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Incubation capacity and clutch size determination in two calidrine sandpipers: a test of the four-egg threshold

Abstract Several groups of vertebrate taxa, including shorebirds, are unusual in that they produce a fixed number of offspring. The aim of this study was to examine whether the incubation capacity of western sandpipers (*Calidris mauri*) and semipalmated sandpipers (*C. pusilla*) limits their maximum clutch size to four eggs. Experimental enlargement of clutch size had no effect on rates of nest abandonment, nest attendance or loss of body mass by incubating sandpipers. The duration of incubation was significantly longer for enlarged five-egg nests, and there were trends towards increased partial clutch loss and asynchrony at hatch, but overall hatching success was unaffected by experimental egg number. I conclude that small, calidrine sandpipers with biparental care are able to compensate for an additional egg in an enlarged nestbowl, despite the constraints of conically shaped eggs and two brood patches. Possibly, shorebirds do not lay more than a fixed clutch size of four eggs because selection on factors acting during egg production or brood-rearing is more important in regulating offspring number.

Key words Invariant offspring number · Clutch size · Incubation capacity · *Calidris* sandpipers

Introduction

The factors that regulate offspring number are a central issue in the theory of life-history evolution (Godfray et al. 1991, Stearns 1992). Research on this topic has often been aimed at explaining intraspecific variation in offspring number (e.g. the individual optimization hypothesis, Pettifor 1993a,b). However, there are many groups of vertebrate taxa that show little variation in reproductive output, and produce a fixed number of offspring in each breeding attempt. This tactic occurs in reptiles (Anolinae, 1 egg, Shine and Greer 1991; Gekkonidae, 2 eggs, Vitt 1986), birds (Alcidae, 1 egg, Ydenberg 1989; Trochilidae, 2 eggs, Johnsgard 1983; Columbidae, 2 eggs, Westmoreland and Best 1987; Laridae, 3 eggs, Reid 1987), and mammals (many groups 1 young, Tuomi 1980; Read and Harvey 1989). An invariant clutch or litter size is usually associated with low mean fecundity (Shine and Greer 1991) and large offspring (Elgar and Heaphy 1989; Read and Harvey 1989).

Two hypotheses that have been proposed to explain evolution of clutch and litter size are: (1) energetic demands on females during egg-laying or gestation may influence the number of offspring they can produce, or (2) offspring number may be adapted to parental expenditures during care of eggs or dependent progeny. Parental ability during either part of the reproductive cycle may act as a proximate constraint that limits clutch or brood size, and possibly to an invariant number of offspring. Selection on parental ability may also play an ultimate role in determination of optimal offspring number, particularly if the fitness consequences of producing or raising additional young are unprofitable.

In animals with altricial young, provisioning young with food after hatch (birds, Murphy and Haujioka 1986; Bryant and Tatner 1988) or parturition (lactation in mammals, Kenagy et al. 1990; Sikes 1995) is generally thought to be the stage of reproduction with the greatest energetic cost. Energetic constraints may be less common at the brood-rearing stage in taxa with precocial young (but see Safriel 1975; Walters 1984) because most forms of parental care are nondepreciable (i.e. the total benefit is distributed equally among the young, Lazarus and Inglis 1986; Schindler and Lamprecht 1987), and because parental effort shows little increase with brood size (Lazarus and Inglis 1978; Lessells 1987; Schindler and Lamprecht 1987; Seddon and Nudds 1994; Williams

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et al. 1994; but see Walters 1982). Mode of development affects the duration of incubation (Rahn and Ar 1974; Nol 1986), and parental expenditures during this period may have influenced the evolution of avian clutch size (Klomp 1970; Winkler and Walters 1983; Murphy and Haukioja 1986; Godfray et al. 1991; Rohwer 1992). The energetic cost of incubation can be high in birds (Piersma and Morrison 1994), and increases with egg number (Biebach 1981; Haftorn and Reinertsen 1985; Moreno and Carlson 1989; Moreno et al. 1991; Erikstad and Tveraa 1995).

Shorebirds (infraorder Charadriides, excluding Laroidea) occur in a wide variety of habitats and show a diverse range of mating systems and parental care (Pitelka et al. 1974; Erckmann 1983; Lenington 1984; Székely and Reynolds 1995), yet almost all species lay a modal clutch size of four eggs (Maclean 1972). Shorebirds differ from most vertebrate taxa that lay a fixed clutch size because they produce more than the usual 1–3 eggs (see also Wiebe and Bortolotti 1993), and because they have precocial young that are nidifugous and self-feeding. The ability of parent(s) to incubate eggs is commonly suggested as a possible constraint on shorebird clutch size (Miller 1979; Hills 1980; Winkler and Walters 1983; Reid 1987; Wiebe and Bortolotti 1993; Erikstad and Tveraa 1995). Shorebird eggs are more conical in shape than the eggs of other birds (Hoyt 1979; Andersson 1978), which may be an adaption for thermal efficiency. Increased surface contact among pyriform eggs may act to reduce heat loss during incubation (Norton 1970, cited in Drent 1975; Andersson 1978; Miller 1979). The brood patch area of the incubating parents may also be important (Andersson 1976; Wiebe and Bortolotti 1993). Shorebirds usually develop two lateral brood patches, and cover two eggs with each oval patch. Experimentally enlarged clutches usually have higher rates of failure in birds that lay a fixed number of eggs, possibly because the number of eggs per brood patch is more easily disrupted than in birds that lay a variable clutch size (Wiebe and Bortolotti 1993).

I manipulated egg number in western sandpipers (*Calidris mauri*) and semipalmated sandpipers (*C. pusilla*) to test whether incubation ability acts as a constraint on shorebird clutch size. Adjustments of egg number may affect parental behaviour and/or the success of their eggs (Hochachka 1992), and I considered both possible effects. I predicted that if experimental clutches are more energetically costly to incubate, parents might show increased nest abandonment (Delehanty and Oring 1993), reduced nest attendance (Jones 1987) or greater loss of body mass (Kålås and Løfaldi 1987; Moreno and Carlson 1989). If parents are unable to cover an enlarged clutch with their brood patches, they might attract predators by rising and settling more often (cf. Beer 1965; Baerends et al. 1970). Similarly, uneven incubation of experimental clutches may result in an extended incubation period (Coleman and Whittall 1988; Smith 1989), increased hatching asynchrony (Reid 1987; Moreno and

Carlson 1989) or may reduce hatching success by causing embryo mortality (Hills 1980, 1983).

Materials and methods

This study of western and semipalmated sandpipers was conducted at a site 21 km east of Nome, Alaska (64°20′N, 164°56′W) during the summers of 1993–1995. The 4-km^2 study area contains shallow tundra ponds interspersed with low, dry ridges where the two species breed in sympatry. The two sandpipers are probably not sibling species (Baker 1992; Székely and Reynolds 1995) but share relevant features of their breeding biology: both are small, male-territorial shorebirds that form monogamous pairs (Gratto-Trevor 1992; Wilson 1994). The female lays the clutch in a shallow ground-nest, and the sexes share incubation duties. Clutch size is usually four eggs. Females may renest if the first nest is depredated, but only one brood is produced per year. The two species are easily distinguished during the breeding season by features of their plumage and by their vocalizations.

To find nests, field workers walked the tundra and observed sandpiper behaviour. Birds attending a nest often flushed from short distances and attempted to use distraction displays to lead the observer away. If the clutch was not found immediately after the parent flushed, the bird was observed from a distance until it returned to the nest. Nests were marked with a line of small sticks and a short stake about 10 m from the nestcup.

Nests were visited daily during laying, irregularly throughout incubation and then daily close to the expected hatch date. The number of eggs was recorded on every visit. If a nest contained fewer than four eggs when first found, it was revisited until clutch size remained unchanged for 3 days. If the nest contained four eggs when found, the eggs were floated in a small cup of warm water and egg buoyancy was used to estimate stage of incubation (Nol and Blokpoel 1983; Alberico 1995; B.K. Sandercock, unpublished work). Dates of clutch initiation and completion of laying were determined from egg-laying schedules, or by back-dating from the estimated stage of incubation. Length of incubation was measured from the date of clutch completion to the date of hatch.

A single protocol was used to create experimental clutches in both western and semipalmated sandpipers. Clutches of three and five eggs were created by exchanging one egg between randomly chosen pairs of four-egg clutches, usually during the first 1–4 days of incubation. The nestcup of addition clutches was enlarged by pressing on the sides of the nest cup to accommodate the fifth egg. Each egg moved to a different nest was marked with a felt pen to distinguish it from the host clutch. Control nests were not treated with sham exchanges because it was necessary to retain a sample of unmanipulated nests for baseline reproductive information. One egg was broken during handling in a few clutches; these nests were included in the removal treatment.

It was difficult to match clutches of similar age because estimates of stage of incubation based on egg buoyancy were somewhat imprecise (± 2 day, B.K. Sandercock unpublished work). If the experimental egg hatched earlier than the host clutch, the parents might have abandoned the rest of clutch to lead the early hatching chick away from the nest (see Reid 1987; Robertson et al. 1995). To avoid this potential problem, experimental eggs were moved from newer nests to older nests. My experiment tests the effect of an additional egg on the success of the host clutch, but the results also have implications for whether parents can successfully incubate five eggs.

Incubating sandpipers were captured with walk-in traps placed over the nest. I attempted to capture both parents on every nest, and each bird was individually marked with combinations of coloured leg bands and a numbered metal band. Birds were trapped twice during incubation, usually 10–14 days apart. A rate of mass change was calculated by dividing the difference in body mass by the number of days elapsed between the two captures.

Western sandpipers were sexed by culmen length (males < 24.5 mm, females > 24.5 mm, Page and Fearis 1971; Cartar 1984), but semipalmated sandpipers could not be reliably sexed by external morphology. In both species, I considered the larger of the two parents on a nest to be the female. A few semipalmated sandpipers were probably sexed incorrectly because individuals that paired with different birds in separate years occasionally had one larger and one smaller mate (4/32 possible cases). Nonetheless, independent criteria indicate this approach is generally accurate for this species (Sandercock and Gratto-Trevor 1997; B.K. Sandercock unpublished work).

In nest visits during incubation, field workers recorded whether a bird was attending the nest, and identified the parent by its colour bands. If no parent was on the nest, the observer touched the eggs with their lips to determine whether they were cold and the nest was unattended. If the eggs were warm, I assumed the parent had been incubating but had flushed while the observer was distant. Total nest attendance was calculated as the proportion of all nest visits that a bird was or had been on the nest. Relative nest attendance by males was calculated as the proportion of nest visits where a parent was identified and it was the male.

Nest fates were defined as one of four possible outcomes: (1) abandoned: eggs left pointing out by an observer were not rotated back into the nest for more than a week, and were consistently cold; (2) depredated (total nest failure): the eggs disappeared before the expected hatch date or there was signs of predator activity (fox urine, smashed eggshells); (3) partial clutch loss: an egg disappeared during incubation; or (4) successful: at least one chick was banded and left the nest. Partial clutch loss may have been caused by predators destroying eggs, but sandpipers may also remove any eggs with mechanical damage from the nest (Sandercock 1996). In nest visits prior to hatch, all eggs were inspected for tapping, starpips, and holepips. The young were not handled until all of the viable eggs had hatched and young were dry enough to be banded. The day the young were banded was taken as the date of hatch. Eggs left in the nestbowl were collected after the young had departed, opened and examined for indications of embryo development.

If the nest survived until hatch, hatching success was calculated as the percentage of eggs that hatched. Three sources contributed to reduced hatching success: partial clutch loss during incubation, abandoned eggs that failed to hatch and young that were unaccounted for at hatch. The experimental egg in addition clutches usually showed signs of hatching but failed because it was out of synchrony with the host clutch; estimates of hatching success for addition clutches were thus based on the four eggs of the host clutch. Young may have been missing at hatch because early-hatching chicks were moving off the nest. I was conservative in calculating estimates of hatching success, and treated missing eggs and young as dead.

Estimates of daily nest survival were calculated using the Mayfield method (Mayfield 1975; Johnson 1979), and compared with program CONTRAST (Hines and Sauer 1989). All other statistics were calculated using standard procedures from SAS (SAS Institute 1990). The tests were two-tailed and considered significant at probability levels less than $\alpha = 0.05$. Sample sizes differ among some tests because complete information was not available for every nest. Weather conditions and timing of laying varied during this study (B.K. Sanderson, unpublished work), but the three years were pooled in the analyses because the clutch size manipulation had similar results in all years.

Results

The clutch size manipulation had a similar effect in western and semipalmated sandpipers. There was no significant difference among treatments in rates of nest abandonment in either species, although western sandpipers deserted several of the experimental three-egg nests (Table 1). Four of five abandoned western sandpiper nests in the removal treatment were deserted immediately after the experimental egg was moved to another nest, but the rest were attended by the parents for several days before they left. Abandoned nests were not included in further analyses. Total nest attendance remained high (> 98% of all nest visits) in all of the three treatments. The relative contribution of each of the sexes to incubation was unaffected by manipulated egg number, males were on the nest during 50–60% of all nest visits (Table 1). Incubating female western sandpipers lost significantly more body mass during incubation than males, but loss of body mass was not affected by manipulated egg number in either species (Table 1).

In both species, there were trends for increased partial clutch loss in the addition treatment (Table 2). In semipalmated sandpipers, there was a significant difference among treatments in daily loss rates (Table 2), but

Table 1 Rates of nest abandonment, male nest attendance and mass loss of semipalmated sandpipers and western sandpipers incubating removal (3 eggs), control (4 eggs) and addition (5 eggs) clutches; sample size of nests appears in the right of each column, means are given ± 2SE

| Treatment | Nest abandonment | | Male nest attendance | | Mass loss during incubation (g/day) | | | |
					Females		Males	
Semipalmated sandpipers								
Removal	0%	22	52% ± 14%	21	−0.05 ± 0.12	9	−0.09 ± 0.18	10
Control	2.1%	97	53% ± 8%	82	−0.03 ± 0.20	20	−0.01 ± 0.10	22
Addition	0%	20	55% ± 18%	14	−0.07 ± 0.14	8	0.04 ± 0.10	9
Statistics	$G_2 = 1.46, P = 0.92$		$\chi_2^2 = 0.10^a, P = 0.95$		Sex: $F_{1,72} = 0.13, P = 0.72$; Trt: $F_{2,72} = 0.23, P = 0.80$			
					Sex × Trt: $F_{2,72} = 0.27, P = 0.76$			
Western sandpipers								
Removal	16.1%	31	62% ± 10%	26	−0.08 ± 0.06	12	0.03 ± 0.08	13
Control	6.0%	83	55% ± 8%	78	0.02 ± 0.16	18	0.02 ± 0.10	22
Addition	0%	22	61% ± 12%	22	−0.15 ± 0.12	14	0.06 ± 0.08	15
Statistics	$G_2 = 6.27, P = 0.28$		$\chi_2^2 = 0.91^a, P = 0.64$		Sex: $F_{1,88} = 5.31, P = 0.02$; Trt: $F_{2,88} = 0.63, P = 0.54$			
					Sex × Trt: $F_{2,88} = 1.80, P = 0.17$			

[a] Kruskal-Wallis test (χ^2 approximation)

Table 2 Partial clutch loss and total nest failure of semipalmated sandpipers and western sandpipers incubating removal (3 eggs), control (4 eggs) and addition (5 eggs) clutches; sample size of nests appears in the right of each column; means are given ± 2SE

Treatment	Partial clutch loss				Total nest failure			
	Percentage of nests with losses		Daily loss rate from the Mayfield method		Percentage of nests depredated		Daily mortality rate from the Mayfield method	
Semipalmated sandpipers								
Removal	0%	22	0	22	40.9%	22	0.026 ± 0.017	22
Control	4.2%	95	0.005 ± 0.004	94	50.5%	95	0.044 ± 0.012	94
Addition	10.0%	20	0.005 ± 0.007	18	50.0%	20	0.032 ± 0.021	18
Statistics	$G_2 = 3.07, P = 0.69$		$\chi_2^2 = 6.02^a, P = 0.049$		$G_2 = 0.68, P = 0.98$		$\chi_2^2 = 3.20^a, P = 0.20$	
Western sandpipers								
Removal	3.8%	26	0.002 ± 0.004	26	30.8%	26	0.017 ± 0.012	26
Control	1.3%	78	0.001 ± 0.002	78	42.3%	78	0.033 ± 0.011	78
Addition	13.6%	22	0.007 ± 0.008	22	31.8%	22	0.016 ± 0.012	22
Statistics	$G_2 = 5.39, P = 0.37$		$\chi_2^2 = 2.18^a, P = 0.34$		$G_2 = 1.56, P = 0.91$		$\chi_2^2 = 5.44^a, P = 0.07$	

[a] Mortality estimates compared with program CONTRAST (Hines and Sauer 1989)

there was no difference between the addition and control treatments in loss rate ($\chi_1^2 = 0.07, P = 0.80$). The partial clutch loss observed in this study was probably caused by mechanical damage to the eggs rather than nest predation. In three addition nests, parents were known to have removed eggs that were broken during incubation. In most of the other cases (10/11 nests), only one egg went missing during incubation. If the partial clutch loss had been due to predation, the predator might be expected to return and continue to remove eggs from the nest. There was no evidence that birds incubating enlarged clutches were able to recognize foreign eggs, all eggs that went missing from the addition nests were eggs of the host and not an egg experimentally added to the clutch. The egg losses in this study were mainly due to total nest failure where a predator destroyed all of the eggs. There was no difference among treatments in the rate of nest loss, whether it was calculated as the percentage of nests destroyed or as a daily mortality rate (Table 2).

The presence of an additional egg had a significant effect on the length of incubation, extending the duration by about one day in both sandpiper species (Table 3). There was increased asynchrony at hatch and a slight reduction in the hatching success of five-egg addition nests, but in neither case was the trend significant (Table 3). In the sample of addition nests, 7/15 pairs of western sandpipers and 3/8 pairs of semipalmated sandpipers hatched all four of their own eggs despite having a fifth egg for 12–19 and 17–18 days of incubation, respectively. There were also several addition nests that were depredated after the eggs had started to hatch but before young could be banded. These clutches showed the same result, all four of the host eggs showing signs of hatching in 2/2 western sandpiper and 3/5 semipalmated sandpiper nests.

There was no difference between treatments in the embryonic development of eggs that failed at hatching and were abandoned in the nest (western sandpipers $G = 5.16, P = 0.40$; semipalmated sandpipers $G = 0.38, P > 0.99$). In the western sandpiper removal and control clutches (pooled), four failed eggs had no visible development, nine had small embryos, and seven had well-developed embryos; the addition treatment had zero, six

Table 3 Length of incubation, duration of hatch and hatch ability of semipalmated sandpipers and western sandpipers incubating removal (3 eggs), control (4 eggs) and addition (5 eggs) clutches; sample size of nests appears in the right of each column; means are given ± 2SE

Treatment	Length of incubation (days)		Duration of hatch (hours)[a]		Hatchability[b]	
Semipalmated sandpipers						
Removal	19.9 ± 0.6	13	47.3 ± 29.2	5	86% ± 12%	13
Control	20.0 ± 0.5	31	48.6 ± 9.8	25	89% ± 6%	47
Addition	21.3 ± 0.5	10	70.1 ± 35.8	5	81% ± 12%	8
Statistics	$F_{2,51} = 3.98, P = 0.02$		$F_{2,32} = 1.29, P = 0.29$		$\chi_2^2 = 2.17^c, P = 0.34$	
Western sandpipers						
Removal	20.9 ± 0.7	18	40.6 ± 11.5	6	91% ± 8%	18
Control	20.8 ± 0.3	30	57.2 ± 11.1	26	91% ± 4%	45
Addition	22.1 ± 0.8	15	77.5 ± 30.6	8	80% ± 12%	15
Statistics	$F_{2,60} = 5.75, P = 0.005$		$F_{2,37} = 2.63, P = 0.09$		$\chi_2^2 = 3.01^c, P = 0.22$	

[a] Time taken by chicks to emerge from eggs that were starpipped
[b] Hatchability in the addition treatment was based on the four host eggs
[c] Kruskal-Wallis test (χ^2 approximation)

and eight eggs, respectively. A similar pattern was observed in semipalmated sandpipers (removal and control 3, 8 and 3 eggs; addition 2, 3 and 2 eggs).

Discussion

Costs of incubation in calidrine sandpipers

This study provides little support for the notion that egg shape (Norton 1970, cited in Drent 1975; Andersson 1978; Miller 1979) and brood patch area (Andersson 1976, Wiebe and Bortolotti 1993) limit the ability of western or semipalmated sandpipers to incubate more than the normal clutch size of four eggs. Anecdotal evidence has suggested that these factors might be important. Sandpipers rotate eggs displaced by an observer so that the narrow ends of the eggs are in the centre of the nest (personal observations). Moreover, the few atypical shorebirds that regularly lay three instead of four eggs usually produce eggs that are more oval in shape (e.g. dotterel *Charadrius morinellus*, Nethersole-Thompson 1973; Kentish plovers *C. alexandrinus*, T. Székely personal communication; black oystercatchers *Haematopus bachmani*, Andres and Falxa 1995).

In this study, total nest attendance remained high and the relative contribution of the sexes was the same for all treatments. Hills (1983) found that western sandpipers returning from incubation breaks took longer to settle on five-egg clutches, but the rate of total nest failure was not higher for experimental clutches in this study. Erckmann (1981, p. 122) found that western sandpipers that were forced to incubate alone lost body mass at 0.49 g/day before deserting the nest. In contrast, the maximum rates of mass loss (*c.* -0.15 g/day) of birds in this study (western sandpipers mean body mass = 27.2 g, semipalmated sandpipers mean body mass = 25.1 g) were much lower. The 2–3 g lost during a 20- to 21-day incubation period could potentially be replaced quickly (migrating western and semipalmated sandpipers can increase body reserves at rates of 1–2 g/day, R.W. Butler and D.B. Lank personal communication).

The increased desertion rate of reduced nests by western sandpipers and other birds (Armstrong and Robertson 1988; Winkler 1991) is probably not a function of their inability to incubate fewer eggs. Parents are likely basing investment decisions on the relative value of their current and future nesting attempts. Egg removals may reduce the value of their current nest relative to the possible benefits of laying a renest of larger clutch size (Winkler 1991), or of deferring breeding given that a predator has detected the nest.

The increased length of incubation and asynchrony at hatch is consistent with parents being unable to cover the entire clutch with their brood patches. With a maximum daily mortality rate of 0.05/day (Table 2), however, an extra day of incubation would not have a substantial effect on total nest failure. Moreover, despite a longer incubation period, parents appeared able to compensate for an extra egg because hatching success was only reduced from 90% to 80%. Given that females could have hatched a fifth egg if it had been in synchrony with the rest of the nest, the minor incubation costs observed in this study do not appear to outweigh the potential 25% increase in reproductive output that females producing an extra egg would gain.

Hills (1980, 1983) conducted similar experiments with calidrine sandpipers at Wales, Alaska but reported quite different results. She found that fewer pairs were able to hatch all of the viable eggs when incubating five instead of four eggs (western sandpipers 0/10 vs. 23/26, semipalmated sandpipers 0/2 vs. 9/10, dunlin *C. alpina* 2/6 vs. 5/6), and that addition nests produced fewer young on average than control nests (western sandpipers 2.6 vs. 3.9, semipalmated sandpipers 3.0 vs. 3.9, dunlin 3.0 vs. 3.8). The disparity between the two studies is intriguing given that the identical species were considered in the same part of their breeding range (Wales and Nome are only 200 km apart in western Alaska).

Two methodological differences may account for the differences we observed in hatching success. Hills (1983) and other manipulative studies (Kålås and Løfaldi 1987; Delehanty and Oring 1993) have used parboiled eggs to create enlarged nests, but shorebird eggs with developing embryos may be less costly to incubate because they lose mass throughout incubation (Lank et al. 1985; Yalden and Yalden 1989). Safriel (1980) suggested that semipalmated sandpipers are able to incubate extra eggs if the nestcup is enlarged. Hills (1983) did not enlarge the nestcup in her experimental nests, which produced egg arrangements where one egg was usually segregated from the rest of the clutch. A consequence of these configurations was that embryo development showed pronounced asynchrony in her five-egg clutches. Addition nests probably had higher hatching success in my study because sandpipers were better able to adjust and incubate five eggs in an enlarged nestcup. The cost of building a larger nestcup would presumably be small in western and semipalmated sandpipers; the males construct many nestscrapes for the female to inspect during courtship (Gratto-Trevor 1992, Wilson 1994).

Uniparental and biparental incubation in shorebirds

Several authors (Erckmann 1983; Lank et al. 1985) have suggested that clutch size may have played a role in the evolution of shorebird mating systems. In general, mate desertion is favoured if one parent is able to successfully incubate the clutch or raise the young (Beissinger 1986; Székely and Reynolds 1995). If clutch size is fixed at four eggs, females may increase their reproductive output by laying multiple clutches, particularly if they are in a resource-rich environment. This scenario may have lead to the evolution of such mating systems as double-clutching (e.g. Temminck's stint *Calidris temminckii*, Hildén 1975) or polyandry (e.g. spotted sandpiper *Actitis macularia*, Lank et al. 1985).

The costs of incubating an additional egg may differ between shorebird species where only the female or male tends the eggs and species with biparental care. Eggs are relatively smaller in shorebirds with multiple-clutch mating systems (Ross 1979; Sæther et al. 1986). However, shorebirds that are uniparental incubators also maintain lower rates of total nest attendance than biparental incubators (Erckmann 1981; Cartar and Montgomerie 1985), which may limit their ability to change foraging patterns to cope with increasing metabolic costs of incubation.

Several studies have manipulated clutch size to investigate incubation costs in shorebirds, and two of these have examined species that regularly lay three eggs (dotterel, Kålås and Løfaldi 1987; Kentish plovers, Székely et al. 1994). Enlargements of clutch size have a detrimental effect on the behaviour of shorebirds that are uniparental incubators. Extra eggs resulted in increased nest abandonment by male Wilson's phalaropes (*Phalaropus tricolor*, Delehanty and Oring 1993) and male dotterel reduced nest attendance after increased loss of body mass (Kålås and Løfaldi 1987). Nonetheless, male spotted sandpipers and dotterel are able to hatch all eggs in supranormal clutches (Bond 1950; Kålås and Løfaldi 1987). Egg additions have less effect on shorebirds with biparental care. Kentish plovers and sandpipers are able to compensate for an additional egg without changing nest attendance or losing body mass (Székely et al. 1994, this study; but see Hills 1980, 1983). Semipalmated sandpipers are able to incubate a four-egg clutch mass that is 40% larger than normal (Safriel 1980). Moreover, clutch enlargements have no effect on the hatching success of sandpipers (this study), American avocets (*Recurvirostra americana*, Shipley 1984; but see Gibson 1971), Kentish plovers (Székely et al. 1994) or spur-winged plovers (*Vanellus spinosus*, Yogev et al. 1996), although enlarged clutches may take 0.5–2 days longer to hatch (this study; Székely et al. 1994; Yogev et al. 1996).

The lower success of uniparental shorebirds with an additional egg is consistent with the observation that daily weather conditions also have a greater impact on these species (e.g. female white-rumped sandpipers *C. fuscicollis*, Cartar and Montgomerie 1985, 1987), than on other arctic-breeding calidrine sandpipers where both sexes incubate (Norton 1972, Erckmann 1981). Further manipulations of clutch size in other shorebird species would be useful in establishing the generality of this observation.

Incubation in birds with a fixed or a variable clutch size

There is a general relationship between clutch size and number of brood patches in birds: birds that lay a variable number of eggs tend to have one large central brood patch, whereas birds that lay a fixed number of eggs usually have a discrete number of brood patches (1–3) that match their clutch size (Reid 1987, Wiebe and Bortolotti 1993). Wiebe and Bortolotti (1993) suggested that number of brood patches may act as a constraint on clutch size, but only in birds that lay a fixed number of eggs, such as shorebirds.

Some experimental evidence supports this idea. In birds that lay a variable clutch size, clutch enlargements sometimes increase the length of incubation (Coleman and Whittall 1988, Baltz and Thompson 1988; Moreno and Carlson 1989; Smith 1989) but usually have no effect on loss of body mass (Rohwer 1985; Jones 1987; Moreno et al. 1991) or hatching success (Slagsvold 1982; Briskie and Sealy 1989; Robertson et al. 1995, but see Klomp 1970; Moreno et al. 1991). The magnitude of manipulation may affect the experimental outcome (Hochachka 1992) and several of these studies increased clutch size by only one or two eggs (Slagsvold 1982, Baltz and Thompson 1988), or created experimental nests within the natural range of clutch size (Briskie and Sealy 1989). Nonetheless, a few remarkable species that lay a variable clutch size can successfully hatch almost twice as many eggs as they lay in a normal clutch (American coots *Fulica americana*, Frederickson 1969; female blue-winged teal *Anas discors*, Rohwer 1985, 1992).

A few birds that lay a fixed number of eggs are unable to cope with enlarged clutches. In larids (Coulter 1973; Andersson 1976), albatrosses (Rice and Kenyon 1962) and white-rumped swiftlets (*Aerodramus spodiopygius*, Tarburton 1987), additional eggs are rolled from the nest, buried or broken. However, it is more common that birds which lay a fixed number of eggs are able to successfully incubate more eggs than their normal clutch size (e.g. gannets *Sula bassana*, Nelson 1964; mourning doves *Zenaida macoura*, Westmoreland and Best 1987; glaucous-winged gulls *Larus glacescens*, Reid 1987; sandpipers, this study). The brood patch hypothesis of Wiebe and Bortolotti (1993) seems weak because most birds appear able to incubate additional eggs whether they lay a variable or a fixed number of eggs.

The ability of birds to incubate eggs and the Lack hypothesis

Studies that have examined the effect of natural or manipulated offspring have frequently shown that the most common brood or litter size is smaller than the size which produces the most recruits (the "Lack clutch size", altricial birds: Klomp 1970; Martin 1987; Dijkstra et al. 1990; VanderWerf 1992; mammals: Morris 1992). The observation above that birds that lay a fixed clutch size are sometimes able to incubate enlarged clutches is analogous to this finding, and several of the criticisms and adaptive explanations that have been used to explain the results of brood size manipulations may also apply to this study.

The manipulative approach I used has been criticized because females did not incur the additional costs of laying the egg (Partridge 1989; Stearns 1992). Heany and Monaghan (1995) have shown that these costs can have

a significant effect on nest success in common terns (*Sterna hirundo*). Similarly, parents may be able to hatch or fledge additional young but if the young are of lower quality they may not survive as well until recruitment (Martin 1987; VanderWerf 1992; Pettifor 1993a).

Most of the adaptive explanations used to explain deviations from the Lack clutch size (reviewed by Morris 1992; Stearns 1992) are aimed at explaining variation in clutch size and are not appropriate for taxa with invariant or fixed reproductive output. I consider here two hypotheses that may be relevant.

1. The cost of reproduction hypothesis (Partridge 1989; Hochachka 1992; Stearns 1992) suggests that four eggs may be the optimal clutch size if there is a tradeoff between fecundity and adult survival, even if the most productive clutch size in sandpipers is greater than four eggs. Survival is a difficult parameter to estimate (Lebreton et al. 1992) and the small samples of most experimental studies hamper detection of differences among treatments (Pettifor 1993b; Graves 1991). The sandpipers in this study might have suffered low post-breeding survival if they incubated five eggs, yet it is unclear why this would be the case if manipulated egg number had no effect on rates of mass loss.

2. The bad-year hypothesis (Boyce and Perrins 1987) suggests that sandpipers may lay clutches of less than maximal clutch mass to hedge against greater failure in bad years. Weather conditions in the arctic are particularly variable and occasionally harsh (Piersma and Morrison 1994). The results of this study should be robust because the experiment had the same result in each of 3 years, although an enlarged clutch may be more detrimental in a year with particularly late snowmelt or cold temperatures.

How does selection limit clutch size in shorebirds and other precocial birds?

I have shown that the ability of parents to incubate does not appear to act as a constraint on clutch size in two biparental calidrine sandpipers. Alternately, selection on parental investment during brood-rearing or egg production may be more important in regulating clutch size. Walters (1984) suggested that parental expenditures during brood-rearing could be important but studies that have manipulated brood size in precocial birds have generally found that parents are able to raise additional young (Rohwer 1985; Lessells 1986; Milonoff and Paananen 1993; Sandercock 1994). The study of Safriel (1975) on semipalmated sandpipers is one notable exception; he found reduced survival in enlarged broods. If sandpiper young are more dispersed in enlarged broods, changes in feeding rates, predation risk, or the probability of getting lost may affect chick mortality (Safriel 1975; Walters 1984). These ideas have not been tested, but Safriel's results are consistent with the minor effect that clutch enlargements had upon incubation costs in this study.

Shorebirds lay relatively large eggs (clutch mass can equal or exceed female body mass, Sæther et al. 1986), but it is unclear whether costs of egg production limit clutch size to four eggs. Some shorebirds are able to produce up to five clutches in a breeding season (Lank et al. 1985; Colwell and Oring 1988) but always with an interval between each clutch (Hildén 1975; Lank et al. 1985; Breiehagen 1989), which the female may use to feed and obtain resources for egg formation. Natural clutches of more than four eggs have been observed in many shorebirds (< 2% of all nests, Bond 1950, Hildén 1978; Shipley 1984; Colwell and Oring 1988; Lanctot and Laredo 1994; but see Gratto-Trevor 1992), but in some cases more than two females probably contributed to the same nest (Giroux 1985; Wilson 1994).

Food addition studies usually affect only date of laying (reviewed by Martin 1987; Daan et al. 1988; Boutin 1990), but sometimes increase clutch size (Arcese and Smith 1988; Carlson 1989), which indicates that food availability acts as a constraint upon egg production. In contrast, egg removals during laying can provide evidence that resources available during egg production do not constrain clutch size, particularly if females produce supranormal clutches at normal egg-laying rates in the same or different nests (indeterminate or continuous egg-laying, Arnold 1992; Sandercock 1993). A caution in such studies is that the extra eggs can be of lower quality (Monaghan et al. 1995). Nonetheless, some birds (e.g. northern flickers *Colaptes auratus*, Eurasian wrynecks *Jynx torquilla*) that lay maximum clutches of 8 and 12 eggs are able to lay up to 60–70 eggs if eggs are removed during laying (references in Haywood 1993). Several shorebirds are indeterminate egg-layers (Haywood 1993, Székely et al. 1994; D. Schamel unpublished work but see Yogev and Yom-Tov 1994), but the costs of egg formation in calidrine sandpipers remain unknown because eggs have not been removed during laying in any species.

Evolution of an invariant clutch size in shorebirds

The constraints that could have limited the ability of sandpipers to incubate in this study (egg shape, number of brood patches, nest size) are all factors that have likely coevolved with clutch size (Slagsvold 1982; Reid 1987), and leave us no closer to understanding the conditions that have may have lead to the evolution of a fixed clutch size in shorebirds or other vertebrate taxa. Shorebirds laying four eggs, geckoes laying two eggs, and anoline iguanids laying one egg are each ecologically diverse lineages that inhabit a broad range of habitats (Erckmann 1983; Shine and Greer 1991). It seems unlikely that a fixed clutch size could be an adaptation to a particular set of environmental conditions. Strong selection for a fixed number of offspring during the evolutionary history of these groups may have resulted in canalization of this trait. An invariant clutch size may have been retained, despite subsequent diversification,

because of phylogenetic conservatism (Shine and Greer 1991).

In sandpipers, a fixed clutch size of four eggs appears to be associated with a suite of life-history traits that are adaptations for the time constraints imposed by long-distance migration. Low reproductive output in shorebirds is consistent with large eggs (Sæther et al. 1986) and high survivorship (Evans and Pienkowski 1984; Evans 1991; Sandercock and Gratto-Trevor 1997). A small clutch requires less time to lay and incubate, which minimizes exposure to predators (Clark and Wilson 1981), but also permits earlier departure from the breeding grounds. Large, yolk-rich eggs (Sotherland and Rahn 1987) produce fast-growing precocial young that are deserted soon after hatch by the parents (Székely and Reynolds 1995), and migrate south independently (Butler et al. 1987). If accurate, this evolutionary scenario would predict that long-distance migration should be the ancestral condition among shorebirds. In the future, phylogenetic analysis (Chu 1994; Székely and Reynolds 1995) may be the best tool to test this hypothesis, and to further investigate the evolutionary pathways that may have led to a fixed clutch size of four eggs.

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