

## Strong pair bonds and high site fidelity in a subarctic-breeding migratory shorebird

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**ABSTRACT**—Interannual mate and site fidelity is common in migratory shorebirds with monogamous mating systems. After long-distance migrations and separation during the winter, birds often relocate their former mate at their previous breeding territory. Although pairs frequently reunite, new pairs are also formed. Why birds change mates is still not completely understood. Mate change can involve active decisions, in which one or both mates actively chooses to divorce from a previous mate, but can also be related to arrival timing or mate availability at the breeding grounds. We explored possible causes of mate change in the Pacific subspecies of the migratory shorebird Dunlin (*Calidris alpina pacifica*) breeding at the subarctic Yukon-Kuskokwim Delta, Alaska, USA (61°36'N, 165°12'W). Interannual return rates of Dunlin to their breeding grounds were higher for males (74%) than for females (54%) and were 14% higher for birds with high previous breeding success. Mate change was rare if both birds returned to the breeding grounds in a consecutive breeding season: only 8% of all pairs divorced when previous mates were available. When former mates failed to return or returned late, however, many individuals formed new pairs (45% of males and 53% of females). Nest initiation dates were not delayed for new pairs compared to reuniting pairs, and nest survival did not differ between new and reuniting pairs; however, renesting after nest failure within a season was faster for reuniting pairs. We conclude that avoiding delayed nesting is a strong determinant of breeding decisions in Pacific Dunlin nesting in the short subarctic summer. Received 25 July 2016. Accepted 22 May 2017.

**Key words:** adult philopatry, breeding success, divorce, Dunlin *Calidris alpina pacifica*, nest initiation, territory.

### Fuertes vínculos de pareja y alta fidelidad a sitio en un ave playera migratoria que anida en el subártico

**RESUMEN** (Spanish)—La fidelidad a pareja y a sitio es común en aves playeras migratorias con sistemas monógamos de apareamiento. Después de migraciones de larga distancia y separación durante el invierno, las aves frecuentemente relocalizan a su antigua pareja en el territorio reproductivo previo. Aunque las parejas frecuentemente se reúnen, también se forman nuevas parejas. El porqué las aves cambian de pareja aún no se entiende del todo. El cambio de pareja puede involucrar decisiones activas, en las que uno o los dos integrantes de la pareja activamente elige divorciarse de su pareja previa, aunque también puede relacionarse a la temporalidad de su llegada o la disponibilidad de parejas en sus sitios de reproducción. Exploramos las posibles causas del cambio de pareja en la subespecie del playero migratorio *Calidris alpina pacifica* que anida en el delta Yukon-Kuskokwim, Alaska, EUA (61°36'N, 165°12'W), en el subártico. Las tasas de retorno de este playero a sus áreas de reproducción fueron más altas para machos (74%) que para hembras (54%), y fueron 14% más altas para aves que previamente tuvieron alto éxito reproductivo. El cambio de pareja fue raro cuando ambas aves regresaron a sus áreas de reproducción en una estación reproductiva consecutiva: solo 8% de todas las parejas se divorciaron cuando estaba presente su pareja previa. Sin embargo, cuando la pareja previa no regresó o regresó tarde, muchos individuos formaron nuevas parejas (45% de los machos y 53% de las hembras). Las fechas de inicio de nidos no se retrasaron para las nuevas parejas comparadas con las parejas reunificadas, y la sobrevivencia de los nidos no difirió entre parejas nuevas y reunificadas. En cambio, el reinicio de anidación después de un nido fallido en la misma temporada fue más rápida para aquellas parejas reunificadas. Concluimos que evitar una anidación retrasada es una determinante de gran peso para la toma de decisiones reproductivas en este playero que anida durante el breve verano subártico.

**Palabras clave:** *Calidris alpina pacifica*, divorcio, éxito reproductivo, Filopatría de adultos, inicio de nidos, territorio.

Most shorebird species migrate long distances between overwintering and breeding areas (García-Peña et al. 2009). Many individuals return to specific breeding areas because of the potential benefits of increased familiarity with the local landscape, foraging areas, and predator community, as well as potentially increasing the probability of obtaining good quality habitat (Fairweather and

Coulson 1995, Morrison et al. 2008). Seasonally returning to a particular breeding area also provides the opportunity for seasonal monogamy (i.e., birds can reunite with a former mate in a consecutive breeding season; Choudhury 1995, Cézilly et al. 2000, Bai and Severinghaus 2012).

Many shorebird species are relatively long-lived (usually 5–10 yr) and frequently form long-lasting socially monogamous pair bonds despite annual migrations over long distances. Examples include Semipalmated Sandpipers (*Calidris pusilla*), Western Sandpipers (*C. mauri*), and Dunlin (*C. alpina*; Sandercock et al. 2000, Gates et al. 2013a). Social pair formation, here viewed independently from possible genetic pair bonding by producing offspring together (Griffith et al. 2002), is common

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in shorebirds despite possible intersexual differences in migratory behavior (García-Peña et al. 2009). Mate fidelity can improve cooperation and coordination between mates and reduce the time needed to find a mate (Schieck and Hannon 1989, Choudhury 1995, Black 1996). It can also come with costs, however, such as searching or waiting for a previous mate (Handel and Gill 2000). Even bird species deemed to have monogamous breeding systems therefore do not always reunite with their mates (Jeschke and Kokko 2008). Within monogamous breeding systems, social mate fidelity can be disrupted by the death of one (or both) of the previous mates, referred to as “widowing” (Culina et al. 2015). In this situation, the widowed individual should either find a new mate, or sustain a high fitness cost by foregoing breeding all together.

In addition to widowing, social mate fidelity can also be disrupted by divorce, occurring when a bird pairs with a new mate even though its former mate is still alive (Jeschke and Kokko 2008, Culina et al. 2015). Divorce can occur either between consecutive seasons or between consecutive breeding attempts within a season and can be caused by many possible factors. These possible causal factors have been the foundation for many different hypotheses on divorce, as recently reviewed by Dhondt (2002) and Culina et al. (2015). In many instances, divorce is viewed as an active choice in which individuals actively decide to divorce their previous mate as a response to, for example, low previous breeding success together (Coulson 1966, Johnston and Ryder 1987, Ens et al. 1993). Mates can also divorce, however, because it is impossible to reunite; for example, in cases where one mate is still alive but either does not return to the same breeding area or returns too late in the breeding season to be available to its previous partner (Dhondt and Adriaensen 1994, Handel and Gill 2000).

Many questions concerning mate and breeding site fidelity in birds remain unresolved (Culina et al. 2015), especially for high-latitude breeding populations that are difficult to study. We aimed to fill several deficits in the literature for the Pacific subspecies of the Dunlin (*Calidris alpina pacifica*; hereafter referred to as Pacific Dunlin) by studying their mate and site fidelity in a subarctic breeding population during 3 breeding seasons on the Yukon-Kuskokwim Delta of Alaska. Dunlin is a

male-territorial, socially monogamous shorebird, of which the *pacifica*-subspecies winters along the west coast of North America (e.g., Mexico, California, and British Columbia) and annually migrates to Western Alaska to breed (Shepherd et al. 2001, Gates et al. 2013b). Specifically, our objectives were to (1) estimate sex-specific breeding site return rates and determine how previous nest success influenced these estimates, (2) estimate current rates of mate fidelity and determine the potential causes of divorce, and (3) determine how nest initiation dates, breeding site fidelity, and nest success were impacted by mate change.

Our specific predictions were related to possible causes and consequences of mate and site fidelity in this population. First, we tested whether the return rate of individual birds to the breeding area depended on their sex and/or previous nest success, expecting females and failed breeders to have lower return rates than males and successful breeders (Oring and Lank 1982, Flynn et al. 1999). Second, we tested whether divorce was possibly caused by unavailability of former mates, failure of previous breeding attempts, or was related to late arrival dates of birds. We considered only social pair bonding and expected (1) divorce to be related to unavailability of former mates for re-pairing, and (2) the frequency of mate change to increase in response to a failed previous nest of a pair (Dubois and Cézilly 2002). Third, we tested whether nest initiation dates of birds depended on their arrival date to the breeding area, sex, and/or whether a bird reunited or formed a new pair. We predicted social pair bonding to accelerate nest initiation (Gates et al. 2013a, Low et al. 2015). Last, we tested whether mate fidelity affected distances between consecutive breeding attempts of males and females. We predicted reuniting pairs would nest closer to previous nesting sites than newly formed pairs, and divorcing males would move less distance between nesting attempts than divorcing females (Sandercock et al. 2000, Gates et al. 2013a).

## Methods

### Study area and field methods

We studied a population of breeding Pacific Dunlin near Kanaryarmiut Field Station, Yukon Delta National Wildlife Refuge, Yukon-Kuskokwim Delta, Alaska (61°36'N, 165°12'W). The 60

ha study plot consisted of graminoid-dominated lowland wet meadows interlaced with various small ponds, surrounded by dry upland tundra and the Aphrewn and Kuyungik rivers. We studied the arrival and nesting behavior of Pacific Dunlin for 3 summer seasons (late Apr to Aug 2004–2006). Every season, our arrival to the study area preceded the arrival of the first Pacific Dunlin by 4 or more days (Table 1). We documented arrival times of previously marked birds in the second and third study-years by searching for Pacific Dunlin using daily surveys throughout the study area. These surveys consisted of 2 observers searching the study area for birds and nests up to 10 h/d, 7 d/week. Search effort was sufficient to survey half the plots every day; hence, effectively the entire plot was surveyed at minimum every other day. Additional surveys regularly took place earlier in the morning (starting 0600 h Alaska Time) and later in the evening (until 1000 h) to ensure detection of birds only active either early or late during the day. The date a bird was first detected was assumed to be its arrival date.

After arrival of Pacific Dunlin to the study area, we continued daily surveys until late July to document and find all nests, located through behavioral observations as well as territory mapping. Male Pacific Dunlin are territorial and defend their territory with aerial displays, songs, and wing lifting (Cramp and Simmons 1983). We used these behaviors and observations of courting and nesting to map territories to facilitate nest searching. Rope dragging was sporadically used in areas where no nests were found but were expected based on the territory mapping. Only once was a marked bird sighted elsewhere by field crews working in other areas than our study area. It therefore returned successfully to Alaska, but might still have been unavailable to its previous mate for pair formation on their former breeding site.

Each nest found was marked with 2 small flags, both placed 10 m from the nest, and locations were recorded using a handheld Global Positioning System (GPS) unit. Each marked nest was visited daily until the clutch was complete, or when the same number of eggs were present for 3 consecutive days, and thereafter every 3 d to ensure it was still active. The date the last egg was laid was defined as the “incubation date” and was used to estimate the hatching date by adding 22 d

to this date (the mean incubation duration of Dunlin; Jamieson 2011). If a clutch already contained 4 eggs when found, eggs were floated in warm water to estimate the stage of incubation (Liebezeit et al. 2007). A nest was considered successful if at least one chick hatched. Pairwise distances among nests were calculated as great circle distances (the shortest distance between 2 points following the spherical surface of the globe) using the recorded GPS locations.

### Capture and handling

We attempted to capture and mark both adults per nest (82.2% had both adults marked, 13.0% had only one marked bird, and 4.8% had no adult marked). We uniquely marked all adults using a combination of 3 colored leg bands and a US Geological Survey metal band.

We sexed individuals by culmen length, assuming male culmen length was <37.7 mm and female >39.8 mm (Gates et al. 2013b: p. 1974). In cases of intermediate culmen lengths (2 males and 10 females), we compared culmen length among mates. Sexing was further verified by behavioral observations such as territorial behavior of males (e.g., display flights, fights, calls).

### Behavioral definitions

Here we define several terms used throughout this publication. “Annual return rates” were calculated based on resighting of individuals within the 60 ha study area. If an individual was not resighted at the study area, we could not determine whether it (1) returned to the nest site but remained undetected by us, (2) had emigrated, or (3) died (Taylor et al. 2015). These estimated return rates are therefore likely underestimates of true survival in the study population because some birds may have returned to our study area but went undetected (Taylor et al. 2015). “Breeding site fidelity” refers to fidelity to particular breeding territories within the 60 ha study area. “Mate change” was defined as individuals not reuniting with their former mate, regardless of the presence of their previous mate in the study area. “Mate fidelity” was defined as individuals that previously nested together, both returning the following season and re-pairing by social bonding and forming a clutch of eggs together (both observed incubating the same clutch). “Divorce” was only

**Table 1.** Seasonal differences in breeding ecology of Pacific Dunlin (*Calidris alpina pacifica*) and environmental conditions near Kanaryarmiut Field Station, Yukon Delta National Wildlife Refuge, Yukon-Kuskokwim Delta, Alaska, from 2004 to 2006.

Year	Survey start	First arrival Dunlin	Mean nest initiation (SD)	Mean incubation duration (SD)	Mean temperature <sup>a</sup>	Ice break-up Kuyungsik River
2004	26 April	30 April	28 May (12 d)	21.2 (1.7) d ( <i>n</i> = 16)	9.7 °C	6 May
2005	27 April	2 May	2 June (14 d)	21.8 (1.4) d ( <i>n</i> = 25)	7.4 °C	24 May
2006	1 May	18 May	4 June (7 d)	21.9 (1.0) d ( <i>n</i> = 22)	5.6 °C	2 June

<sup>a</sup> mean daily temperature from April to July from Bethel weather station monitored by the Alaska Climate Research Center (2009).

considered a possible active choice if a previous mate was also available for re-pairing at the time of nest initiation. “Renests” were defined as replacement clutches of failed breeding attempts by marked individuals (Jamieson 2011).

### Data analyses

We used mixed-effect modeling to investigate (I) annual return rates of Pacific Dunlin, (II) mate change between seasons, (III) nest initiation dates, and (IV) distances moved between consecutive nesting attempts for (a) first nests and (b) renests. Possible explanatory variables of interest were (1) sex: the sex of the individual (binomial variable); (2) previous nest success: the number of hatched eggs in the previous nest of an individual (following Culina et al. 2015); (3) individual arrival date: the date a previously marked individual was first observed at the study area; (4) former mate availability: whether an individual’s previous mate was encountered in the study area prior to the date of nest initiation (binomial variable); and (5) mate history: whether an individual initiated a new nest with its previous mate or formed a new pair (binomial variable). To assess mate history, at least one bird had to be marked and thus also had previous breeding experience on this site. Prior to analyses, we centered all continuous variables to have a mean of zero.

Model I examined effects of sex and previous nest success on annual return rates, using whether or not a bird returned (yes/no) as a binomial dependent variable. Model II examined effects of sex, arrival date to the breeding site, and the (lack of) return of a former mate on mate change by an individual (binomial, yes/no). Model III examined effects of sex, mate history, and arrival date on nest initiation dates. Models IVa and IVb examined

effects of mate history and previous nest success on the distance between former nests and first nests (IVa), and former nests and renests (IVb) of an individual. The natural log-transformed distance between consecutive nests was the dependent variable, which normalized the residuals.

Model selection was based on Akaike information criterion values for small sample sizes (AICc) on datasets with complete data for all individuals. We compared all possible model combinations including all second-order interactions using maximum likelihood estimation (Burnham and Anderson 2002). We present and discuss results for all terms included in models  $<2.0$  AICc from the top-ranked model (following Arnold 2010). All dates were included as Julian dates. In all models, bird ID and year were included as random factors to accommodate the effects of repeated observations on individuals and variation in environmental conditions between years (Table 1).

In addition to the mixed models, we also compared possible effects of mate change on the number of days it took mates to reneest within seasons, using a Student’s *t*-test because the data were normally distributed and variances were homoscedastic between reuniting and new pairs. The effect of mate change on nest survival was compared between new and reuniting pairs by 2 methods. First, hatching success was compared between reuniting and new pairs using  $\chi^2$ -tests on the number of nests in each category. Second, the number of days that nests were incubated (before either predation or hatch) was compared between groups using Welch’s 2-sample *t*-tests to account for inequality of variances. All analyses were performed using R 3.2.3 (R Development Core Team 2016). Mixed-effect models were computed with package *lme4* (Bates et al. 2015). Values are

reported as means (SD), the  $\alpha$ -level of significance was set to 0.05, and all tests were 2-tailed.

## Results

From 2004 to 2006 we found and monitored 147 Pacific Dunlin nests in the study area (45 in 2004, 57 in 2005, and 45 in 2006, of which 30, 36, and 39, respectively, were classified as first nests). In total 128 birds were marked. Of all nests, 71 (48.3%) successfully hatched after a mean incubation period of 21.7 (SD 1.3) d (varying with different climatic conditions; Table 1).

### Annual return rates

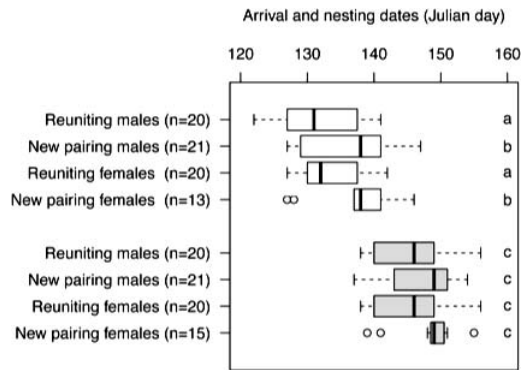
The mean interannual return rate for Pacific Dunlin to the breeding grounds on the Yukon-Kuskokwim Delta was 63% ( $n = 134$ , calculated over 2 yr). Mean return rate per year was significantly higher for males (74%) than for females (54%; Tables 2 and 3). Return rates of males and females combined were 60% for birds hatching 0 or 3 eggs in their previous breeding attempt and 14% higher (74%) for birds that had hatched 4 eggs (Model I; Tables 2 and 3).

### Mate change

The mate fidelity of returning individuals depended mostly on the return of their previous mate to the breeding grounds (Model II; Tables 2 and 3). Mate change, including cases where the former mate failed to return, was 55% for males and 47% for females. Between-season divorce in situations where both pair members returned to the study area and were present at the time of nest initiation was assessed for 38 pairs and only occurred in 3 of those pairs (8%). Reuniting individuals arrived on average 3.5 d earlier than those that formed new pairs, which was marginally significant considering the 85% confidence interval (CI; Model II; Fig. 1, Tables 2 and 3).

### Nesting dates

Nest initiation dates were not statistically different between reuniting pairs (mean [SD] = 25 May [5.2 d], range = 18 May to 5 June,  $n = 20$ ) and new pairs (mean = 27 May [5.6 d], range = 17 May to 4 June,  $n = 29$ ; Model III; Fig. 1, Tables 2 and 3). After depredation of a first nest in the season, however, reuniting pairs took 7–10 d to



**Figure 1.** Arrival (open boxes) and nest initiation (filled boxes) dates of Pacific Dunlin (*Calidris alpina pacifica*) of varying pairing status breeding on the Yukon Kuskokwim Delta, Alaska. Statistics are presented in models II and III, Tables 2 and 3. The boxes range from 25th to 75th percentiles, the whiskers extend to 1.5 times the interquartile range (IQR), the solid lines in the boxes are the medians, and trailing dots are outliers. Groups sharing common letters do not statistically differ.

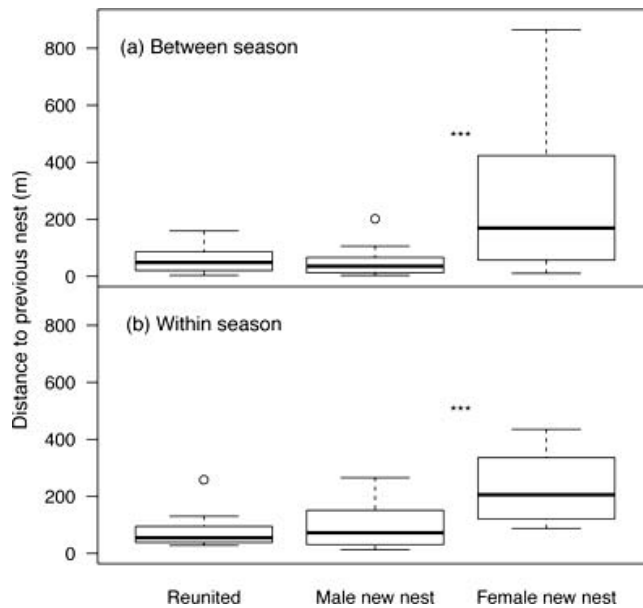
initiate a new nest (mean = 8.5 [1.3] d,  $n = 16$ ), significantly faster than reinitiation of new pairs (ranging from 8 to 18 d, mean = 13.1 [4.9] d,  $n = 21$ , 2-sample  $t$ -test:  $t = -4.69$ ,  $df = 32$ ,  $P < 0.001$ ). Nest initiation dates were not significantly affected by the arrival timing of birds, although arrival timing was among possibly influential factors (Model III; Table 2, Fig. 1).

### Breeding site fidelity

Reuniting pairs nested close to their previous nest, independently of their previous nest success. Divorcing birds nested farther away from their previous nest after a failed previous breeding season (interaction previous nest success  $\times$  mate history in Model IVa; Tables 2 and 3, Fig. 2). Females moved significantly farther after a divorce (285 [SD 275] m) than after reuniting (67 [54] m; Fig. 2), but this was not the case for males (71 [71] m and 68 [55] m, respectively). This pattern held for both first nests of the seasons and renews within seasons (Fig. 2; significant interaction of sex  $\times$  mate history in Models IVa and IVb; Tables 2 and 3).

### Nest survival

The percentage of successfully hatched first nests of the year did not differ between reunited pairs or newly formed pairs (Fisher's exact tests; males:



**Figure 2.** The distances moved between consecutive nesting attempts of female and male Pacific Dunlin (*Calidris alpina pacifica*) breeding at the Yukon-Kuskokwim Delta, Alaska (a) between seasons and (b) within season renests, depending on whether or not they reunited or formed a new pair. The boxes range from 25th to 75th percentiles, the whiskers extend to 1.5 times the interquartile range (IQR), the solid lines in the boxes are the medians, and trailing dots are outliers. Significant differences among groups are indicated with asterisks (for details see Table 3).

odds ratio = 0.85,  $P = 0.80$ ,  $n = 41$ ; females: odds ratio = 0.95,  $P = 1.00$ ,  $n = 35$ ; Table 4). The number of days that nests remained active was highly variable between nests and not statistically different between reuniting (overall mean 19.0 [SD 5.6] d,  $n = 20$ ) and newly formed (overall mean 16.1 [7.0] d,  $n = 29$ ) pairs (Welch's 2-sample  $t$ -test:  $t = 1.6$ ,  $df = 45.9$ ,  $P = 0.11$ ). After failure of a first nest in the season, reneating success was also similar for reuniting pairs (7 of 19 nests [47%] hatched) and new pairs (9 of 16 nests [56%] hatched; Fisher's exact test, odds ratio = 0.66,  $P = 0.55$ ). The number of days that renests remained active was highly variable between nests and did not statistically differ between reuniting and new pairs (reuniting pairs: 16.4 [SD 7.7] d,  $n = 16$ ; new pairs: 11.6 [8.7] d,  $n = 19$ ;  $t = 1.7$ ,  $df = 33$ ,  $P = 0.10$ ).

## Discussion

The high annual return rate of Pacific Dunlin to the study area is characteristic for many subarctic and Arctic-breeding shorebird species. Similar or higher rates have been found in other Dunlin populations (Soikkeli 1970, Thorup 1999, Koloski

2015) and other shorebird species such as Black Turnstones (*Arenaria melanocephala*; Handel and Gill 2000), Western Sandpipers (Johnson and Walters 2009), and Semipalmated Plovers (*Charadrius semipalmatus*; Flynn et al. 1999). We predicted that return rates would decrease in response to a failed breeding season, as known for Spotted Sandpipers (*Actitis macularia*), Semipalmated Plovers, and Southern Dunlin (*Calidris alpina schinzii*; Oring and Lank 1982, Jackson 1994, Flynn et al. 1999), but this expectation received only some support. Return rates were 14% higher for individuals hatching 4 eggs compared to those hatching none or 3 eggs, a difference potentially related to individual quality, but this requires further study. Most returning birds nested close to their previous season's nesting location, and only divorcing females moved over longer distances in response to failed breeding. This nesting behavior confirms previous findings in Dunlin and other shorebird species (e.g., Soikkeli 1967, Holmes 1971a, Gratto et al. 1985, Sandercock et al. 2000, Gates 2011).

A high probability of a previous mate's return can facilitate mate fidelity (Bried et al. 2003,



**Table 2.** Continued.

Model	Dependent variable	Terms										K	Dev	AICc	ΔAICc	$\omega_j$	
		Sex	Mate	Previous nest success	Sex × previous nest success	Sex × mate history	Previous nest success × mate history	Sex × previous nest success × mate history									
<b>IVa</b>	In(distance between first nests)	X	X	X		X	X	X				9	230.4	251.14	0.00	0.45	
		X	X	X	X		X	X				10	229.4	252.86	1.72	0.19	
		X	X	X		X						8	235.1	253.28	2.14	0.16	
		X	X	X	X		X	X	X			11	229.1	255.29	4.14	0.06	
		X	X	X	X	X						9	234.9	255.70	4.56	0.05	
		X	X	X	X	X		X	X			9	235.7	256.43	5.28	0.03	
		X	X	X	X			X	X			8	239.6	257.81	6.67	0.02	
		X	X	X	X							6	245.0	258.26	7.11	0.01	
		X	X	X								6	245.9	259.18	8.03	0.01	
		X	X	X	X							5	248.4	259.29	8.15	0.01	
		X	X	X	X	X						7	244.0	259.70	8.55	0.01	
<b>IVb</b>	In(distance between re-nests)	X	X	X		X					5	251.3	262.18	11.04	0.00		
		X	X	X							4	254.1	262.70	11.56	0.00		
		X	X	X	X						5	252.6	263.45	12.30	0.00		
		X	X	X	X						6	250.8	264.02	12.88	0.00		
		X	X	X	X	X						7	130.8	147.04	0.00	0.49	
		X	X	X	X	X	X					8	129.6	148.54	1.50	0.23	
		X	X	X	X	X	X	X				9	128.4	150.18	3.15	0.10	
		X	X	X	X	X	X	X	X			9	129.1	150.87	3.83	0.07	
		X	X	X	X	X	X	X	X			10	128.2	152.88	5.84	0.03	
		X	X	X	X	X	X	X	X			6	139.5	153.14	6.11	0.02	
		X	X	X	X	X	X	X	X			5	142.9	154.03	6.99	0.01	
X	X	X	X	X	X	X	X			9	133.3	155.03	7.99	0.01			
X	X	X	X	X	X	X	X			4	146.3	155.10	8.06	0.01			
X	X	X	X	X	X	X	X			5	144.1	155.28	8.25	0.01			
X	X	X	X	X	X	X	X	X		11	127.6	155.33	8.29	0.01			

<sup>a</sup> sex; the sex of the individual (binomial variable).  
<sup>b</sup> previous nest success; the number of hatched eggs in the previous nest of an individual.  
<sup>c</sup> individual arrival date; the date first observed on the study plot.  
<sup>d</sup> former mate availability; whether an individual's previous mate was encountered in the study area prior to the date of nest initiation (binomial variable).  
<sup>e</sup> mate history; whether an individual initiated a new nest with its previous mate or formed a new pair (binomial variable).



**Table 3.** Details for all informative mixed-effects models examining site and mate fidelity of Pacific Dunlin (*Calidris alpina pacifica*) breeding on the Yukon-Kuskokwim Delta, Alaska, from 2004 to 2006.

Model	Dependent variable	Explanatory predictor variable	Variance explained by random factor	Estimate	85% CI <sup>a</sup>
I	Return yes/no		Bird ID	0.00	
			Year	0.0005	
			Residual	0.21	
		intercept		0.52	
II	Mate change yes/no	sex <sup>b</sup>		0.28	0.15 to 0.40
		previous nest success <sup>c</sup>		0.03	0.003 to 0.069
			Bird ID	0.00	
			Year	0.00	
III	Nest initiation date		Residual	0.06	
		intercept		2.03	
		former mate availability <sup>d</sup>		0.84	0.73 to 0.95
		arrival date		-0.01	-0.017 to 0.0012
IVa	ln(distance between first nests)		Bird ID	0.00	
			Year	22.80	
			Residual	5.38	
		intercept		145.67	
IVb	ln(distance between re-nests)	arrival date		0.14	-0.015 to 0.30
		mate history <sup>c</sup>		0.47	-0.35 to 1.30
			Bird ID	0.00	
			Year	0.07	
			Residual	1.22	
		intercept		3.84	
		sex <sup>b</sup>		1.64	1.24 to 2.61
		mate history <sup>c</sup>		-0.62	-1.21 to 0.092
previous nest success <sup>c</sup>		-1.07	-1.45 to 0.03		
sex × mate history		-1.63	-2.54 to -0.32		
sex × previous nest success		-0.59	-0.77 to 0.60		
previous nest success × mate history		1.42	0.27 to 2.86		
IVc	ln(distance between re-nests)		Bird ID	0.00	
			Year	0.04	
			Residual	0.53	
		intercept		4.09	
		sex <sup>b</sup>		1.29	0.81 to 1.76
		mate history <sup>c</sup>		0.08	-0.33 to 0.47
previous nest success <sup>c</sup>		0.30	-0.10 to 0.70		
sex × mate history		-1.29	-1.72 to -0.68		

<sup>a</sup> If the 85% confidence intervals cross zero, these variables can be considered non-informative according to Arnold (2010).

<sup>b</sup> intercept: male.

<sup>c</sup> intercept: fail.

<sup>d</sup> intercept: not available.

<sup>e</sup> intercept: new pair.

Jeschke and Kokko 2008). This idea was confirmed in our study population by high mate fidelity, comparable to other Dunlin populations in North-America (Hill 2012) and Europe (Soikkeli 1967, Thorup 1999, Flodin and Blomqvist 2012). Mate change was predominantly associated with the absence of previous mates to the study site, regardless of whether this absence was due to late arrival or no return to the study area. Of all individuals, 92% reunited with their previous mate if this mate was available at the time nests could be

initiated, illustrating strong between-season monogamy in this species. These findings are mostly in accordance with the Bet-hedging and Musical Chairs hypotheses. The Bet-hedging Hypothesis states that an individual should pair with a new mate if costs of waiting for the old mate at the start of the season exceed a particular threshold (Handel and Gill 2000). The Musical Chairs Hypothesis attributes divorce to arrival asynchrony of mates (Dhondt and Adriaensen 1994), expecting arriving individuals to select the best available territory,

**Table 4.** Mate fidelity, nest survival, and nest initiation dates of Pacific Dunlin (*Calidris alpina pacifica*) breeding on the Yukon-Kuskokwim Delta, Alaska, from 2004 to 2006.

	Number	Breeding status	Number	Hatched	Nest survival day (SD)	Nest initiation Julian date (SD)
<b>Males</b>						
Marked 2004	26					
Returned 2005	18 (72%)	Reunited	11 (61%)	7 (64%)	18.7 (5.1)	141 (3)
		New pair <sup>b</sup>	6 (33%)	2 (33%)	11.3 (6.2)	139 (2)
		Did not breed	1 (6%)			
Marked 2005	39					
Returned 2006	26 (67%) <sup>a</sup>	Reunited	9 (35%)	7 (78%)	19.4 (6.3)	150 (2)
		New pair <sup>b</sup>	15 (58%)	9 (65%)	17.4 (7.0)	151 (2)
		Did not breed	2 (8%)			
<b>Females</b>						
Marked 2004	25					
Returned 2005	16 (64%)	Reunited	11 (69%)	7 (64%)	18.7 (5.1)	141 (3)
		New pair <sup>b</sup>	3 (19%)	2 (67%)	20.3 (0.6)	140 (1)
		Did not breed	2 (13%)			
Marked 2005	44					
Returned 2006	21 (48%) <sup>a</sup>	Reunited	9 (43%)	7 (78%)	19.4 (6.3)	150 (2)
		New pair <sup>b</sup>	12 (57%)	8 (67%)	17.7 (7.0)	150 (2)
		Did not breed	0 (0%)			

<sup>a</sup> Calculated based on the number of marked birds that left the surveyed area in 2005 with known bands from both the 2004 and 2005 seasons. Nineteen birds marked in 2004 were still seen breeding on the plot in 2006, and all of those were also seen in 2005.

<sup>b</sup> New pair refers to individuals nesting with another mate than during previous nesting attempts. Numbers of marked males and females can therefore vary because some individuals had multiple breeding attempts.

and if the former mate arrives too late (or not at all), the territory (chair) will already be occupied.

Support for these hypotheses contrasts with a recent study in temperate regions that found support for active mate choice in a population of Southern Dunlin in Sweden (Flodin and Blomqvist 2012). Divorcing female Southern Dunlin increased their reproductive success in accordance with the Better Option Hypothesis (Ens et al. 1993), which suggests that individuals actively divorce their previous mate because they have an opportunity to pair with a higher quality individual, or that they chose to move to a higher quality breeding territory. Although we cannot completely exclude this possibility in our population, overall levels of active divorce were low. Longer monitoring of our population would possibly result in more instances of active divorce and could perhaps explain the discrepancy between our subarctic and the Swedish population (which was monitored for 15 seasons). A larger dataset is especially advantageous because recording a reuniting pair requires the detection of only one nest, whereas 2 nests must be located for a divorcing pair (Sandercock et al. 2000). Despite our confidence that a large proportion of all nests

was detected, our estimated divorce rates are likely underestimates for this reason. An alternative explanation for lower levels of divorce in the subarctic breeding population could be more pragmatic breeding behavior by birds during shorter breeding seasons (Holmes 1971b), as also confirmed by low divorce rates in an Arctic-breeding population of Arctic-breeding Dunlin (*Calidris alpina arctica*) in Northern Alaska (Gates 2011). More detailed comparisons between temperate-, subarctic-, and Arctic-breeding populations are required to explore this further.

Time was identified as an influential factor throughout this study; arrival timing of individuals seemed important, and reuniting accelerated re-nesting after a failed clutch. These observations may be linked to the many advantages of timely nest initiation for shorebirds (Hill 2012), including lower predation rates (e.g., Sandercock 1998, Jamieson 2011), advanced southward migration, and increased (chick) survival during migration (Warnock et al. 2013). Early nest initiation is additionally important for successful re-nesting after possible depredation of a first nest and can possibly even facilitate double brooding (recently shown in Pacific- and Arctic-breeding Dunlin;

Gates 2011, Jamieson 2011, Gates et al. 2013a). Interestingly, Arctic-breeding Dunlin were recently found to be more likely to reunite with their previous mate after their nest was depredated late in the season than if depredated early in the season (Gates et al. 2013a). This finding suggests that if time becomes more limited, reuniting may become more advantageous, although this idea requires further study. Whether or not early nesting and faster renesting is also advantageous for individuals attempting to double brood remains little explored because possible costs of survival to double brooding have not yet been fully quantified (but see Hill 2012).

In conclusion, this study indicates that subarctic-breeding Pacific Dunlin strongly prefer previous breeding locations and previous mates when available in consecutive breeding attempts. If sites or mates are unavailable, however, their behavior prioritizes early nest initiation and fast renesting over mate and site fidelity, illustrating the high importance of timing for migratory birds nesting in the short subarctic summer.

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