

Seasonal declines in the fecundity of arctic-breeding sandpipers: different tactics in two species with an invariant clutch size

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The breeding biology of Western and Semipalmated Sandpipers was studied for four years near Nome, Alaska. Despite a short breeding season and a putatively invariant clutch size, there were seasonal declines in the fecundity of both sandpiper species. Most females produced only one clutch (> 98%), but often laid fewer than four eggs (7.6–34.5% of first nests). Clutches of 2–3 eggs were initiated significantly later (6–8 d) and contained smaller eggs (2.9–3.5%) than 4-egg clutches. Small clutches were not re-nesting attempts, and were not caused by disturbance during laying or partial clutch loss. This is one of the first reports of seasonal declines in egg number among birds considered to have an invariant clutch size.

We evaluated four explanations for the seasonal declines in fecundity. The data did not support a clutch size-egg size tradeoff or the nutrient-reallocation hypothesis, but it was not possible to evaluate the cost-of-delay hypothesis. Variation in parent quality was the most likely explanation for the seasonal declines in fecundity. Females that were familiar with the study area bred significantly earlier in Western Sandpipers (4.5 d) but not Semipalmated Sandpipers (3.5 d, $p = 0.07$). Timing of clutch initiation was not related to female age in Western Sandpipers or to familiarity with a mate in either species.

The two sandpiper species adjusted different components of fecundity: Western Sandpipers typically laid four eggs, and in three of four years there were significant seasonal reductions in egg size among 4-egg clutches. In contrast, Semipalmated Sandpipers laid significantly fewer eggs than Western Sandpipers, but females laying 4-egg clutches did not produce smaller eggs if they laid late in the breeding season. Semipalmated Sandpipers may reduce clutch size because their smaller eggs are close to a minimum threshold size necessary to produce viable precocial young in the arctic.

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All animals are expected to use reproductive tactics which maximize their fitness. Avian young produced early in the breeding season can have higher survival and be more likely to recruit (Cooke et al. 1984, Daan et al. 1988, Hochachka 1990). Number of breeding attempts and clutch size affect the number of potential recruits. Cross-fostering experiments have shown that residual egg size affects offspring survival (Bolton 1991, Dawson and Clark 1996), presumably because big eggs produce structurally larger young that have greater nutrient reserves (Williams 1994). Reproductive traits may covary for two reasons. First, environmental con-

ditions such as food supply affect phenotypic variation in timing of breeding, and to a lesser extent, clutch and egg size (Drent and Daan 1980, Rohwer 1992, Svensson 1995). On the other hand, life-history theory predicts there may be genotypic interactions among reproductive traits because of differential allocation of resources (Roff 1992). To better understand covariation among timing of laying, clutch and egg size, it could be useful to examine birds where these aspects of fecundity are constrained.

The reproductive tactics of migratory shorebirds that breed in the arctic are highly constrained. The breeding

period at high latitude sites is usually limited: local conditions are suitable for only a short time (Miller 1983, Pienkowski 1984), and early departure is necessary if migrants are to successfully reach distant wintering areas (Myers 1981, Reynolds and Székely 1997). Most arctic-breeding sandpipers lay four eggs (MacLean 1972), and shorebird clutch size may be a case where phylogenetic inertia constrains current reproductive strategies (Ligon 1993, Sandercock 1997a). Birds that are unable to adjust reproductive effort by varying timing of laying or clutch size may be more likely to adjust egg size (Birkhead and Nettleship 1982). However, the heritability of egg size is high in many birds (Boag and van Noordwijk 1987), suggesting that environmental factors account for little of the phenotypic variation in this trait. Here, we report seasonal declines in the clutch and egg size of two arctic-breeding shorebirds thought to have an invariant clutch size: the Western Sandpiper *Calidris mauri* and the Semipalmated Sandpiper *C. pusilla*. We review four hypotheses for seasonal declines in fecundity, and discuss the evolutionary implications of this variation.

Methods

The breeding biology of Western and Semipalmated Sandpipers was studied at a 4 km² study site, 21 km east of Nome, Alaska (64°20'N, 164°56'W) during 1993–1996. The two species share similar breeding biology: both are small, male-territorial shorebirds that form monogamous pairs (Holmes 1971, 1972, Gratto-Trevor 1992). Western and Semipalmated Sandpipers are closely related (Haig et al. 1997), but were easily distinguished during the breeding season by their plumage coloration and vocalizations. Western Sandpipers are larger than Semipalmated Sandpipers (mean female body mass: 28.8 vs 25.9 g) and lay larger eggs (mean volume: 7.1 vs 6.3 cm³).

Sandpipers arrived at Nome in the first to second week of May, and the courtship displays associated with pair formation began immediately. Pairs held feeding territories on the margins of shallow brackish ponds, but nests of the two species were interspersed on low tundra ridges. Females usually initiated clutches soon after they were first sighted (ca. 5 d), and laid eggs in scrapes on the ground. Both sexes shared incubation duties. Nests were located by searching the tundra and observing incubating birds that flushed from the nest and gave distraction displays. If a clutch was not found immediately, the bird was observed from a distance until it returned to the nest. If a clutch contained fewer than four eggs when first discovered, we revisited the nest until egg number remained unchanged for three days; this was taken as clutch size. New eggs were numbered with a felt marker on each nest visit. If a

clutch contained four eggs, the eggs were floated in a small cup of warm water and egg buoyancy was recorded. Nests were visited every 6–7 d during incubation and then daily close to the estimated hatching date.

Laying rates at Nome were 0.8 eggs/day, and the duration of incubation averaged 20 and 21 days in Semipalmated and Western Sandpipers, respectively (Sandercock 1998a). Date of clutch initiation was calculated by backdating from the observed egg-laying schedule (15–24% of all nests, accuracy of ± 1 d), date of hatching (36–38%, ± 1 –2 d), or stage of incubation (39–50%, ± 2 –3 d, Sandercock 1998a). Egg length (L) and breadth (B) were measured to 0.1 mm with dial calipers. Egg volume was measured directly for a subsample of the eggs by water displacement in a volumeter. We calculated egg volume from egg length and breadth using $V = 0.47LB^2$ (B. K. Sandercock, unpubl.). All analyses were based on the mean egg volume of each clutch because eggs from one female are not independent observations, and because within-clutch repeatability of egg size was high.

Sandpipers were captured with walk-in traps placed over the clutch during incubation. Both parents were captured on most nests, and birds were individually marked with combinations of coloured leg bands and a numbered metal band. We recorded the identity of mated pairs, and determined familiarity with a mate by comparing associations in consecutive years. Sandpipers were sexed by behaviour (i.e. courtship displays, copulatory position) and culmen length (Cartar 1984, Sandercock 1998b). In 1996, Western Sandpipers were aged by the coloration on the edges of the inner tertial and wing coverts (white in adults, buff or chestnut in yearlings). This technique has been used elsewhere to age wintering Western Sandpipers (P. D. O'Hara, unpubl.), and other calidrine sandpipers (Page 1974, Prater et al. 1977). Eight birds of known age were assigned to the correct age class at Nome (2 yearlings, 6 adults). Partial wing moult has been used to identify yearling Semipalmated Sandpipers in eastern North America (Gratto and Morrison 1981), but only 3 of 209 (1.4%) breeding birds had plumage in this condition at Nome.

Data were analysed using SAS procedures (SAS Institute 1990). ANOVA and ANCOVA models were computed with PROC GLM, and multiple contingency models with maximum likelihood estimates were calculated with PROC CATMOD. Clutches of less than four eggs were pooled in all analyses because sample sizes were small. Clutch size was adjusted in some nests as part of an incubation experiment (Sandercock 1997a), but we used unmanipulated nests to calculate rates of abandonment and partial clutch loss. Rates of partial clutch loss were estimated using the Mayfield method (Johnson 1979). I have previously shown that female body size explains little of the variation in timing of laying, clutch size and egg size ($r^2 < 15\%$, Sandercock

1998b), and we focus on covariation among these traits in this paper. Tests were two-tailed and considered significant at probability levels of $\alpha < 0.05$. Sample sizes differ among some sections because complete information was not available for all clutches.

Results

Variation in clutch size

The modal clutch size of Semipalmated and Western Sandpipers was four eggs in all years (Table 1). Maximum likelihood analysis showed that an interaction between species and year did not significantly affect clutch size ($\chi^2_3 = 0.81$, $p = 0.85$). In a reduced model that contained only main effects, both species ($\chi^2_1 = 4.71$, $p = 0.03$) and year ($\chi^2_3 = 13.5$, $p < 0.005$) had a significant effect on clutch size. Semipalmated Sandpipers had a significantly smaller clutch size than Western Sandpipers (Table 1). When we considered the species separately, we found that there was significant annual variation in the clutch size of Semipalmated Sandpipers ($\chi^2_3 = 9.73$, $p < 0.021$), but not Western Sandpipers ($\chi^2_3 = 4.22$, $p < 0.24$). Female Semipalmated Sandpipers produced more 2- and 3-egg clutches in 1994 (Table 1). Clutches of less than four eggs were viable and were not abandoned at higher rates than 4-egg clutches in either Western (< 4 eggs: 2.5%, $n = 22$; 4 eggs: 4.5%, $n = 132$, Fisher's Exact Test, $p = 0.12$) or Semipalmated Sandpipers (< 4 eggs: 0%, $n = 37$; 4 eggs: 1.7%, $n = 121$, Fisher's Exact Test, $p > 0.99$).

A few renesting attempts were found during this study (Western: 4 of 238 nests (1.7%), Semipalmated: 1 of 208 (0.5%)), and all were close to the site of the first nest (mean distance: $77.0 \text{ m} \pm 27.2 \text{ SD}$, $n = 5$). Three female Western Sandpipers were captured on two nests: two females laid four eggs twice, and one female laid four and then three eggs. The first nests were depredated soon after the start of incubation ($7.7 \text{ d} \pm 5.8 \text{ SD}$, $n = 3$) and the interval before renesting was short ($6.6 \text{ d} \pm 3.4 \text{ SD}$, $n = 3$). The re-nests were excluded from further analyses.

Clutches of fewer than four eggs might be expected if disturbance caused laying females to deposit eggs out-

side of the nestbowl. Two- and 3-egg clutches tended to be found more often during laying (Western: 8 of 20 (40.0%), Semipalmated: 8 of 38 (21.1%)) than 4-egg clutches (Western: 41 of 194 (21.1%), Semipalmated: 19 of 157 (12.1%)), but the difference was not significant (Western: $G_1 = 3.26$, $p = 0.07$, Semipalmated: $G_1 = 1.88$, $p = 0.17$). Small clutches might also be expected if eggs were destroyed by predators prior to discovery of the nest. There were no losses of marked eggs from clutches observed during laying (Western: 0 losses in 135 d, Semipalmated: 0 losses in 147 d, Mayfield estimates of daily survival rate (d.s.r.) = 1). Most nests were found soon after incubation had started (Western: $2.1 \pm 4.5 \text{ SD d}$, $n = 214$, Semipalmated: $3.0 \pm 5.0 \text{ SD d}$, $n = 195$), and egg loss during incubation was also rare (Western: 4 losses in 1957.5 d of exposure, d.s.r. = $0.998 \pm 0.001 \text{ SE}$, Semipalmated: 7 losses in 1728.5 d of exposure, d.s.r. = $0.996 \pm 0.002 \text{ SE}$). Partial clutch loss did not explain the variation in clutch size because the observed number of 2- and 3-egg clutches (Table 1) was significantly higher than the frequencies expected from the rates of egg loss (i.e., < 3 per species, Western: $G_1 = 115.6$, $p < 0.001$, Semipalmated: $G_1 = 154.2$, $p < 0.001$).

Variation in the timing of clutch initiation

Timing of laying was synchronous: 80% of the clutches were usually initiated within 1–2 weeks (range: Western 9–18 d, Semipalmated 7–19 d). There were highly significant differences in laying date between 2–3 and 4-egg clutches in both Western (2-way ANOVA, clutch size: $F_{1,201} = 27.7$, $p < 0.0001$) and Semipalmated Sandpipers (2-way ANOVA, clutch size: $F_{1,186} = 26.7$, $p < 0.0001$). Females that laid clutches of less than four eggs initiated nests 6–8 days later, on average, than females that produced 4-egg clutches (Table 2). There was also significant annual variation in the laying date of Western Sandpipers (year: $F_{3,201} = 3.83$, $p = 0.01$, clutch size \times year: $F_{3,201} = 0.69$, $p = 0.57$), but not Semipalmated Sandpipers (year: $F_{3,186} = 1.55$, $p = 0.20$, clutch size \times year: $F_{3,186} = 1.46$, $p = 0.23$).

Table 1. Clutch size distributions of Western and Semipalmated Sandpipers breeding at Nome, Alaska. No. of nests (% of nests).

Year	Western Sandpiper				Semipalmated Sandpiper			
	2 eggs	3 eggs	4 eggs	n	2 eggs	3 eggs	4 eggs	n
1993 ^a	1 (2.1)	3 (6.3)	44 (91.7)	48	1 (1.5)	10 (15.2)	55 (83.3)	66
1994	2 (3.3)	9 (15.0)	49 (81.7)	60	1 (1.7)	18 (31.6)	38 (66.7)	57
1995	–	5 (10.0)	45 (90.0)	50	1 (1.8)	7 (12.3)	49 (86.0)	57
1996	–	5 (7.6)	61 (92.4)	66	2 (8.0)	–	23 (92.0)	25
Total	3 (1.3)	22 (9.8)	199 (88.8)	224	5 (2.4)	35 (17.1)	165 (81.0)	205

^a One Western Sandpiper clutch of 7 eggs was not included because two females may have used the same nestcup.

Variation in egg size

There was a significant difference in mean egg volume between 2–3 and 4-egg clutches in both Western (2-way ANOVA, clutch size: $F_{1,215} = 7.14$, $p < 0.01$) and Semipalmated Sandpipers (2-way ANOVA, clutch size: $F_{1,196} = 5.43$, $p = 0.02$). Eggs in the 2- and 3-egg clutches were 2.9% (Western) and 3.5% (Semipalmated) smaller than eggs in 4-egg clutches (Table 3). There was no annual variation in the egg volume of either Western (year: $F_{3,215} = 1.75$, $p = 0.16$, clutch size \times year: $F_{3,215} = 1.18$, $p = 0.32$) or Semipalmated Sandpipers (year: $F_{3,196} = 1.68$, $p = 0.17$, clutch size \times year: $F_{3,196} = 1.99$, $p = 0.12$).

To further investigate the relationship between egg volume and laying date, we controlled for clutch size and limited our sample to 4-egg clutches (Fig. 1). In this subset of the data, the egg volume of Western Sandpipers declined significantly with laying date in three of four years ($p = 0.10$ in 1995, Fig. 1). The egg volume of Semipalmated Sandpipers increased significantly in one year, but was otherwise unaffected by the timing of laying (Fig. 1). Overall, the seasonal decline in egg volume was highly significant in Western Sandpipers (ANCOVA, laying date: $F_{1,182} = 17.7$, $p < 0.0001$, year: $F_{3,182} = 0.67$, $p = 0.57$, year \times laying date: $F_{3,182} = 0.69$, $p = 0.56$), but not in Semipalmated Sandpipers (laying date: $F_{1,149} = 0.76$, $p = 0.38$, year: $F_{3,149} = 0.78$, $p = 0.51$, year \times laying date: $F_{3,149} = 0.91$, $p = 0.44$). Egg size declined by 5–12% over the breeding season in Western Sandpipers.

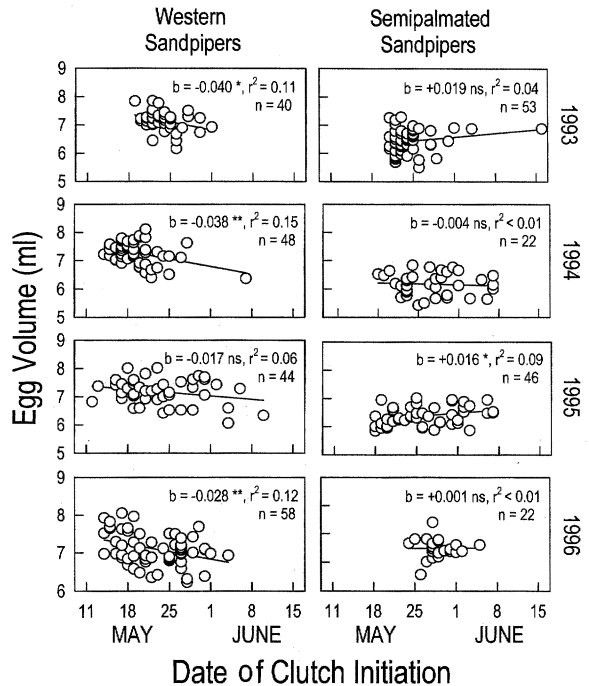


Fig. 1. Mean egg volume in Western and Semipalmated Sandpipers as a function of date of clutch initiation. Each point is the mean egg volume for a 4-egg clutch, smaller clutches were not included. * $p < 0.05$, ** $p < 0.01$.

Factors covarying with timing of clutch initiation

In Western Sandpipers, there was no significant difference in timing of clutch initiation between yearlings and

Table 2. Timing of clutch initiation in relation to the clutch size of Western and Semipalmated Sandpipers. Mean date \pm 1 SD (n of nests), where 152 = 1 Jun.

Year	Western Sandpiper		Semipalmated Sandpiper	
	2–3 eggs	4 eggs	2–3 eggs	4 eggs
1993	151.5 \pm 0.7 (2)	143.9 \pm 2.9 (40)	151.9 \pm 6.0 (8)	144.6 \pm 4.2 (53)
1994	147.9 \pm 5.5 (8)	139.7 \pm 4.1 (48)	152.0 \pm 3.3 (19)	147.3 \pm 5.6 (36)
1995	153.8 \pm 9.3 (5)	143.7 \pm 6.6 (44)	155.5 \pm 6.4 (8)	146.5 \pm 6.0 (46)
1996	147.0 \pm 7.0 (3)	142.5 \pm 5.4 (59)	152.5 \pm 0.7 (2)	149.0 \pm 2.7 (22)
Total ^a	7.1 \pm 6.4 (18)	-0.7 \pm 5.0 (191)	4.8 \pm 5.0 (37)	-1.1 \pm 5.0 (157)

^a Residuals corrected for annual variation in timing of clutch initiation. Negative values indicate laying dates prior to the annual means.

Table 3. Mean egg volume (ml) in relation to the clutch size of Western and Semipalmated Sandpipers. Mean \pm 1 SD (n of nests).

Year	Western Sandpiper		Semipalmated Sandpiper	
	2–3 eggs	4 eggs	2–3 eggs	4 eggs
1993	6.60 \pm 0.52 (4)	7.15 \pm 0.34 (44)	6.04 \pm 0.40 (10)	6.45 \pm 0.43 (55)
1994	7.08 \pm 0.61 (11)	7.27 \pm 0.41 (49)	6.14 \pm 0.40 (19)	6.17 \pm 0.39 (38)
1995	6.95 \pm 0.51 (5)	7.17 \pm 0.46 (45)	6.31 \pm 0.19 (8)	6.38 \pm 0.36 (49)
1996	7.08 \pm 0.40 (5)	7.09 \pm 0.43 (60)	6.16 \pm 0.01 (2)	6.49 \pm 0.35 (23)
Total	6.96 \pm 0.55 (25)	7.17 \pm 0.41 (198)	6.15 \pm 0.36 (39)	6.37 \pm 0.40 (165)

Table 4. Residual date of clutch initiation (corrected for annual variation) as a function of female age, familiarity with a mate and familiarity with the study area^a. Data from 1994–1996 are pooled, data from 1993 were not included because all birds were newly banded in the first year of the study. Mean residual date \pm SD (n of nests).

Variable		Western Sandpiper	Semipalmated Sandpiper
Female age ^b			
Adult		0.8 \pm 5.5 (29)	–
Yearling		2.8 \pm 2.6 (8)	–
Familiarity with a mate ^c			
Remated pair		–3.9 \pm 2.9 (25)	–1.5 \pm 5.1 (33)
New pair		–1.7 \pm 5.2 (21)	–3.2 \pm 3.7 (12)
Familiarity with the study area ^d			
Female	Male		
Recapture	Recapture	–1.6 \pm 5.2 (21)	–3.2 \pm 3.7 (12)
Recapture	Band	–3.2 \pm 5.3 (18)	0.2 \pm 5.2 (5)
Band	Recapture	0.1 \pm 5.5 (25)	1.1 \pm 4.1 (16)
Band	Band	2.9 \pm 5.9 (54)	1.9 \pm 6.5 (25)

^a Negative values indicate laying dates prior to the annual mean.

^b Females unfamiliar with mate and study area (all newly banded in 1996).

^c Adult birds familiar with study area (all banded in a previous year). Familiarity with a mate was determined from nesting records in the previous year.

^d Birds unfamiliar with their mate (I assumed a pair was new if both birds were newly banded), age class not controlled. Banding status was used as index of familiarity with the study area, where 'recapture' and 'band' indicate the bird was banded on the study area in a previous or current year, respectively.

newly settled adults ($t_{15,8} = -1.46$, $p = 0.16$), although yearlings nested two days later on average (Table 4). Similarly, newly mated and reuniting pairs did not differ significantly in timing of clutch initiation in either Western ($t_{30,5} = 1.78$, $p = 0.09$) or Semipalmated Sandpipers ($t_{43} = -1.06$, $p = 0.30$). New pairs of Western Sandpipers nested two days later than reuniting pairs but the opposite trend was observed in Semipalmated Sandpipers (Table 4). Male experience with the study area had no effect on the timing of clutch initiation in Western (2-way ANOVA, male: $F_{1,114} = 0.33$, $p = 0.57$) or Semipalmated Sandpipers (2-way ANOVA, male: $F_{1,54} = 1.58$, $p = 0.21$). However, female Western Sandpipers that had previously bred on the study area nested significantly earlier (female: $F_{1,114} = 12.5$, $p < 0.001$) than birds that were captured for the first time (by 4.5 d, Table 4). The difference (3.5 d, Table 4) was not significant in Semipalmated Sandpipers (female: $F_{1,54} = 3.30$, $p = 0.07$), nor was there an interaction in timing between the sexes in either species (female \times male, Western: $F_{1,114} = 3.78$, $p = 0.054$, Semipalmated: $F_{1,54} = 0.59$, $p = 0.44$).

Discussion

The fecundity of Western Sandpipers and Semipalmated Sandpipers at Nome had two unusual aspects. First, despite short and synchronous breeding seasons, there were seasonal declines in the fecundity of both species. Clutches of two and three eggs were initiated later in the season and contained smaller eggs than 4-egg clutches. Second, the two sandpiper species adjusted different aspects of their fecundity over the

course of the breeding season. Semipalmated Sandpipers laid smaller clutches than Western Sandpipers, whereas the egg size of Western Sandpipers declined with laying date (among 4-egg clutches).

The variation in clutch size that we observed (Table 1) is surprising because past studies have reported a clutch size of four eggs in Western and Semipalmated Sandpipers (Holmes 1972, Gratto et al. 1983, Gratto-Trevor 1992). The frequency of 4-egg clutches ranges from 85–100% for most arctic (Mayfield 1978, Parmelee 1992, Lanctot and Laredo 1994) and temperate-breeding shorebirds (Miller 1979, Berg 1992). Tomkovich and Morozov (1983) provide one exception: they found that only 63.4% ($n = 82$) of Western Sandpiper nests contained four eggs in eastern Russia. Most studies of shorebirds have attributed clutches of fewer than four eggs to partial nest predation, disturbance or renesting, but we can reject these explanations here (see also Sandercock 1997b).

Undetected egg predation could be high during laying if sandpiper nests are left unattended (Sandercock 1998a), and females that lose first-laid eggs might change nest sites to lay a smaller clutch (cf. Ganter and Cooke 1993). However, no eggs were lost from sandpiper nests monitored during laying, and egg losses during incubation were likely due to parents removing broken eggs for nest-cup sanitation (Sandercock 1996). The trend for clutches of fewer than four eggs to be found during laying is consistent with a disturbance effect. However, if disturbance led to small clutches, the difference in clutch initiation should have been 0–2 days instead of 6–8 days. Similarly, disturbance does not explain why small clutches were initiated later in the season or why eggs were smaller in these attempts. We

detected few renests in this study (0.5–1.7%), a frequency comparable to past studies of Western Sandpipers (6.4%, Holmes 1971, 0%, Tomkovich and Morozov 1983), Semipalmated Sandpipers (4.2%, C. L. Gratto-Trevor, unpubl.) and other arctic-breeding species (0%, Stilt Sandpiper *Calidris himantopus*; Jehl 1973, Ringed Plover *Charadrius hiaticula*; Pienkowski 1984). Sandpipers only replaced clutches that were lost during early incubation (see also Berg 1992), but most nest failure occurred late in the breeding season (Sandercock 1998a). Renesting cannot explain the seasonal declines in clutch size because the frequency of small clutches was much higher than that of renests.

Seasonal declines in the clutch size and egg size of shorebirds

Seasonal declines in clutch size are widespread among birds that lay a variable number of eggs (Klomp 1970, Murphy 1986, Rohwer 1992). Several groups of birds lay an invariant or truncated clutch size (Sandercock 1997a), and Rohwer (1992) suggested that these birds should be an exception to the general pattern. For example, seabirds that lay one egg (Alcidae, Diomedidae) obviously cannot reduce clutch size any further, although females may opt not to breed if conditions are unfavourable. To our knowledge, this is one of the first studies to demonstrate that there can be a covariation between laying date and clutch size in a bird with a putatively invariant clutch size. We conclude that the phenomenon of seasonal declines in clutch size is more ubiquitous than previously recognized. Birds that do lay a fixed number of eggs might adjust egg size to cope with different environmental conditions, or as a condition-dependent tactic (Miller 1979, Galbraith 1988). Seasonal declines in the egg size of Western Sandpipers, other shorebirds (Byrkjedal and Kålås 1985, Redmond 1986), and some seabirds that lay one egg (Harris 1980, Birkhead and Nettleship 1982) are consistent with this expectation. Many hypotheses have been offered to account for seasonal declines in clutch and egg size (Murphy 1986, Rohwer 1992), and we review here four explanations that are relevant to sandpipers.

The Clutch Size-Egg Size Tradeoff Hypothesis

Theoretical models (Smith and Fretwell 1974, Winkler and Wallin 1987) predict that there may be tradeoffs between offspring number and the investment per offspring. Birds nesting late in the season could potentially lay fewer eggs and reduce the duration of breeding, but lay larger eggs to improve the survival of their young. That was not the case in this study, since late-nesting sandpipers that produced 2- or 3-egg clutches laid smaller eggs than birds laying 4-egg clutches. Positive phenotypic correlations among life-history traits are

common, and may be caused by variation in parental ability or territory quality.

The Nutrient Reallocation Hypothesis

The nutrient reallocation hypothesis was first suggested to explain seasonal declines in the clutch size of arctic-nesting geese (Rohwer 1992, Ganter and Cooke 1996). Under this model, females arrive on the breeding grounds with limited endogenous resources, which they use for body maintenance if environmental conditions delay the onset of laying. The relative importance of endogenous versus exogenous nutrients for shorebird reproduction is currently unresolved (Galbraith 1988, Blomqvist and Johansson 1995), but Nol et al. (1997) reported a reduction in the clutch size of Semipalmated Plovers *Charadrius semipalmatus* during a year of late spring phenology. In this study, Western Sandpipers showed annual variation in laying date but there was no concomitant change in clutch size. Conversely, there was annual variation in the clutch size of Semipalmated Sandpipers, but it was not related to yearly differences in the timing of laying. The nutrient reallocation hypothesis was not supported here, but our four years of data provide a relatively weak test of this idea.

The Cost-of-Delay Hypothesis

If the success rate of nests or the recruitment rate of young decline during the breeding season, reductions in clutch or egg size may be advantageous if they save time needed to acquire nutrients for additional or larger eggs (Drent and Daan 1980). Nesting success was higher for early-breeding sandpipers at Nome (Sandercock 1998a), but the opposite trend has been reported in most other shorebird studies (Byrkjedal 1980, Pienkowski 1984, Reynolds 1987). It was not possible to assess seasonal changes in sandpiper recruitment because < 3% of banded nestlings were recaptured on the study area as breeding birds (Sandercock 1997b). Low natal philopatry is common in shorebirds (Sandercock and Gratto-Trevor 1997), although Lank et al. (1985) were able to show that recruitment of Spotted Sandpipers *Actitis macularia* is not affected by seasonal timing. Further evaluation of this hypothesis requires better estimates of survivorship for shorebird young.

The Parent-Quality Hypothesis

Timing of arrival and laying are correlated in several migratory shorebirds (Soikkeli 1967, Hildén and Vuolanto 1972, Jönsson 1987), and possibly in Western and Semipalmated Sandpipers as well. Pairs that bred early in the breeding season laid both larger clutches and bigger eggs. These results are consistent with the notion that birds of lower phenotypic quality nest later in the breeding season. Many conditional factors can affect 'quality' of a breeding bird, but we considered

age, experience with the breeding area and experience with a mate. Previous studies of shorebirds have tested these factors by using relative age (Hildén and Vuolanto 1972, Thompson and Hale 1991, Oring et al. 1994) or by comparing the fecundity of new and old pairs (Jönsson 1987). Age and experience are confounded in both instances, and we attempted to distinguish among these factors in our analyses.

Fecundity rates increase with parent age in many birds and these changes may be due to accumulated experience, or to age-specific breeding tactics based on the relative value of future reproduction (Rohwer 1992, Martin 1995). Adult Western Sandpipers bred 2 days earlier than yearlings on average, but the difference was not significant. Gratto et al. (1983) found that adult Semipalmated Sandpipers in Manitoba laid larger eggs and nested 2–3 days earlier than yearlings. Seasonal declines in the fecundity of Semipalmated Sandpiper could have been due to age-specific variation in effort, but only if undetected yearlings were numerous. However, female age cannot be a general explanation for seasonal reductions in fecundity of birds because declines in clutch size have been documented within homogeneous age groups (Rohwer 1992, Smith 1993).

Familiarity with a mate or a local breeding area could affect timing of laying because breeding site-fidelity is high among monogamous shorebirds with a male-territorial breeding system (Sandercock and Gratto-Trevor 1997, Sandercock 1997b). In three other species of calidrine sandpipers, reuniting pairs nested earlier than newly-formed pairs (Soikkeli 1967, Jehl 1973, Miller 1983, Jönsson 1987). In these previous studies, newly-formed pairs may have included birds that were young or unfamiliar with the study area. When we controlled for these two factors, we found that experience with a partner had no effect on the timing of laying. Female experience with the study area had a significant effect on the timing of laying in Western Sandpipers. Female Western Sandpipers bred 4.5 days earlier if they had nested on the study area before. We were unable to control for age in this analysis. However, the difference in timing between yearling and adult females was only 2 days, thus experience with the local area appears to have a residual effect on female reproductive timing. Male experience presumably had no effect because clutch initiation is controlled by females. Overall, seasonal declines in the clutch and egg size of Western and Semipalmated Sandpipers seem most consistent with the Parent-Quality hypothesis, but the Nutrient-Reallocation and Cost-of-Delay hypotheses deserve further study.

Variation in the reproductive tactics of Western and Semipalmated Sandpipers

Why were there seasonal declines in the egg size of

Western Sandpipers, whereas clutch size was reduced in Semipalmated Sandpipers? Absolute egg size may have been important. Calidrine sandpipers are small-bodied compared to other precocial birds (Rahn et al. 1975), and produce some of the smallest eggs among birds with this mode of development (Reynolds and Székely 1997). Surface area to volume ratios are important in the development of homeothermy (Visser and Ricklefs 1993), and could set a lower boundary on the size of shorebird young in arctic environments. The eggs of Semipalmated Sandpipers were 12% smaller than those of Western Sandpipers, and could be close to a minimum size for viable precocial young. If so, there may have been seasonal reductions in the clutch size of Semipalmated Sandpipers because reductions in egg size would have had a greater effect on fitness.

Seasonal trends in clutch or egg size have not been previously found in Western or Semipalmated Sandpipers. However, birds at Nome, Alaska are morphologically (Harrington and Morrison 1979) and genetically distinct (Haig et al. 1997) from populations in other regions of North America. The patterns of fecundity that we observed could be adaptations to local conditions. For example, Semipalmated Sandpipers at Nome start breeding a month earlier than more easterly populations of this species (Gratto and Cooke 1987). Reductions in clutch size among Semipalmated Sandpipers could be an adaptation to the greater time constraints associated with a longer migration to western Alaska. Seasonal declines in clutch and egg size may also indicate that the costs of egg production are important at our study site. To better understand local variation in fecundity, future studies should determine whether females rely on exogenous nutrients for egg production, and measure the seasonal availability of important foods.

Evolutionary implications of variation in sandpiper fecundity

Shorebirds exhibit a wide array of mating systems and patterns of parental care. Phylogenetic analysis has shown that the reproductive behaviour of shorebirds is labile, but the evolutionary transitions between different forms of parental care remain controversial (Székely and Reynolds 1995). An invariant clutch size has presumably led to diversification because reproductive output can only be increased by investment in more than one clutch (Ligon 1993). Interestingly, shorebirds with multiple-clutch mating systems produce relatively small eggs (Sæther et al. 1986), and sometimes have a fixed clutch size of three eggs (e.g. Dotterel *Charadrius morinellus*, Kålås and Løfaldi 1987; Kentish Plover *C. alexandrinus*, Székely et al. 1994). These differences have been previously interpreted as a secondary adapta-

tion to increases in egg production. Our results suggest a different evolutionary pathway. Phenotypic variation in fecundity is likely to change the payoffs for deserting a mate during incubation. Thus, seasonal variation in clutch and egg size is intriguing because it could be a preadaptation that has favoured transitions from biparental to uniparental care.

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