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HIGH RENESTING RATES IN ARCTIC-BREEDING DUNLIN (*CALIDRIS ALPINA*): A CLUTCH-REMOVAL EXPERIMENT

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Abstract.—The propensity to replace a clutch is a complex component of avian reproduction and poorly understood. We experimentally removed clutches from an Arctic-breeding shorebird, the Dunlin (*Calidris alpina arcticola*), during early and late stages of incubation to investigate replacement clutch rates, renesting interval, and mate and site fidelity between nesting attempts. In contrast to other Arctic studies, we documented renesting by radiotracking individuals to find replacement clutches. We also examined clutch size and mean egg volume to document changes in individual females' investment in initial and replacement clutches. Finally, we examined the influence of adult body mass, clutch volume, dates of clutch initiation and nest loss, and year on the propensity to renest. We found high (82–95%) and moderate (35–50%) rates of renesting for early and late incubation treatments. Renesting intervals averaged 4.7–6.8 days and were not different for clutches removed early or late in incubation. Most pairs remained together for renesting attempts. Larger females were more likely to replace a clutch; female body mass was the most important parameter predicting propensity to renest. Clutches lost later in the season were less likely to be replaced. We present evidence that renesting is more common in Arctic-breeding shorebirds than was previously thought, and suggest that renesting is constrained by energetic and temporal factors as well as mate availability. Obtaining rates of renesting in species breeding at different latitudes will help determine when this behavior is likely to occur; such information is necessary for demographic models that include individual and population-level fecundity estimates. *Received 24 March 2012, accepted 28 November 2012.*

Key words: Arctic, *Calidris alpina arcticola*, fecundity, renest, replacement clutch, shorebird.

Altas Tasas de Anidación Recurrente en *Calidris alpina*: un Experimento de Remoción de la Nidada

Resumen.—La predisposición a reemplazar una nidada es un componente complejo de la reproducción de las aves que es pobremente entendido. Removimos experimentalmente nidadas de un ave playera anidante del ártico, *Calidris alpina arcticola*, durante etapas tempranas y tardías de la incubación para investigar las tasas de reemplazo de la nidada, el intervalo entre nidadas recurrentes, y la fidelidad al sitio y a la pareja entre los intentos de anidación. En contraste con otros estudios hechos en el ártico, documentamos la anidación recurrente por medio del rastreo por radio de los individuos para encontrar las nidadas de reemplazo. También examinamos el tamaño de las nidadas y el volumen promedio de los huevos para documentar cambios en la inversión de las hembras en las nidadas iniciales y de reemplazo. Finalmente, examinamos la influencia de la masa corporal de los adultos, el volumen de la nidada, las fechas de inicio y pérdida de las nidadas, y el año sobre la predisposición a anidar recurrentemente. Encontramos tasas altas (82–95%) y moderadas (35–50%) de anidación recurrente para los tratamientos de anidación temprana y tardía. Los intervalos entre nidadas recurrentes fueron en promedio de 4.7 a 6.8 días y no fueron diferentes entre las nidadas removidas temprano y tarde en la incubación. La mayoría de las parejas permanecieron juntas para los nuevos intentos de anidación. Las hembras más grandes fueron las más propensas a reemplazar la nidada; la masa corporal de las hembras fue el parámetro más importante para predecir la predisposición a anidar de nuevo. La probabilidad de ser reemplazadas fue menor para las nidadas perdidas tarde en la temporada reproductiva. Presentamos evidencia de que la anidación recurrente es más común entre las aves playeras anidantes del ártico de lo que se pensaba, y sugerimos que la anidación recurrente está restringida por factores energéticos y temporales, así como por la disponibilidad de parejas. Obtener estimados de tasas de anidación recurrente en especies que se reproducen en diferentes latitudes podría ayudar a determinar cuándo es más probable que ocurra este comportamiento; tal información es necesaria para los modelos demográficos que incluyen estimados de fecundidad a nivel individual y de la población.

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Replacement of failed clutches (i.e., renesting) is a common strategy employed by birds subjected to high nest-mortality rates to compensate for clutch loss (Sandercock et al. 2005, Fontaine and Martin 2006, Arnold et al. 2010). Several factors affect female renesting propensity, including age, experience, and physiological condition (Grand and Flint 1996, Amat et al. 1999, Arnold et al. 2010), food quality and availability (Amat et al. 2001), stage of incubation when clutch is lost (Fondell et al. 2009), date of nest loss within the breeding season, latitude, and environmental conditions (Martin and Wiebe 2004, Sandercock et al. 2005, Martin et al. 2011). Female age and experience likely increase propensity to renest because older and more experienced individuals tend to be in better physical condition upon arrival and nest earlier (Hipfner et al. 1997, Roper 2005, Smith and Moore 2005). Arctic-breeding (high-latitude) shorebirds are dependent on local and seasonally abundant food resources to sustain metabolic demands and produce eggs during a short breeding period (Meijer and Drent 1999, Klaassen et al. 2001, Hobson and Jehl 2010); thus, their ability to lay multiple clutches is likely constrained (Drent and Daan 1980). Individuals that initiate nests earlier may gain a longer window of opportunity for renesting, so renesting propensity is also likely to be affected by timing of clutch loss; species breeding at higher latitudes and elevations may be less likely to renest because they have shorter breeding seasons (Johnson et al. 1992, Martin and Wiebe 2004, Sandercock et al. 2005).

Renesting can make important contributions to an individual's annual fecundity and lifetime reproductive success (Milonoff 1991, Murray 1991, Hipfner 2001, Morton 2002). In general, propensity to renest is poorly understood, and demographic models frequently lack accurate estimates of renesting rates (Koons et al. 2006, Sandercock et al. 2008, Arnold et al. 2010), which can lead to underestimates of fecundity and overestimates of population size. For example, methods used by the Arctic Program for Regional and International Shorebird Monitoring to estimate sizes of breeding populations rely on counts of nests to develop detection ratios; however, observers cannot detect renesting attempts because adults are not marked (Bart and Earnst 2002, Frederick et al. 2006). By not incorporating renesting, the double sampling protocol may inflate estimates of population size; depending on the magnitude of this effect, recent assessments to estimate populations of Arctic-breeding shorebirds may be biased high (Bart et al. 2012). Although several studies have reported low to moderate rates of replacement-clutch laying in several Arctic shorebird species (Holmes 1966a, Soikkeli 1967, Norton 1972, Schamel and Tracy 1977, Tulp 2007), documentation of clutch replacement was mostly anecdotal, and renesting was often assumed after a nest was lost and another appeared in the same area later (i.e., no adults were marked and followed between nests). A long-term breeding ecology study at Barrow, Alaska, documented replacement laying in 5 of 11 shorebird species; all appeared to have extremely low rates of renesting (<1%, $n = 934$ nests; Naves et al. 2008).

To definitively assess rates of renesting, we used an experimental approach to investigate renesting propensity by removing clutches and following individuals equipped with radiotransmitters in an Arctic-breeding shorebird, the Dunlin (*Calidris alpina arcticola*). On the basis of previous estimates of renesting rates in the Arctic, we predicted that clutches removed in early (~5 days) and late (~13 days) incubation would have low to moderate (<50%) and very low rates (<5%) of clutch replacement, respectively. Assuming physiological constraints on females, we further predicted that replacement clutches would have fewer (clutch size) and smaller (clutch volume) eggs than initial clutches, and that the number of days between clutch loss and replacement would be greater for clutches removed later in incubation. Because Dunlin are socially monogamous and have biparental incubation (Warnock and Gill 1996), we predicted that pairs would remain together to renest because few unmated individuals would be available later in the breeding season (see Holmes 1966a). Finally, we used a modeling approach to examine potential physiological, seasonal, or ecological constraints on renesting. Understanding factors that affect renesting propensity in shorebirds will help us predict when replacement clutches will be laid and how important renesting is to individual- and population-level fecundity.

Methods

Study area.—Experiments were conducted near the city of Barrow (71.15°N, 156.48°W), adjacent to the Chukchi and Beaufort seas in northern Alaska, in diverse tundra vegetation communities with xeric to mesic hydrologic conditions (Pitelka et al. 1974, Walker et al. 1980, Naves et al. 2008). The experimental study area was ~10 km^2; the area becomes mostly snow free by the first week of June. Dunlin are an important component of a diverse avian breeding community, with densities averaging ~19 nests km^2 in nearby standardized plots (2007–2009; R. B. Lanctot unpubl. data). They arrive in Barrow before the area is snow free, typically during the last week of May, and depart around the first week of August (R. B. Lanctot unpubl. data). Mammalian predators of shorebird eggs in the study area included Short-tailed and Least weasels (*Mustela erminea* and *M. nivalis*), Arctic Foxes (*Alopex lagopus*), and Polar Bears (*Ursus maritimus*); avian predators included Parasitic Jaegers (*Stercorarius parasiticus*), Long-tailed Jaegers (*S. longicaudus*), Pomarine Jaegers (*S. pomarinus*), Glaucous Gulls (*Larus hyperboreus*), and Common Ravens (*Corvus corax*). Beginning in 2005, Arctic Foxes were removed from the Barrow area in the summer months to protect nesting Steller's Eiders (*Polysticta stelleri*) and their broods (U.S. Fish and Wildlife Service 2002). Because the Arctic Fox is one of the primary predators of shorebird nests (Liebezeit and Zack 2008, McKinnon and Bêty 2009), the lack of foxes likely increased nest survival and allowed us to find more nests than was otherwise possible.

Nest searching.—We intensively searched for Dunlin nests from late May through the second week of July, 2007–2009. Nests were located by (1) following adults back to their nests, (2) flushing adults from nests during area searches, and (3) rope dragging (Naves et al. 2008). During nest visits, we attempted to minimize nest predation by pretending to check nests at sites that were without nests, to confuse and mislead visual (e.g., jaegers) and olfactory (e.g., foxes) predators. We located replacement clutches by tracking radio-equipped adults back to their nests (see below). We determined nest initiation dates from observed laying dates, or by backdating by estimates of egg age derived from floating eggs or known hatch dates, presuming a 21-day incubation period; we defined nest initiation as the date the first egg was laid and assumed that females laid 1 egg day^{-1} (Warnock and Gill 1996). Error (± SE) associated with egg flotation methods is 1.2 ± 0.1 days during early incubation and 1.7 ± 0.2 days during late incubation (Liebezeit et al. 2007).

Experimental clutch removal.—We experimentally removed clutches during early (5.2 ± 0.2 days) and late (13.0 ± 0.2 days) stages of incubation (means ± SE). To control for the effect of nest initiation date on replacement laying, we used a systematic random approach to assign nests to the early or late clutch-removal treatments. We removed entire clutches after both mates were successfully captured, although in a few cases the nest was depredated (i.e., all eggs lost) or abandoned (i.e., all eggs intact and no adult present for >3 days) before both adults could be captured, limiting our ability to assess mate fidelity. A few clutches failed outside of the experimental periods; these nests were included only in calculations of renesting rates.

For all clutches, we recorded clutch size and measured egg length (L) and breadth (B) to the nearest 0.1 mm with dial calipers. Egg volume was calculated using linear egg measures and a species-specific volume coefficent (K_V) derived for Dunlin (Governali et al. 2012) and Hoyt's (1979) egg volume equation ($V = K_V * LB^2$). To get a ratio of clutch mass to female body mass, we measured the mass of each egg (to nearest 0.01 g) within a subset of clutches (n = 24) that were found at the beginning of incubation (less than 1–2 days).

Marking and resighting adults.—We used bow nets to capture adults on nests and uniquely marked them with color bands; a single, blank, dark green flag; and a U.S. Geological Survey aluminum leg band. We glued a 1.4-g VHF transmitter (Holohil Systems, Carp, Ontario) to each adult's back, placing it ~5 mm above the uropygial gland (Warnock and Warnock 1993). We weighed each bird and measured the lengths (mm) of culmen, diagonal tarsus, head (including bill), and flattened and straightened wing chord to determine body condition and, in some cases, sex. We also collected ~100 µL of blood from the brachial vein or collected breast feathers for genetic sexing. We used one of three methods to determine sex: (1) molecular (86%, n = 161), (2) discriminant function analysis (13%, n = 24; Gates 2011), and (3) presence of a distended cloaca (1%, n = 2). For molecular methods, we extracted DNA from blood or feathers, and amplified the CHD-W/CHD-Z genes using the P2 and P8 primers (Griffiths et al. 1998). Because we were not confident in our estimates of age, we did not include age as a variable in our analyses.

We waited 3 days after clutch removal before attempting to locate replacement nests to minimize disturbance. Thereafter, we radiotracked adults using hand-held Yagi antennas and receivers (Advanced Telemetry Systems, Isanti, Minnesota); individuals were monitored every 1–2 days until a replacement clutch was found, or up to 21 days after clutch removal. Pairs that we consistently observed during this period but never located at a new nest were categorized as "non-renesters." Likewise, we considered pairs that we lost (moved beyond the search area) or saw irregularly as "non-renesters." We used aerial telemetry to search for birds in early July, ~15 km beyond the study area. If birds were detected on aerial surveys, we subsequently searched for them by foot to determine whether they had renested. When replacement nests were found, we noted the identity of the attending adult(s) and contents and stage of the nest (e.g., laying and incubation). We considered adults site faithful if they nested within their initial territory boundaries; pairs were considered mate faithful if both members were found incubating the replacement clutch. When renesting pairs appeared to have divorced, we attempted to locate both birds to confirm whether they obtained new mates and renested. We identified new mates through capture, banding, and resighting.

Data analysis.—To evaluate potential bias in our experimental sample, we first estimated daily survival rates for early and late renesting attempts (Dinsmore et al. 2002), and used the Mayfield method to estimate nest age (Miller and Johnson 1978, Johnson and Shaffer 1990). On the basis of these analyses, we estimated the number of renesting attempts that we failed to locate (McPherson et al. 2003, Martin et al. 2009). We combined data for all years (2007–2009) and generated separate estimates for early- and late-removal nests. We used body mass as a proxy for an individual's body condition (Piersma and Davidson 1991, Brown 1996, Schamber et al. 2009), and tested for differences in body mass between females in early- and late-removal treatments using a t-test.

To evaluate sex differences in breeding effort, we summarized rates of renesting for females and males separately. We defined renesting interval as the number of days between clutch loss and the day that the first egg was laid in the replacement clutch. For mate-faithful pairs (n = 58), we examined factors that affected renesting interval using an analysis of covariance with year and clutch-removal treatment (early and late) as factors and initiation date as a covariate. For divorced individuals (n = 6), renesting intervals were summarized but sample sizes were too small to compare statistically. We compared clutch initiation dates of nests removed during early and late incubation using a two-way analysis of variance with year and clutch-removal treatments as factors. We used post hoc Tukey HSD multiple-comparison tests to examine differences between factors ($\alpha = 0.05$).

We compared mean egg volumes for initial and replacement clutches in each treatment group using paired t-tests. We estimated distance between initial and replacement clutches using a great-circle distance calculator (Schneider 2011).

We used logistic regression to examine the effect of year, initiation date of initial clutch, clutch loss date, number of days of incubation at clutch loss, female mass, male mass, and clutch volume on the probability of renesting. We created 29 biologically relevant additive models using these parameters to represent potential physiological, seasonal, or ecological constraints on renesting. We imputed missing values using restricted maximum likelihood procedures for 30 cases (where some cases had multiple missing values): clutch volume (n = 13), male mass (n = 11), and female mass (n = 15; Little and Rubin 1987). We calculated Akaike's information criterion value adjusted for small sample size (AIC_c) and Akaike weights (w_i) to evaluate model support. We considered the model with the lowest AIC_c value the best and defined ΔAIC_c as the difference between the AIC_c values of the current and the best model. We calculated model-averaged parameter estimates, unconditional standard errors, and 85% confidence intervals (CIs) for models with $\Delta\text{AIC}_c \leq 4$ (Burnham and Anderson 1998, Anderson and Burnham 2002, Arnold 2010). We ranked the relative importance of independent variables using the cumulative sum of Akaike weights (Burnham and Anderson 1998, Anderson and Burnham 2002). We identified uninformative parameters using importance rankings and whether CIs around the model-averaged parameter estimates included zero (Arnold 2010). Statistical analyses were conducted using JMP, version 8.0.2, and summarized data are presented as means ± SE.

RESULTS

Experimental clutch removal.—Of the nests initially selected for experimental clutch removal, 14 were lost to predation and 4 were abandoned before we could capture and band both adults. Of the

Table 1. Summary (mean ± SE) of nest age, renesting intervals, and inter-nest distances for renesting Dunlin whose clutches were experimentally removed during early and late incubation near Barrow, Alaska, 2007–2009. The range of days, followed by sample sizes, are shown in parentheses. Renest interval and distance between initial and replacement clutches are reported for mate-faithful pairs only.

	Early removal				Late removal		
	2007	2008	2009	All years	2008	2009	All years
Nest age at removal (days)	4.8 ± 0.4 (2–7, 16)	5.2 ± 0.3 (3–8, 21)	5.6 ± 0.3 (3–8, 23)	5.2 ± 0.2 (2–8, 60)	13.0 ± 0.3 (12–16, 20)	13.0 ± 0.4 (12–15, 9)	13.0 ± 0.2 (12–16, 29)
Renesting interval (days)	6.8 ± 0.8 (5–15, 12)	4.7 ± 0.4 (2–7, 18)	6.4 ± 0.7 (2–14, 17)	6.0 ± 0.4 (2–15, 47)	6.6 ± 0.6 (4–8, 7)	5.3 ± 1.1 (3–7, 4)	6.5 ± 0.9 (3–8, 11)
Inter-nest distance (m) [a]	232 ± 36 (70–394, 12)	161 ± 27 (22–451, 18)	187 ± 34 (32–455, 17)	192 ± 20 (22–455, 47)	185 ± 64 (84–549, 7)	201 ± 40 (98–287, 4)	194 ± 34 (8–549, 11)

[a] Great-circle distance between initial and replacement clutches.

89 remaining nests, we removed 60 clutches in early-removal and 29 in late-removal treatments (Table 1). Nest initiation of these clutches occurred between late May and the first week of June; experimental clutch removal took place during the first 2 weeks of June in all years (Fig. 1). Mean nest initiation dates were different among years ($F = 18.47$, df = 2 and 85, $P < 0.0001$), but nests that had clutches removed early and late in incubation were initiated at roughly the same time within a year ($F = 0.34$, df = 1 and 85, $P = 0.56$). Initiation dates in 2009 were, on average, 3 days earlier than those in 2007 and 2008 ($q_{0.05} = 2.39$). Body mass of females in our experiment did not differ between the two treatment groups (early: 61.9 ± 0.5 g, range: 51.5–68.0 g, $n = 60$; late: 61.0 ± 0.6 g, range: 54.5–67.5 g, $n = 29$; $P = 0.27$).

Replacement clutches.—Dunlin replaced clutches at high (82–95%) and more moderate (35–50%) rates after early and late clutch removal, respectively (Table 2). We found 48 replacement nests from the early treatment; the oldest was 21 days (sum of number of eggs + incubation days) when discovered, and 31 survived to 21 days. We estimated that survival probability during this interval was 0.54 ± 0.07 and that 57 replacement nests were initiated (31/0.54 = 57.4). We found 15 late-replacement nests; the oldest was 11 days old, and 12 survived to 11 days. Nest survival was 0.79 ± 0.08 for this interval, and we estimated that 15 were initiated (12/0.79 = 15.2). Thus, we estimate that we found 84% and 100% of early- and late-replacement nests, respectively. The high rates of renesting yielded a bimodal distribution of initiation dates (Fig. 1).

Both females and males in the early-removal treatment renested more frequently (44% and 52%, respectively) than those in the late treatment. Generally, both sexes participated in second nests at equal rates, regardless of when nests were experimentally removed (Table 2). Out of 64 pairs that renested, 58 stayed together for the second nest; these nests were within 100–300 m of their initial nest (Table 2). Divorce rates were low (<13%) for the early-removal treatment, and no pairs divorced in the late-removal treatment (Table 2). When divorce occurred, males remained on their initial territory and nested again (distance between initial and replacement nests: 259 ± 139 m, range: 120–398 m, $n = 2$) or attempted to attract a new mate, whereas divorced females moved greater distances to find a new mate and nest again (5.3 ± 1.4 km, range: 2.0–8.1 km, $n = 4$).

Four breeding pairs, and eight other individuals belonging to different pairs, returned to the study area to breed in multiple years and were subjected to different clutch-removal treatments among years. The four pairs that were faithful between years replaced their clutches 89% of the time. One pair returned in all 3 years of the study and replaced its clutches each year. Returning

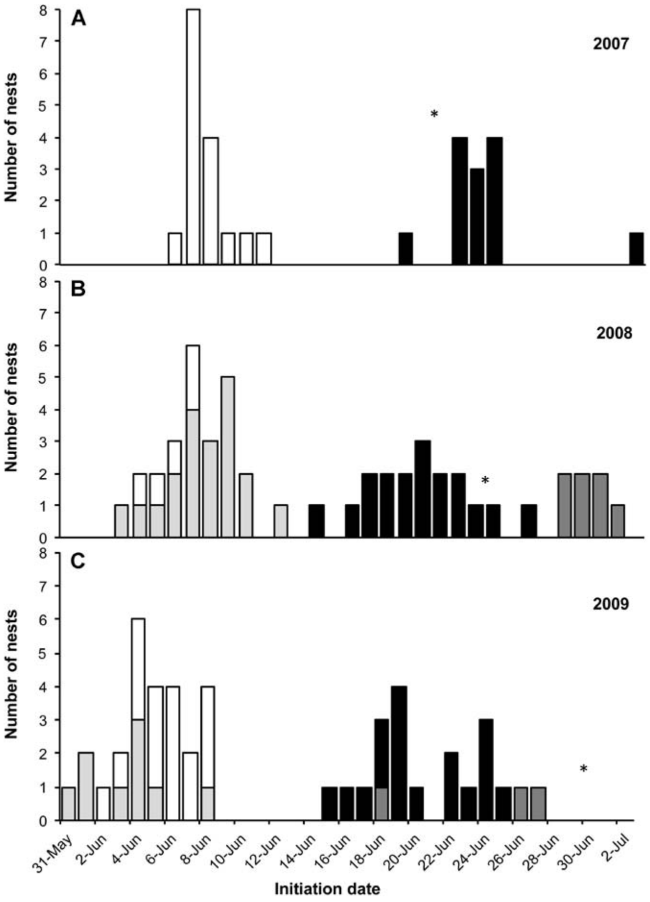

Fig. 1. Nest initiation dates of initial and replacement clutches from Dunlin at Barrow, Alaska, 2007–2009. Initial nests were removed during early (white) and late (light gray) incubation and subsequently replaced (early = black, late = dark gray). Asterisks indicate the last dates of nest initiation of Dunlin nests in nearby standardized plots (2007, $n = 32$; 2008, $n = 35$; 2009, $n = 46$; R. B. Lanctot unpubl. data).

Table 2. Annual renesting and divorce rates for Dunlin near Barrow, Alaska, whose clutches were experimentally removed early (2007–2009) or late (2000–2009) in the incubation period. Values in parentheses: number of individuals that renested/number of individuals whose clutches were removed.

	Early removal [a]				Late removal [a]		
	2007	2008	2009	All years	2008	2009	All years
Renesting rate							
Female	85% (17/20)	95% (18/19)	82% (14/17)	88% (49/56)	35% (7/20)	50% (2/4)	43% (9/24)
Male	90% (17/19)	81% (17/21)	85% (17/20)	85% (51/60)	35% (7/20)	30% (3/10)	33% (11/30)
Divorce rate	6%	5%	13%	8%	0	0	0

[a] Early clutch removal occurred primarily when nests were between 3 and 8 days into incubation, although 3 nests were removed 9, 9, and 10 days into incubation in 2007, and 3 nests were removed 10, 11, and 11 days into incubation in 2009. These nests were not included in other analyses. Late removal occurred between 12 and 16 days into incubation.

individuals that did not retain between-season pair bonds had a 55% replacement rate; all individuals that failed to replace their clutches were in the late-removal treatment.

Within a season, we found no relationship between renesting interval and date that the first nest was initiated ($F = 0.07$, df = 1 and 56, $P = 0.80$), the date that the clutch was removed ($F = 0.36$, df = 1 and 56, $P = 0.55$), or year ($F = 1.96$, df = 2 and 56, $P = 0.15$) for the 58 experimental clutches where mates stayed together. Among divorced birds, renesting intervals were 5.3 ± 1.0 days (range: 4–8, $n = 4$) for females and 8.0 ± 3.0 days (range: 5–11, $n = 2$) for males.

All initial nests had 4-egg clutches, whereas 14% of early replacement clutches and 27% of late replacement clutches contained ≤3 eggs. We found no difference in mean egg volume between initial (11.38 ± 0.09 cm^3; 95% CI: 11.19–11.57, $n = 35$) and replacement (11.31 ± 0.09 cm^3; 95% CI: 11.12–11.49, $n = 35$) clutches in the early treatment. In the late-treatment clutches, mean egg volume was lower in replacement clutches (11.01 ± 0.20 cm^3; 95% CI: 10.56–11.46, $n = 9$) than in initial clutches (11.46 ± 0.27 cm^3; 95% CI: 10.84–12.09, $n = 9$) ($t = 3.4$, $P = 0.005$, $n = 9$). Females weighed, on average, 62.3 ± 0.6 g (range: 55.0–67.0 g, $n = 24$; thus, a single egg and a 4-egg clutch represented 19.1 ± 1.1% and 76.5 ± 4.6% of a female's total body mass, respectively.

The top logistic models ($\Delta AIC_c \leq 4$) explaining the probability of renesting included all initial explanatory factors except year (Table 3). However, male mass, initiation date, clutch volume, and year all had 85% CIs that included zero and low relative variable importance (0.09–0.25), indicating that these factors were uninformative (Table 4). Female body mass was the only factor found in all seven top models, and date of clutch loss was present in most models; both had high relative variable importance (female body mass = 0.84; clutch loss date = 0.55; Table 4). Renesting propensity was positively affected by a female's body mass, indicating that heavier females were more likely to lay replacement clutches ($\beta_{FM} = 0.19$), and negatively affected by clutch loss date, indicating that clutches lost later in the season were less likely to be replaced ($\beta_{CL} = -0.21$; Table 4 and Fig. 2). Similarly, females that incubated clutches longer were less likely to replace clutches ($\beta_{CI} = -0.22$), although the relative importance of this variable was lower (Table 4).

Table 3. Logistic regression models used to assess factors that affected the probability of Dunlin laying a replacement clutch in Barrow, Alaska, 2007–2009. All models with $\Delta AIC_c \leq 4$ are shown. K is the number of parameters, and w_i is the Akaike model weight. Abbreviations in model descriptions: CL = Julian date of clutch, CV = clutch volume, DI = number of days of incubation at clutch loss, FM = female body mass, ID = Julian initiation date of initial clutch removal/loss, MM = male body mass. AIC$_c$ of top-ranked model = 95.91.

Model	K	Log likelihood	ΔAIC_c	w_i	$\sum_r w_i$
FM + CL	3	−44.814	0.000	0.296	0.296
FM + ID + DI	4	−44.488	1.541	0.137	0.434
FM + CL + MM	4	−44.703	1.972	0.111	0.544
FM + DI	3	−45.815	2.001	0.109	0.653
FM + CL + CV	4	−44.792	2.150	0.101	0.754
FM + ID + DI + CV	5	−44.472	3.757	0.045	0.799
FM + CL + ID + MM	5	−44.493	3.798	0.044	0.844

Discussion

Contrary to our expectations, renesting propensity in Dunlin was high, especially for clutches removed during early incubation. Despite using an experimental approach and our intensive efforts to track birds to replacement clutches, these rates are likely still biased low because of depredation of replacement nests before discovery, radio failure or loss, and individuals emigrating from the study area; we estimated that we may have missed nine renesting attempts for the early-removal treatment. Thus, our results suggest that virtually all females that lost clutches during early incubation replaced them; a smaller but high proportion of females that lost clutches in late incubation also replaced them. Other studies documented low to moderate rates of replacement-clutch laying in Arctic and sub-Arctic breeding shorebirds (Soikkeli 1967 [16%], Gratto-Trevor 1992

Table 4. Logistic regression model parameters, including model-averaged parameter estimates (all models with AIC$_c \leq 4$), standard errors (SE), 85% confidence intervals (CIs), and relative variable importance (summed Akaike weights) for the probability of Dunlin renesting after clutch removal in Barrow, Alaska, 2007–2009. Asterisks indicate uninformative parameters (i.e., their relative variable importance scores and CIs included zero).

	Model-averaged parameter				
			85% CI		
	Estimate	SE	Lower	Upper	Relative variable importance
Intercept	21.25	14.55	0.30	42.19	–
Female body mass	0.19	0.07	0.09	0.30	0.84
Clutch loss date	−0.21	0.07	−0.30	−0.12	0.55
Days of incubation	−0.22	0.07	−0.31	−0.12	0.29
Initiation date*	−0.10	0.14	−0.30	0.10	0.23
Male body mass*	−0.05	0.09	−0.18	0.08	0.15
Clutch volume*	0.00	0.09	−0.13	0.13	0.15
2007*	0.32	0.51	−0.42	1.05	0.00
2008*	0.30	0.47	−0.38	0.98	0.00

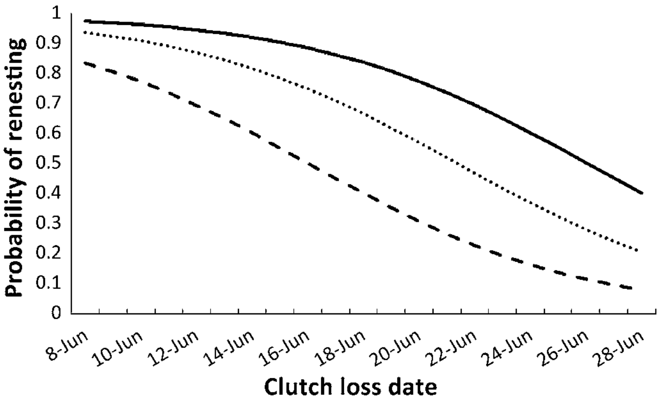

Fig. 2. Probability of female Dunlin renesting in relation to date of cluch loss and body mass. The dotted line represents the population's median body mass, and the solid and dashed lines represent the 10th and 90th percentile, respectively, of the distribution of body mass in the population at Barrow, Alaska, 2007–2009.

[47%], Tulp 2007 [53%], Johnson et al. 2008 [33%]), although Jamieson (2011) recorded a higher rate (75%) in a sub-Arctic population of Dunlin (*C. alpina pacifica*). We suspect that these studies underestimated the actual renesting rates in their populations because of the many difficulties associated with definitively documenting a renesting attempt (Naves et al. 2008).

Dunlin molt their flight feathers during the breeding season, which is unusual in birds (Holmes 1966b, Holmgren and Hedenström 1995, Warnock and Gill 1996, Summers et al. 2004) and adds a considerable energetic demand (Murphy 1996). Regardless, we found that Dunlin renested despite the high energetic costs of molting during incubation (Holmes 1966b). In addition, there are some energetic costs of producing two clutches during one season; we estimated that each clutch constituted 70–80% of a female's body mass. Thus, we were surprised that renesting intervals did not vary (about 5–6 days), regardless of whether clutches were removed in early or late incubation. Because of the assumed energetic costs of molting and producing another clutch, and because gonadal atrophy occurs as the breeding season progresses (Holmes 1966a), we expected longer intervals between nests for individuals that lost clutches late in incubation. However, ecological and physiological mechanisms that underlie rapid egg-follicle development are poorly understood in wild bird populations (Donham et al. 1976, Williams 2005, Martin et al. 2011). Renesting intervals for Dunlin (*C. a. pacifica*) breeding in the sub-Arctic averaged 9.3 days (Jamieson 2011), ~3 days longer than our Arctic-breeding population. The more rapid renesting rate found in our study may be due to the higher energy-expenditure rates of Arctic-breeding shorebirds compared with temperate congeners (Piersma et al. 2003), resulting in higher metabolic rates and shorter physiological responses. Alternatively, Dunlin breeding at sub-Arctic latitudes may simply have a longer breeding season; Dunlin breeding around Barrow leave in early to mid-August. Given the demonstrated high propensity for Dunlin to replace their clutches, combined with predicted increases in breeding-season length resulting from a warming environment in the Arctic (ACIA 2005), we might expect an increase in overall fecundity in some Arctic-breeding populations.

Despite the high rates of clutch replacement, we found some evidence that females were limited energetically. First, larger females were more likely to replace a clutch; in fact, female body mass was the most important parameter predicting propensity to renest. Second, clutch sizes were slightly smaller in replacement clutches than in initial clutches, and mean egg volume was lower in nests replaced later in the season. There was also evidence that a female's ability to replace a clutch decreased as the breeding season progressed. The date that an initial clutch was lost was an important determinant of nest replacement; females whose clutches were removed early in the season and lost early in incubation were much more likely to replace them. Although both energy and time appear to impose some constraints on renesting in Dunlin, they did not appear to be as limiting as was previously assumed for Arctic and alpine bird populations (Martin and Wiebe 2004).

The ability of Dunlin to lay replacement clutches may also be limited by their access to mates. Virtually all the Dunlin in our experiment, except a few pairs in the early-removal treatment, remained with the same partner after clutch removal; all these mate-faithful pairs also renested close to their initial nest. The low divorce rates we found suggest that individuals may be limited in their mate choice because mates are either unavailable or of insufficient quality (Ens et al. 1996, van de Pol et al. 2006). The former explanation is supported by a likely male-biased sex ratio (due to lower survival rates in females [0.41] than in males [0.60]; Hill 2012), which may make females more choosy and give males fewer individuals to attract as mates. A lethal-removal experiment conducted on Dunlin at Barrow indicated that mates might not be available, especially later in the breeding season (Holmes 1966a). Male-biased sex ratios have been reported in many bird species (Székely et al. 2006, Donald 2007), and species with biased sex ratios may have lower rates of renesting because of difficulty in finding new mates.

Given our results, we predict that most Arctic-breeding shorebird species would replace lost clutches given sufficient within-season time, food, and availability of mates. However, we expect renesting propensity to vary with life-history traits. Late-nesting species (e.g., Long-billed Dowitchers [*Limnodromus scolopaceus*]) or species with long incubation and brood-rearing periods (e.g., Bar-tailed Godwits [*Limosa lapponica*]) would be less likely to replace clutches. These species are more temporally constrained and may initiate replacement clutches only if the first nest is lost very early in the breeding season. Less is known about how food availability may limit the laying of second clutches. Other studies found that seasonal variation and decline in food availability had little effect in constraining renesting propensity in three waterbird species (Arnold 1993, Grand and Flint 1996, Arnold et al. 2010). In the Arctic, data on invertebrates during the breeding season suggest that peak abundance corresponds with peak shorebird hatch and declines thereafter (Holmes 1966b, MacLean and Pitelka 1971, Schekkerman et al. 2003, Hill 2012). Because replacement clutches are typically laid before peak invertebrate abundance, there should be sufficient food resources for females to produce a new clutch. However, survival rates of chicks produced from these clutches are not well known; for Dunlin from late-removal nests, the survial rate is only 0.03 ± 0.61 (Hill 2012).

Implications of high renesting rates.—Replacement clutches compensate for a proportion of first-nest losses (Parker 1985, Amat et al. 1999) and can make important contributions to a species' annual productivity and an individual's lifetime reproductive success, especially in areas with high egg mortality (Hipfner 2001, Morton 2002). Our results demonstrate that clutch replacement is a frequent reproductive compensation response for Dunlin and is therefore an important parameter to include in productivity estimates. The high likelihood of renesting in Dunlin is consistent with the idea that selection should favor individuals with the ability to rapidly replace failed nests (Milonoff 1991, Roper 2005) in areas with high predation rates (such as the Arctic regions of Northern Alaska; Liebezeit et al. 2009), but inconsistent with the short growing season that should limit laying of replacement clutches due to high chick mortality (Farnsworth and Simons 2001). The relatively high overwinter mortality rates experienced by female Dunlin may have allowed females to retain this trait, given that adults can occasionally fledge young from renests (see Milonoff's [1991] exertion hypothesis). Further studies are necessary to examine physiological and ecological mechanisms that constrain renesting propensity. In particular, more studies are needed on how an individual's age and experience, as well as food availability and quality, affect laying of replacement clutches. Additional experimental studies on species with different life-history strategies and in variable environmental conditions will aid in understanding the mechanisms that underlie renesting propensity.

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