YKD (7 October) or the Alaska Peninsula (13, 18 October). On the YKD, the mean maximum distance from the banding site at which juveniles were relocated (63.9 ± 68.8 km, median 36.3 km, IQR 122.8 km, $n = 17$) was greater than that of adults (12.6 ± 14.4 km, median 8.8 km, IQR 21.7 km, $n = 17$; Kruskal-Wallis $\chi^2_1 = 4.19$, $p < 0.04$).

The minimum stay ranged from 3 to 56 days for adults (median 23 days, IQR 39.5 days) and from 1 to 49 days for juveniles (median 19 days, IQR 16 days). Among 15 a priori general linear models considered to explain length of stay, the best-supported model (minimum AIC_c) included the single variable body mass, but other models with combinations of mass, culmen, and age also had substantial support ($\Delta AIC_c < 2$; Table 2). The sum of Akaike weights across the entire candidate model set provided strong evidence for the relative importance of mass ($\sum w_i = 0.98$) as an explanatory variable compared to culmen length (0.49), age (0.36), or date of marking (0.23). In the best-supported model, average length of stay on the YKD was predicted to decrease by 2.5 ± 0.8 days per additional gram of body mass at time of capture.

DISCUSSION

Residency Times

Our radio-marking study confirmed that Dunlin use extensive intertidal mudflats of the YKD in autumn as a staging area rather than as a stopover site (sensu Piersma, 1987; Warnock, 2010). At least 40% of marked individuals resided there for a minimum of three weeks, well into September or early October, during which time they underwent body and wing molt before continuing on their southward migration. Body mass was a more important explanatory variable than age in predicting residency time on the

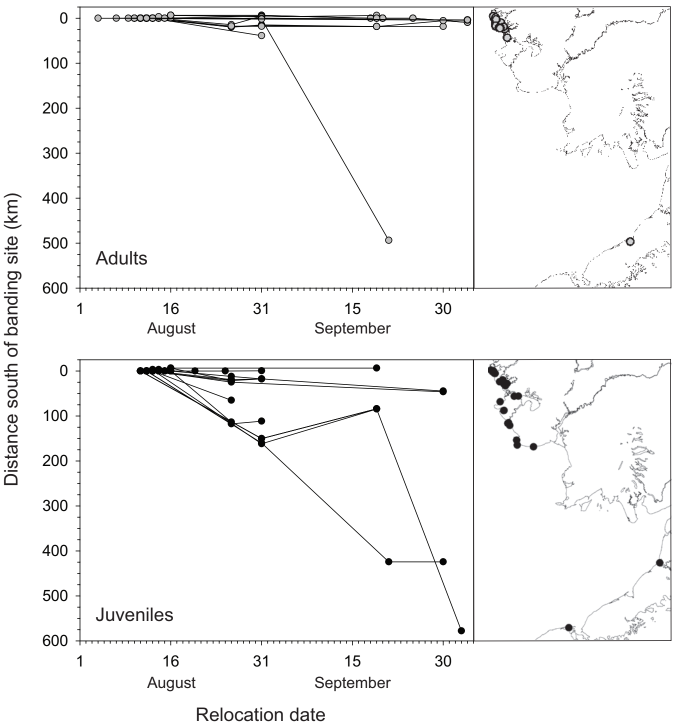

FIG. 2. Relocations of radio-marked adult (top; n = 17) and juvenile (bottom; n = 17) Dunlin during ground and aerial surveys in western Alaska during 2005 (see Table 1 for dates and locations of surveys). Lines connect relocations of individual birds and illustrate distances moved southward from Angyoyaravak Bay, where birds were originally marked during early August.

YKD, although adults and juveniles differed in their spatiotemporal patterns of use. Fewer than 10% of individuals were detected on other important staging areas along the north coast of the Alaska Peninsula (Gill and Jorgensen, 1979) before migrating south. Together, these patterns appear to reflect differential age-related requirements for molt and migration for Alaskan populations of Dunlin and provide further evidence for the importance of the rich intertidal food resources available to birds on the YKD during autumn.

We consider our estimated residency times of radio-marked Dunlin on the YKD to be minimum estimates for several reasons. First, we do not know when birds actually entered our study area, but only when we marked them. Second, given the sheer size of the YKD and our relatively moderate search efforts, it would have been easy for us to miss radio-marked birds, especially if they were at sites inland from the coast or if birds went north of the south end of Hooper Bay. Earlier studies of postbreeding Dunlin in the Angyoyaravak Bay area (Handel and Gill, 1992) showed that occasionally birds could also be found well inland from the coast. Our incidental flights to and from the main coastal survey area detected similar local inland movements, as well as short movements north from capture sites in Angyoyaravak Bay. Thus, we cannot estimate how many marked birds we may have missed that might have moved either inland from the coast of the YKD or along the coast north of our study area. In addition, Dunlin are also known to concentrate in late summer along the Bristol Bay coastline from the Kuskokwim River mouth south to the base of the Alaska Peninsula (Alaska Shorebird Group, 2008; R. Gill, unpubl. data), but we did not search that area. Third, given the length of stay of Dunlin on the YKD in the autumn, radios may have fallen off or batteries may have failed. Radios were built to last at least eight weeks, which for our earliest marked birds (4–8 August) would have been around the end of September. We detected a few marked birds as late as the first week of October, but we may have missed others because of battery failure.

TABLE 2. Model-selection results for effects of mass, culmen, age, and banding date on minimum length of stay of 34 radio-marked Dunlin on the Yukon-Kuskokwim Delta, Alaska, during autumn 2005. Fifteen a priori models were considered (see text) and those with Akaike weight (w_i) > 0.01 are shown here. K is the number of parameters in each model, AIC_c is the Akaike information criterion value corrected for small sample size, and ΔAIC_c is the difference between each model and the best-supported model.

Model	K	AIC_c	ΔAIC_c	w_i
Mass	3	193.22	0.00	0.27
Mass + culmen	4	193.55	0.33	0.23
Mass + culmen + age	5	194.42	1.20	0.15
Mass + age	4	195.06	1.84	0.11
Mass + date	4	195.76	2.54	0.08
Mass + culmen + date	5	196.31	3.09	0.06
Mass + culmen + age + date	6	196.68	3.46	0.05
Mass + age + date	5	197.12	3.90	0.04

The reasons that Dunlin stay longer into the autumn in this region than in other subarctic regions are likely related to energetic requirements for molt and migration, as well as relative safety from predators. On the North Slope of Alaska at different coastal estuaries, peak abundance of staging *C. a. arcticola* occurs between late July and late August (Holmes, 1966a; Taylor et al., 2010), and some of those birds move to western Alaska before heading to Asia (Taylor et al., 2011; Gill et al., 2013). A proximate reason for the late departure from the YKD is the timing and duration of prebasic molt (Holmes, 1971; Greenwood, 1986), which usually is not completed at northern staging areas such as the YKD until mid-September (Holmes, 1971; Gill and Handel, 1990; Warnock and Gill, 1996), and sometimes not until late September (R. Gill, unpubl. data). Molt can be energetically expensive (Vézina et al., 2009), and the YKD may be an ideal place to accumulate energy for molting since it has a rich intertidal invertebrate community (Lindström et al., 2011; A. Dekinga et al., unpubl. data).

Compared to other subspecies of Dunlin, those breeding in western Alaska and Canada (*C. a. pacifica* and *C. a. hudsonia*, respectively) have a unique molt strategy, in which adults and juveniles initiate and complete prebasic molt on or adjacent to breeding grounds before migrating south to wintering grounds (Holmes, 1966b; Engelmoer and Roselaar, 1998). Dunlin breeding in northern Alaska (*C. a. arcticola*) and other subspecies breeding in the Russian Far East also initiate molt on or near breeding grounds but complete it during southward migration or on wintering grounds in Asia (Holmes, 1966b; Tomkovich, 1998; Choi et al., 2010, 2011). Both of these strategies differ from those of Dunlin populations breeding in the western Palearctic, which do not initiate prebasic molt until after significant southward movements from their breeding sites (Pienkowski and Dick, 1975; Gromadzka, 1989; Holmgren et al., 1993). In Sweden, autumn-migrating Dunlin (*C. a. alpina*) spend 2.5–9 days, on average, at stopover sites; the duration depends on age, but not on stage of molt (Holmgren et al., 1993). These birds have already migrated up to 3000 km from breeding areas in western Siberia (Gromadzka and Ryabitsev, 1998) and have shorter distances to go from Sweden to wintering areas in western Europe (Gromadzka, 1983; Pienkowski and Evans, 1984).

Dunlin staging on the YKD are not only replacing flight feathers, but also preparing for what is thought to be a rapid, nonstop, transoceanic flight southward to wintering grounds (Gill and Jorgensen, 1979; Gill et al., 2013; R. Gill, unpubl. data). For individual *C. a. pacifica*, these flights may range in length from 2000 to 4500 km across the eastern North Pacific to wintering destinations between southern Canada and Mexico (Warnock and Gill, 1996; Fernández et al., 2010). For *C. a. arcticola*, migratory flights across the Pacific from the YKD to wintering grounds in central-east Asia could exceed 4500 km. Such flights require large stores of fuel, mostly in the form of fat (Alerstam et al., 1986; Warnock, 2010), which birds readily acquire on autumn staging areas in western Alaska. In August, the average mass of adult Dunlin on the YKD and the Alaska Peninsula is about 52 g for males and 56 g for females; in October, average masses for both sexes at these sites are 70–80 g (Warnock and Gill, 1996). Other late-staging shorebirds on the YKD, such as the Bar-tailed Godwit (*Limosa lapponica*) and Sharp-tailed Sandpiper (*C. acuminata*), also undergo prodigious gains in body mass in the autumn in order to complete their nonstop, long-distance migrations to wintering grounds (Piersma and Gill, 1998; Gill et al., 2009; Handel and Gill, 2010; Lindström et al., 2011).

The extended stay of Dunlin in western Alaska may also relate to differences in predation pressure on the staging and wintering grounds. Falcons and accipitrine hawks are uncommon in western Alaska during autumn, at least along the coast of the YKD (Handel and Gill, 1992; Lindström et al., 2011; R. Gill and B. McCaffery, unpubl. data), whereas they exert steady predation pressure on Dunlin wintering along the Pacific Coast of North America (Page and Whitacre, 1975; Buchanan, 1996; Buchanan et al., 1988; Ydenberg et al., 2010). Thus, a combination of minimal predation pressure plus ample food resources to fuel molt and long, nonstop flights may select for the late migration strategy used by Dunlin and other shorebirds in western Alaska (Gill et al., 2009; Handel and Gill, 2010).

Requirements for long migratory flights may explain why we found that radio-marked Dunlin with lower body masses tended to stay longer on the YKD than heavier Dunlin. This result is contrary to studies that have examined this relationship at other autumn (e.g., Holmgren et al., 1993) and spring stopover sites (Warnock et al., 2004), where no significant relationship between body mass and length of stay was noted, and where birds were either well into migration or embarking on shorter flights. However, this result should be taken with caution since we were unable to account for potentially confounding influences of sex and subspecific status on body mass. Likewise, it is not clear how molt status influences this relationship, although in a study that examined the relationship between molt status and stopover length of Dunlin in Sweden, no significant relationship was found (Holmgren et al., 1993).

Movement Patterns

Away from the breeding grounds, Dunlin can make single-day movements of tens to hundreds of kilometers (Warnock, 1996; Warnock et al., 2004; Conklin and Colwell, 2007). In our study, autumn-staging Dunlin on the YKD moved comparable distances prior to migrating to wintering grounds. Initially after banding, Dunlin moved out to feed on the mudflats of the Bering Sea at low tide and then back to the mouth of the Tutakoke River near their capture site to roost, as also observed by Handel and Gill (1992). This pattern lasted only about a week after birds were marked, before they moved off to other coastal roost sites and feeding areas both north and south of the Tutakoke River mouth. These local movements were usually less than 20 km. The short length of stay of radio-marked Dunlin at Tutakoke, combined with the abrupt departure of all Dunlin from the immediate banding area, suggests that environmental factors may have influenced local site use. Tide cycle and wind direction are known to influence roost use at Tutakoke (Handel and Gill, 1992), and these factors likely affected the movements of the radio-marked Dunlin from Tutakoke within Angyoyaravak Bay.

While the majority of the Dunlin radio-marked in our study limited their movements to the area around Angyoyaravak and Hazen Bays (i.e., within 40 km of the banding site), more than 25% of the marked Dunlin moved 50–200 km south of the banding site, with few significant movements back north. Juveniles were more likely to move south beyond Hazen Bay, and the maximum distance they traveled on the YKD from their capture site averaged more than five times the distance traveled by adults. Had we been able to survey the coastline between the Kuskokwim River and the Alaska Peninsula, the age-related discrepancy in movements would likely have been even more pronounced. Some marked juveniles that we failed to detect after late August likely continued to drift southward along this section of coast; however, given that we found no marked adults between Hazen Bay and the Kuskokwim River and only one on the Alaska Peninsula during any of the surveys, it is likely that few adults, if any, had moved to the non-surveyed section of coast.

Reasons for this age-related difference in movement are not clear, but various, not necessarily mutually exclusive, explanations may apply. First, movements by adult Dunlin at this time are likely to be more energetically expensive than movements by juveniles because only the adults are molting flight feathers. Second, adults may know from past experience on the YKD where best to feed, where to roost, and how to avoid predators under various tide and weather conditions whereas juveniles may need to explore and learn about the region. Age-related differences in spatial use patterns have also been found among Dunlin on wintering areas. In northern California, juvenile Dunlin move farther between consecutive nocturnal high-tide roosts than adults do (Conklin and Colwell, 2007). Juveniles and adults also use different habitats within California estuaries (Warnock, 1990, 1994; Conklin and Colwell, 2007), most likely because juveniles lack local knowledge about safe and profitable foraging sites (Warnock, 1990, 1994). Although others have suggested that differential habitat segregation by adult and juvenile shorebirds may be a result of intraspecific competition (Groves, 1978; Goss-Custard et al., 1982), evidence for such competition in Dunlin is not strong (Warnock, 1994). Closely related Western Sandpipers (*C. mauri*) wintering with Dunlin in San Francisco Bay, California, show similar age-related patterns in which juveniles have larger winter home ranges than adults, and these differences have also been attributed to prior knowledge of local resources by adult birds (Warnock and Takekawa, 1996). Juvenile birds in general may be programmed to prospect around areas more in their first year as a way of increasing their experience with variable conditions, thereby presumably increasing the probability of their survival (Reed et al., 1999).

After a period of local movements and regional dispersal, the majority of Dunlin that stage on the central YKD appear to depart on migration directly from the YKD, headed to temperate wintering areas along the west coast of North America (*C. a. pacifica*) or the east coast of Asia (*C. a. arcticola*) (Gill et al., 2013). We detected only three radio-marked birds (< 10%) more than about 200 km from the banding site. Given our small samples, the large areas we were searching (over 1500 km of coast), our later survey start dates on the Alaska Peninsula, and our moderate search effort, this proportion should be viewed as a preliminary estimate of interchange between these two staging areas, which are both of great importance to many of North America's and Asia's waterbird populations (Gill and Handel, 1981, 1990; Reed et al., 1989; Gill, 1996; Gill et al., 1997; Alaska Shorebird Group, 2008). Such limited mixing, however, is concordant with the significant but incomplete latitudinal segregation found among *C. a pacifica* Dunlin marked during autumn on the YKD and Alaska Peninsula and subsequently resighted or recovered on North American wintering grounds (Gill et al., 2013).

Why a few birds moved more than 600 km south to the Alaska Peninsula while most apparently migrated directly to wintering areas from the YKD remains an intriguing, unresolved question. Perhaps such movements allow individuals in poorer body condition to reduce migration distance or to remain longer in ice-free areas and accumulate the reserves needed for migration. We cannot rule out the possibility that marking Dunlin at multiple roost sites around the YKD might have revealed other movement. Elucidating the factors influencing the differential postbreeding movements of juvenile and adult Dunlin will require more research under varying climatic conditions. Additionally, it would be informative to track Dunlin from western Alaskan staging grounds to wintering grounds to determine the exact timing and routes of migration. The Dunlin is a species thought to be in decline in parts of its range (Bart et al., 2007; Fernández et al., 2010), and understanding how sites are connected for different populations of birds may be critical for the effective conservation of this tundra breeder (Gill et al., 2013).

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