FACTORS AFFECTING THE BREEDING DEMOGRAPHY OF

WESTERN SANDPIPERS (*Calidris mauri*) AND SEMIPALMATED SANDPIPERS

(*C. pusilla*) AT NOME, ALASKA

by

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FACTORS AFFECTING THE BREEDING DEMOGRAPHY OF WESTERN SANDPIPERS (CALIDRIS MAURI) AND SEMIPALMATED SANDPIPERS (CALIDRIS PUSILLA) AT NOME, ALASKA

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ABSTRACT

The breeding demography of Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*C. pusilla*) was studied at Nome, Alaska for four years (1993-1996). These abundant arctic-nesting sandpipers are long-distance migrants, lay a modal clutch size of four eggs, and have biparental care. I monitored nests and banded breeding birds to determine sandpiper fecundity and survival rates. I also performed an experiment to test one of the factors that may limit clutch size.

Breeding seasons were short, and both sandpipers had similar egg-laying rates, duration of incubation, and hatching rates. Clutch and egg size declined seasonally in both species: 2- and 3-egg clutches contained smaller eggs and were initiated later than 4-egg clutches. Small clutches were not renests, and were not caused by disturbance or clutch loss. This is one of the first reports of clutch size variation in birds thought to have a fixed clutch size. Of four explanations tested, seasonal variation in fecundity was most consistent with the parental-quality hypothesis. Adult females that were familiar with the study area and their mate tended to nest earlier. The cost-of-delay hypothesis was not tested because low natal philopatry precluded assessment of recruitment.

Egg number was manipulated to determine whether incubation ability limits shorebird clutch size. Contrary to a widespread view, incubation capacity does not select for a maximal clutch size of four eggs in biparental sandpipers. Experimental clutch enlargement did not affect rates of abandonment, nest attendance or loss of body mass. Incubation length and hatching asynchrony were increased, but hatching success was unaffected. Other stages of reproduction warrant further investigation.

Both species showed female-biased sexual size dimorphism, but there was no evidence of assortative mating for body size. Timing of laying was related to body size, but not in the expected direction. Mate choice could not explain dimorphism but intrasexual selection could be important because large females laid larger eggs.

Local survival was high in sandpipers, presumably because breeding site-fidelity was strong. Females moved further than males to remate, but overall, mate-fidelity was relatively high. Low fecundity and high survival rates suggest that Western and Semipalmated Sandpipers may be vulnerable to environmental change and thus require conservation effort in the future.

DEDICATION

I dedicate my dissertation to the memory of

my brother

Craig A. Sandercock
28 March 1968 - 27 December 1992

and my grandfather

William F.G. Adams
10 March 1909 - 27 July 1993

my tenure at Queen's University and Simon Fraser University. The Cooke lab in particular, has been a large and somewhat amorphous group whose total or specific membership is often difficult to identify. I have received (in no particular order): camaraderie, requests for assistance, beer, recent papers, billiards lessons, sympathy, teasing, encouragement, bad poker hands, theoretical insights, and shared laughter from many participants. These have enhanced my university experience, and to all I am very grateful.

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Chapter I

General Introduction

Introduction

Many species of shorebirds are migratory, with annual cycles that include movements among breeding sites in the arctic, stopover areas in temperate regions, and tropical wintering grounds (Myers et al. 1987). The advantage of long-distance travel is that it allows shorebirds to utilize the flush of food resources that occurs at high latitudes in the summer. Migration has two consequences, however, that make shorebirds a particularly vulnerable group of birds. First, some species concentrate in phenomenal numbers during migration (Senner et al. 1981, Hicklin 1987), and aggregation makes these populations vulnerable to catastrophic events of natural (e.g., anomalous weather) and anthropogenic origin (e.g., oil spills). Second, most shorebird species complete migration by making a series of flights (O'Reilly and Wingfield 1995, Iverson et al. 1996), and by replenishing body reserves at stopover sites (Davidson and Evans 1988). Shorebird migration has been compared to a 'stepping-stone' model because geographic barriers often separate the series of estuaries and wetlands that are used by the birds (Piersma 1987 *in* O'Reilly and Wingfield 1995). Unfortunately, the habitats needed by shorebirds are often heavily impacted by human activity (Myers et al. 1987, Gill et al. 1994, Rattner et al. 1995). Industrial development, agricultural runoff or disturbance in one area could be devastating if it hampers the ability of shorebirds to accumulate the resources for movement to consecutive sites.

Effective conservation biology depends on the accurate assessment of population status and the ability to identify changes that are most likely to have detrimental effects. Population viability analyses (PVA) have been increasingly used to address these problems in recent years (Beissinger 1997). In this approach, detailed demographic and enviromental data are used to simulate populations into the future, and to evaluate their risk of extinction. Stage-structured models have been applied to only a few shorebirds, including Semipalmated Sandpipers (*Calidris pusilla*, Hitchcock and Gratto-Trevor 1997) and the endangered Piping Plover (*Charadrius melodus,* Ryan et al. 1993). The success of PVA is largely dependent on the quality of demographic information that is available for a selected species. Shorebirds are thought to have a life-history strategy that includes low reproductive rates and high survivorship (Evans and Pienkowski 1984, Evans 1991), but accurate empirical estimates of these rates are limited to a few species (Thompson and Thompson 1991). In this project, I conducted an intensive study of the breeding demography of the Western Sandpiper (*Calidris mauri*) and the Semipalmated Sandpiper (*C. pusilla*) at Nome, Alaska. The two major aims of my dissertation were: *i*) to derive empirical estimates of fecundity and survival, and *ii*) to assess the factors that influence these rates.

The Two Study Species

The Western Sandpiper is the most abundant shorebird on the Pacific flyway of North America (Senner et al. 1981, Wilson 1994), and the Semipalmated Sandpiper shares the same status on the Atlantic coast (Hicklin 1987). The two species appear to be closely related because they share unique morphological features (e.g., partially webbed feet, Paulson 1993); recent biochemical evidence has supported this idea (Haig et al. 1997). Western and Semipalmated Sandpipers are arctic-breeding shorebirds that are highly migratory, lay a modal clutch size of four eggs and have biparental care. Both sexes participate equally in incubation (Holmes 1972, Ashkenazie and Safriel 1979), but males provide most parental care after hatching (Gratto-Trevor 1991). These aspects of their biology make Western and Semipalmated Sandpipers useful as 'model species' for understanding the biology of migratory shorebirds. My dissertation complements previous work and concurrent studies that are being conducted on the two species at wintering sites, during migration and on the breeding grounds.

Western and Semipalmated Sandpipers winter throughout central and South America, but the nonbreeding biology of these species is poorly known (Gratto-Trevor 1992, Wilson 1994). In Western Sandpipers, there appear to be latitudinal clines in the wintering areas of the sexes, with males staying further north (Page et al. 1972, Harrington and Haase 1994). Recent work in the San Francisco Bay area has shown that some individuals maintain home ranges and exhibit a high degree of site-fidelity (Warnock and Takekawa 1995, 1996). Further demographic information on wintering birds will be available when ongoing studies in Panama (P.D. O'Hara, unpubl.) and Mexico are completed (H. de la Cueva, unpubl.).

Western Sandpipers have been studied during migration at the Fraser (Butler et al. 1987) and Copper River Deltas (Senner et al. 1981). Recent projects using radio-marked (Iverson et al. 1996) and colour-banded birds (Butler et al. 1996) have improved our understanding of the migration tactics and routes of this species. Western Sandpipers from Nome have been resighted in the Pacific Northwest to as far south as Mexico (Butler et al. 1996), and have been recaptured in Panama (P.D. O'Hara and B.K. Sandercock, unpubl.). Few Semipalmated Sandpipers from Nome have been resighted elsewhere, although two birds from Ecuador were resighted on the study area (B.K. Sandercock, unpubl.). The migration routes (Harrington and Morrison 1979, Gratto-Trevor and Dickson 1994) and stopover behaviour (Lank 1989, Skagen and Knopf 1994, Lyons and Haig 1995) of Semipalmated Sandpipers in North America have been relatively well-studied.

The breeding range of the Western Sandpiper is confined to coastal areas in western Alaska (Wilson 1994), whereas the Semipalmated Sandpiper breeds throughout the arctic regions of North America (Harrington and Morrison 1979, Gratto-Trevor 1992). The breeding biology of the Western Sandpiper is known mainly from two studies, one in the Yukon-Kuskokwim River Delta, Alaska (Holmes 1971, 1972), and one in eastern Russia (Tomkovich and Morozov 1983). The Semipalmated Sandpiper has been studied in northern Alaska (Ashkenazie and Safriel 1979), but most of the information on fecundity (Gratto et al. 1983; 1985, Gratto and Cooke 1987, Gratto-Trevor 1991) and survival (Gratto 1988, Sandercock and Gratto-Trevor 1997) comes from a study of a population in Manitoba. This information has been useful for a comparative basis, and the populations at Nome appear to differ from other areas in several aspects of their fecundity.

Dissertation Outline

This dissertation has been prepared in the 'paper' format that is commonly used in Europe, and each chapter is intended to be complete if separated from the thesis. Nonetheless, the topics addressed in each of the six main chapters are closely related. In Chapter II, I describe the nesting chronology of Western and Semipalmated Sandpipers at Nome, Alaska. Laying rates, length of incubation and duration of hatching were estimated, and flotation of eggs was used to estimate stage of incubation. This information was used to determine dates of clutch initiation, and to investigate seasonal variation in nest success. Sandpipers remove eggshells from nests at hatching, which makes it difficult to determine whether a nest was successful or was depredated. In Chapter III, I evaluate two explanations for eggshell removal: *i*) the risk of nest predation, and *ii*) the risk of egg-capping. Seasonal declines in fecundity are common in birds but have rarely been found in species with an invariant clutch size. In Chapter IV, I document seasonal variation in sandpiper clutch and egg size. I evaluate four hypotheses that may explain seasonal reductions in reproductive effort: *i*) tradeoffs between the components of fecundity, *ii*) nutrient reallocation, *iii*) the cost of delay, and *iv*) variation in parent quality. The factors that regulate clutch size in birds with an invariant clutch are poorly known. In Chapter V, the incubation capacity of sandpipers was investigated by experimentally manipulating number of eggs. I considered the effects that clutch reduction and enlargement had upon the parents (e.g., behaviour, condition) and the success of the clutch (e.g., length of incubation, hatching success). Males are territorial and compete for mates in many monogamous sandpipers, but surprisingly, females are usually the larger sex. In Chapter VI, I examine the evidence that negative assortative mating and size-dependent fecundity has led to female-biased sexual size dimorphism. Reliable estimates of survival are available for few migratory shorebirds. In Chapter VII, I determine

the survival rates of sandpipers and evaluate the biases in these estimates with corollary data on site-tenacity and mate-fidelity. In Chapter VIII, I summarize the contributions I have made to understanding the biology of shorebirds, and I provide suggestions for future directions in research.

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Chapter II

Chronology of Nesting Events in Western and Semipalmated Sandpipers Near the Arctic Circle

Abstract. The chronology of nesting events was examined in Western Sandpipers *(Calidris mauri)* and Semipalmated Sandpipers (*C. pusilla*) breeding at Nome, Alaska. The duration of laying (5 d for a 4-egg clutch) and hatching (53.0±26.6SD h, dry chicks to emerge from star-pipped eggs) was similar for both species. Laying rates of Semipalmated Sandpipers at Nome were slower than other populations, possibly because laying intervals were greater than 30 h. Length of incubation was significantly longer in Western (21.5±0.5 d) than Semipalmated Sandpipers (20.3±1.9 d). Early clutches had significantly higher hatching success than late clutches in Semipalmated Sandpipers (60.0%, n=105 vs. 22.9%, n=70) but not Western Sandpipers (68.2%, n=88 vs. 47.3%, n=55).

Introduction

Time constraints strongly influence the biology of migratory birds that breed in the arctic. Local conditions are usually suitable for only a short period, and early departure may be critical if migrants are to reach wintering areas successfully. Many shorebirds have compressed breeding schedules at high latitudes (Miller 1983, Pienkowski 1984), and northern populations may have adaptations that reduce the length of the breeding period. The nesting chronology of shorebirds can be difficult to investigate because it is hard to find nests before laying is complete, and because predation rates are often high (Evans and Pienkowski 1984). Nonetheless, Dunlin (*Calidris alpina*) have faster egg-laying rates in the northern parts of their breeding range (Holmes 1966, Soikkeli 1967), Red Phalaropes (*Phalaropus fulicaria*) have a shorter length of incubation (Schamel and Tracy 1987), and female Semipalmated Sandpipers (*C. pusilla*) desert their young to depart earlier (Gratto and Cooke 1987). The aims of this study were to determine: the egg-laying rates, length of incubation, duration of hatching and seasonal rates of nest success in Western Sandpipers (*C. mauri*) and Semipalmated Sandpipers breeding at a site near the Arctic Circle.

Methods

Field methods

The reproductive 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 May-July in 1993-1995. The two species breed in the same habitat at this site, and nests are placed on low, dry ridges that are close to shallow tundra ponds.

Nests were located by walking the tundra and observing sandpiper behavior. Incubating birds flushed from the nest at short distances and used distraction displays to lead the observer away. If the clutch was not found immediately after the parent flushed, the bird was observed from 20-30 m until it returned to the nest. Nests were marked with a line of small sticks and a wooden stake 10 m

from the nestcup. Date and the time of day were recorded on all nest visits; most effort was in the daylight hours of 0800-0100 h.

Nests found with fewer than four eggs were visited 1-2 times per day until clutch size remained unchanged for three days. These nests were revisited during incubation to float eggs. If a nest contained four eggs (the maximum clutch size) when it was found, 2-4 eggs were immersed in a small, clear cup of warm water. Eggs were pushed to the bottom before release to prevent egg damage from dropping and to ensure they were not held by surface tension. Only undamaged eggs were floated. If eggs touched the bottom of the cup, the angle between the bottom of the cup and the center axis of the egg (flat or 20-90°) was measured. If eggs floated freely in the water, it was recorded whether or not the eggshell broke the surface. Floating eggs does not affect hatchability in shorebirds (Van Paassen et al. 1984, Alberico 1995)

Nests were visited every 6-7 d during incubation and then daily close to estimated hatching date. Observers held eggs close to the ear to listen for the sound of young tapping on the eggshell. If tapping was heard, we lightly touched the blunt end of the egg with a fingertip to detect raised eggshell or 'star-pips'. In the next stage of hatching, young punctured a small opening or 'hole-pip' in the eggshell; these holes were visible without handling the eggs. Young were not banded until all viable eggs had hatched, and preferably when the chick down feathers had dried. The young usually departed the nest soon after all were dry.

Estimation methods

The number of nests was not adequate to test for annual or seasonal variation in most cases, so data from the three years were usually pooled. Sample sizes differ among analyses because complete information was not available for every nest.

Egg-laying rates were calculated for four-egg clutches that were found during laying. Three-egg clutches were excluded because a long laying interval could be caused by eggs lost to partial nest depredation or disturbance during laying. The few nests that were not visited at least daily during laying were also excluded. The laying interval between successive eggs was calculated by using the elapsed time between two different nest visits. To obtain a minimum estimate, I assumed that an egg had been laid just previous to the first visit, and I only included cases where an additional egg was known to have been laid subsequent to the last nest check. If egg number did not change between two daily visits, the elapsed time was a minimum estimate of one laying interval (e.g., 3 eggs on day 1 at 1000 h to 3 eggs on day 2 at 1800 h gives a laying interval of 32 h). If egg number increased by one during a 2-3 d period, the elapsed time was a minimum estimate of two laying intervals (e.g., 2 eggs

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on day 1 at 1300 h to 3 eggs on day 4 at 1300 h gives a mean laying interval of 36 h). Both estimates are clearly sensitive to check frequency, thus minimum intervals of less than 15 h were discarded. The estimates may be biased towards longer laying intervals because it was not possible to determine the time of laying when an egg appeared between two daily nest visits.

The duration of incubation was estimated by subtracting the date the last egg was laid from the date of hatching. For nests found during laying, the date of last laying was the day the last egg was found. For nests that contained complete clutches of eggs that floated flat (see below), date of last laying was assumed to be the day the nest was found.

The duration for each stage of hatching was the elapsed time between the nest visit where some eggs in the nest showed signs of hatching and the nest check where the last viable egg had hatched. There was usually some hatching asynchrony among the eggs of a clutch, and nests were categorized on the basis of the most advanced egg.

Determining nest success

Nest fate was defined as one of three outcomes: (1) *abandoned*: eggs were consistently cold for a week or more; (2) *depredated*: eggs disappeared before the expected hatching date, or there were signs of predator activity (broken egg shells, fox urine in the nestbowl); or (3) *hatched*: at least one chick was banded and left the nest. Predators often remove all eggs from shorebird nests (pers. obs.), but the fate of an empty nestbowl can be ambiguous because parents remove eggshells from the nest at hatching (Chapter III). To clarify uncertainty in nest fate, I used flotation of eggs to determine stage of incubation (Rahn and Ar 1974, Van Passen et al. 1984, Alberico 1995). If a nest was found after laying was completed and subsequently disappeared, I compared the date it was last seen with the estimated stage of incubation and predicted hatching date. Egg buoyancy was a good predictor of stage of incubation, the number of days of incubation could be estimated with an error of ±2-3 d if the nest was found within the first week after laying (Figure II-1). This accuracy is comparable to float curves for other shorebirds (Van Paassen et al. 1984).

All tests were two-tailed and considered significant at probability levels less than ∝=0.05. Means are presented ±1SD.

Figure II-1. Changes in the buoyancy of sandpiper eggs during incubation. Day 0 is the estimated date of laying for the last egg; it was determined from either observations during egg-laying or by back-dating from the date of hatch. Observers recorded the angle between the centre axis of the egg and the bottom of the float cup. Numbers above each bar indicate the sample size of eggs, the totals are based on 90 visits to 71 Western Sandpiper nests and 80 visits to 64 Semipalmated Sandpiper nests. The egg that was flat on day 6 was probably infertile.
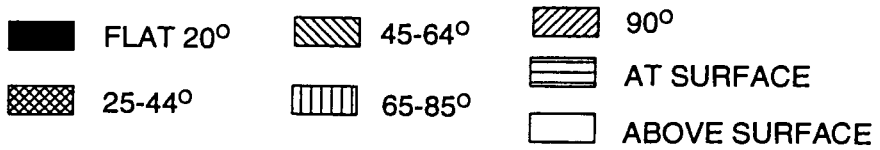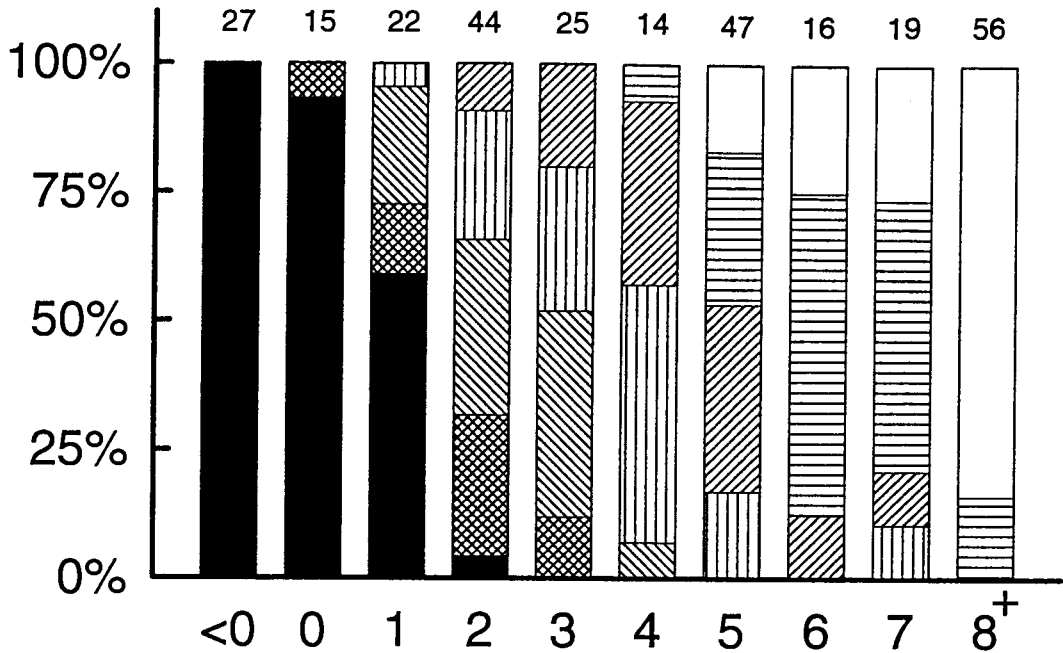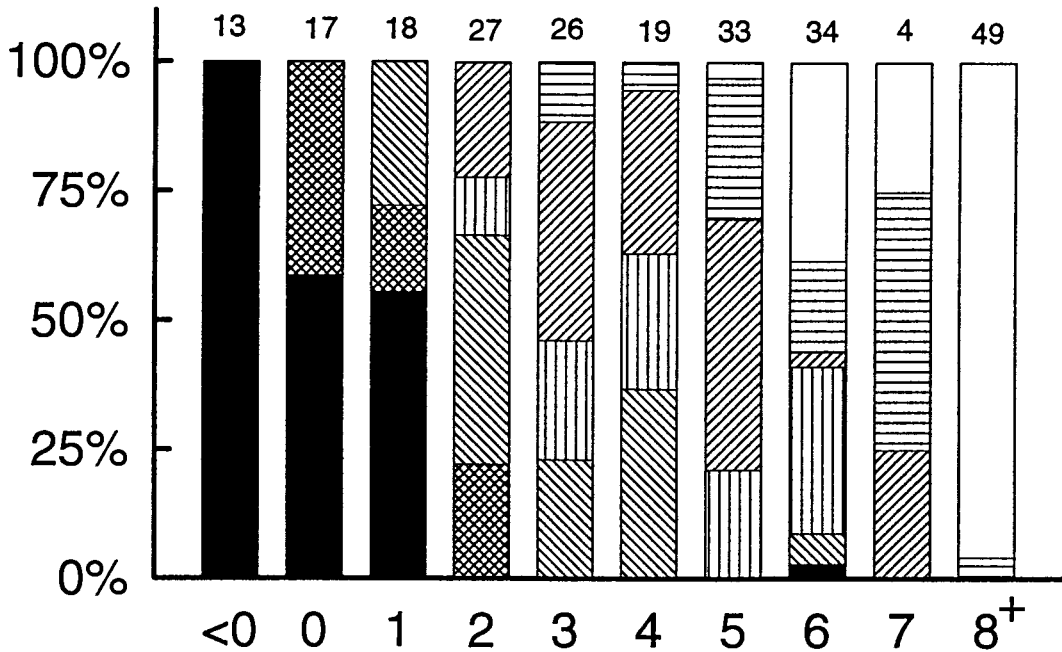
Results

Sandpiper nests were usually found after laying was completed (Western: 79.3%, n=164, Semipalmated: 85.8%, n=183). Most of the clutches found during laying that eventually contained four eggs were discovered when the clutch was almost complete (Western, 1-egg: 7.4%, 2-egg: 25.9%, 3-egg: 66.6%, n=27; Semipalmated, 1-egg: 5.5%, 2-egg: 33.3%, 3-egg: 61.1%, n=18). Nests found early in laying were more likely to have a laying schedule that included visits where there was no new egg (100% of nests found at 1-egg, n=3; 63.6% of 2-egg nests, n=11; 25.0% of 3-egg nests, n=24; Fisher's exact test, P<0.01 [pooling 1- and 2-egg clutches]). In the following laying schedules, numbers indicate days where new eggs were found during nest visits. A dash indicates a day where egg number was unchanged in Western (1-2-34, n=1; 12-3-4, n=1; 2-3-4 ,n=1; 2-34, n=2; 23-4, n=1; 234, n=2; 3-4, n=4; 34, n=10) and Semipalmated Sandpipers (1-2-34, n=1; 2-34, n=1; 23-4, n=2; 234, n=2; 3-4, n=2; 34, n=8). The days that eggs were not found did not appear more frequently towards either the start or end of laying.

The estimates of the minimum interval between two sequential eggs in Western (mean=23.1 h ±3.2, range=17.7-28.5 h, n=12) and Semipalmated Sandpipers (mean=24.1 h ±5.0, range=17.2-31.4, n=8) were sometimes as high as 30 h. The estimates of the mean minimum interval between three sequential eggs were as high as 36 h in Western (mean=30.5 h ±5.8, range=23.4-36.4 h, n=6) and Semipalmated Sandpipers (mean=28.6 h ±7.2, range=23.9-36.9 h, n=3). Both estimates were based on a sample of 16 nests that included visits where no new egg was found.

Length of incubation was significantly shorter in Semipalmated Sandpipers (mean=20.3 d ±1.0, n=7) than Western Sandpipers (mean=21.5 d ±0.5, n=12, Mann-Whitney test, U=7.8, P<0.01). There was no significant difference between the two species in the duration of hatching (all tests, P>0.05). The elapsed time between hatching of the last chick and the different stages of hatching (both species pooled) were: tapping eggs 71.5 h ±42.6 (n=16), star-pipped eggs 53.0 h ±26.6 (n=51), hole-pipped eggs 28.1 h ±19.9 (n=18), and wet chicks 13.7 h ±5.7 (n=16).

I examined the success rate (hatched vs. depredated) of nests laid before and after the mean annual laying dates. Abandoned clutches were not included in the totals because few nests were deserted each year (Western, n=0-7; Semipalmated, n=0-2). In Semipalmated Sandpipers, the success rate of early nests (60.0%, n=105) was significantly higher than that of late nests (22.9%, n=70, Fisher's exact test, P<0.001). The success rate of early Western Sandpiper nests (68.2%, n=88) was also higher than late nests (47.3%, n=55) but the difference was not significant (Fisher's

exact test, P=0.15). The pattern was the same in all years, and similar conclusions were reached if survival rates were calculated with the Mayfield method.

Discussion

Egg-laying rates

Western and Semipalmated Sandpipers at Nome took 5 d to lay a 4-egg clutch, and there were often days when no new egg was found. In contrast, Holmes (1972) observed laying schedules at seven Western Sandpiper nests at a more southerly site in coastal Alaska, and concluded that the laying intervals averaged 24-25 h. Estimates of laying intervals between eggs in Semipalmated Sandpipers range from less than 24 h (n=1, Norton 1972), 1 egg/d or 24 h (n=4, Ashkenazie and Safriel 1979), and up to 32 h (Gratto-Trevor 1992). In a study of Semipalmated Sandpipers in Manitoba, C.L. Gratto-Trevor (unpubl.) found that 72% of nests (n=25) discovered at the 1-egg stage had a laying schedule (1234) consistent with a laying interval of 24 h. In the remaining nests (28%), no new egg was found after the first (1-234) or second egg (12-34) was laid.

Gaps in laying schedules may be due to the time of day a nest visit occurs, to a fixed laying interval that is greater than the visitation rate, or to skipped days where an egg is not laid (Schubert and Cooke 1993, Wiebe and Martin 1995). An apparent gap would be found if a new egg was laid after the observer's daily visit. A 24-h visitation rate is an unlikely explanation for laying gaps in this study because I never observed an increase of two eggs after a visit where there was no new egg. Furthermore, I used the same methods and visitation rates as C.L. Gratto-Trevor (unpubl.), but we found that the laying rates in two populations of Semipalmated Sandpipers were different.

The laying schedules and estimates of laying interval I observed in Western and Semipalmated Sandpipers are consistent with a fixed interval greater than 30 h. In other shorebirds, the time between consecutive eggs is usually greater than 24 h. Estimates include 23-26 h (phalaropes, Kagarise 1979, Colwell and Oring 1988), 30 h (n=17, Least Sandpiper *C. minutilla*, Miller 1983), 32 h (n=6, Temminck's Stint *C. temminckii*, Breiehagen 1989), 36 h (n=8, Curlew *Numenius arquata*, Mulder and Swaan 1992), 46 h (n=15, Greenshank *Tringa nebularia*, Nethersole-Thompson and Nethersole-Thompson 1979) and 47 h (n=1, Long-billed Curlew *N. americanus*, Allen 1980). However, Western and Semipalmated Sandpipers may have had gaps in their laying schedules if the laying interval was 24 h but females occasionally skipped a day. Indeed, several of the above studies noted that laying gaps were sometimes greater than 48 h (Miller 1983, Colwell and Oring 1988, Breiehagen 1989). Daily visits are not adequate to test conclusively between the last two explanations, and this question warrants further research.

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It was surprising that the more northerly population of Semipalmated Sandpipers at Nome, Alaska (64°N) had slower egg-laying rates than birds breeding at La Pérouse Bay, Manitoba (58°N). This is the opposite of Dunlin which have faster egg-laying rates at Barrow, Alaska (72°N, 1 egg/d or 24 h, Holmes 1966) than in Finland (62°N, 36 h, Soikkeli 1967). However, slow rates of egg-laying are consistent with two other aspects of Semipalmated Sandpiper reproduction at Nome. This population is unusual in that females often produce clutches of less than four eggs and rarely renest (Chapter IV). Interpopulation differences in the fecundity of this species may be related to differences in timing of breeding (birds at Nome nest 3-4 wk earlier than birds at other sites, Gratto and Cooke 1987, Chapter IV), or to site-specific nutritional constraints on females during egg production.

Length of incubation

Incubation averaged 21 d in Western Sandpipers and 20 d in Semipalmated Sandpipers, which is consistent with previous reports (Holmes 1972, Ashkenazie and Safriel 1979, Gratto-Trevor 1992). Length of incubation in other calidrine sandpipers varies from 20 d (n=5, Least Sandpiper, Miller 1983), 21 d (n=6, Temminck's Stint, Breiehagen 1989), 21-22 d (n=23, Dunlin, Soikkeli 1967) to 22 d (n=1, White-rumped Sandpiper *C. fuscicollis*, Parmelee et al. 1968). Interspecific variation in shorebird laying intervals and length of incubation is probably related to variation in egg size, all of these factors are also positively correlated with body size (Rahn and Ar 1974, Sæther et al. 1986).

Nest attendance (and possibly incubation) is initiated before laying is complete in Semipalmated Sandpipers (Norton 1972, Ashkenazie and Safriel 1979) and most other shorebirds (Maxson and Oring 1980, Miller 1983, Reynolds 1987). In this study, the majority of the nests found during laying contained three eggs. If the probability of finding a nest is proportional to the amount of time parents tend the nest (cf. Wiebe and Martin 1995), my observations indicate that some Western Sandpipers also begin attending the nest during laying.

Hatching chronology

I found that sandpiper young usually finished hatching about 3 d after they had begun tapping on the eggshell. Past estimates of hatching duration in Western Sandpipers (24 h, Holmes 1972) and Semipalmated Sandpipers (24 h, Ashkenazie and Safriel 1979) appear to have been calculated from the hatching of the first egg to the last egg. If so, they are comparable to my estimates of 28 h for the hatching of nests with hole-pipped eggs. In a comparative study of other calidrine sandpipers, Norton (1972) also found that hole-pips preceded hatching by 12-48 h. The total time required by

sandpiper young to emerge from eggs is longer than previously recognized. Future studies should be explicit in defining how estimates of different hatching stages are measured.

Nesting success

Predation on the nests of both sandpiper species increased as the breeding seasons progressed at Nome. Western Sandpipers had higher nest success because they tended to breed earlier than Semipalmated Sandpipers (Chapter IV). In contrast, nest predation rates decreased seasonally in Ringed Plovers (*Charadrius hiaticula*, Pienkowski 1984) and Red-necked Phalaropes (*Phalaropus lobatus*, Reynolds 1987). Rates of nest predation in arctic shorebirds are often linked to numbers of predators and their alternate prey (Pienkowski 1984, Underhill et al. 1993, Gratto-Trevor 1994). Microtine rodents were not observed at Nome, but foxes (*Alopex lagopus*, *Vulpes vulpes*), jaegers (all *Stercorarius* spp.), and Sandhill Cranes (*Grus canadensis*) were present. Nest predation may have increased seasonally because predator encounter rates and activity were affected by the cumulative number of initiated clutches. Pienkowski (1984) argued that nest predation declined because the availability of other prey increased. Despite many hours afield, we rarely observed predator encounters with nests of any bird. Alternately, late-nesting sandpipers may have suffered higher predation rates because they were younger or more inexperienced birds. Late-breeding sandpipers at Nome are usually new birds that are unbanded (Chapter IV), but whether their nests were more vulnerable is unknown.

Shorebird numbers are affected by variation in productivity (Ryan et al. 1993), but variable nesting success should not have a major effect on population size because adult survival rates are high in shorebirds (Evans 1991, Sandercock and Gratto-Trevor 1997). Recent population models support this notion, and show that sandpiper numbers are most sensitive to changes in the rates of adult mortality (Hitchcock and Gratto-Trevor 1997).

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Chapter III

Egg-capping and Eggshell Removal by Western and Semipalmated Sandpipers

Abstract. Shorebirds are unusual among nidifugous birds in that they remove eggshells from the nestbowl at hatching. I found that fragments of shell from hatched eggs smothered later-hatching young in 1.6-3.0% of sandpiper nests, and affected the hatchability of 0.4-0.8% of the eggs. Parents carried eggshells at least 20 m from the nestbowl, which suggests that nest conspicuousness and the risk of clutch loss is important (the predation hypothesis). Shorebirds may suffer a greater risk of egg-capping than waterfowl and grouse. Sandpipers lay conical eggs and have a peculiar mode of hatching that produces eggshell fragments that are often irregular in shape. Removal of eggshells could be adaptive in sandpipers if it reduces the risk of hatching interference (the egg-capping hypothesis).

Introduction

Parents of birds with nidicolous young that remain in the nest after hatching generally remove eggshells from the nest after the chicks emerge from the eggs. In contrast, birds with nidifugous young usually leave eggshells and unhatched eggs in the nest when the brood departs on the day of hatching. Shorebirds (Suborder Charadrii) are a curious exception to this pattern. Despite having well-developed precocial young that leave the nest soon after hatching, many shorebirds remove shells of hatched eggs from the nest (e.g. Red Knot *Calidris canutus*, Whitfield and Brade 1991; White-rumped Sandpiper *C. fuscicollis*, Parmelee 1992; Buff-breasted Sandpiper *Tryngites subruficollis*, Lanctot and Laredo 1994; Black-necked Stilt *Himantopus mexicanus*, American Avocet *Recurvirostra americana*, Sordahl 1994).

Tinbergen et al. (1962) suggested five reasons that parents might remove eggshells: *i*) if sharp shell edges injure chicks, *ii*) if shells from hatched eggs interfere with brooding, *iii*) if material on remaining shells increases the risk of bacterial infection, *iv*) if the white linings of eggshells from hatched eggs increase the conspicuousness of the nest to a predator (here called the predation hypothesis), or *v*) if the shells from a hatched egg can become affixed to a later-hatching egg, forming a double shell layer that a pipping chick cannot break through (here called the egg-capping hypothesis, Derrickson and Warkentin 1991, Arnold 1992). The first three explanations seem unlikely for shorebirds because the young do not remain long in the nest. In this paper, I evaluate the predation and egg-capping hypotheses as explanations for parental removal of eggshells at hatching by Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*C. pusilla*).

Methods

Observations on eggshell removal and egg-capping were conducted as part of an ongoing study of the reproductive biology of Western and Semipalmated Sandpipers near Nome, Alaska (64°20'N,

164°56'W). Field workers intensively searched for nests by walking on the tundra and observing the behavior of flushed birds. Stage of incubation was estimated by floating eggs in water (Chapter II); nests were revisited daily close to the expected hatching date.

Results

Eggs that were known to have been broken during incubation disappeared from the nest (n=3 nests); presumably because the parents removed them. Repeated visits to the nests during hatching showed that eggshells were sequentially removed from the nestcup as the young emerged from the eggs. A few tiny fragments produced during pipping were usually left in the debris of the nest. Eggshells were never found near the nestcup; parents observed removing eggshells (n=4 nests) flew with them at least 20 m from the nest. Shells from hatched eggs were occasionally found on the study area, but not near known nest locations. Eggs that failed to hatch (possibly infertile) were abandoned in the nestcup by Western (21 of 248 eggs [8.5%] in 19 of 66 nests [28.8%]) and Semipalmated Sandpipers (16 of 238 [6.7%] eggs in 14 of 62 nests [22.6%]).

In the three years of this study (1993-1995), egg-capping was observed in both Western (2 of 248 eggs [0.8%] in 2 of 66 nests [3.0%]) and Semipalmated Sandpipers (1 of 238 eggs [0.4%] in 1 of 62 nests [1.6%]). In a 6-year study (1976-1979, 1994-1995) at Cape Espenberg, Alaska (66°30'N, 163°30'W), D. Schamel (unpubl.) detected egg-capping in Semipalmated Sandpipers (1 of 202 eggs [0.5%] in 1 of 55 nests [1.8%]) but not Western Sandpipers (0 of 208 eggs in 0 of 59 nests). Only nests that were known to have hatched eggs are included in the totals. In one Western Sandpiper nest, the rounded end of an eggshell from a hatched egg was attached to the rounded end of a later-hatching egg. In the two Semipalmated Sandpiper nests, a fragment from the conical end of an egg adhered to the rounded end of another hatching egg. In these three cases, the chicks had reached an advanced stage of hole-pipping but failed to hatch, presumably because the presence of the additional shell fragment smothered the emerging young. In the second Western Sandpiper nest, the capping shell fragment was removed by an observer from the encapsulated egg; the egg subsequently hatched normally.

Discussion

Removal of eggshells has been previously observed in both Western (Wilson 1994) and Semipalmated Sandpipers (Gratto-Trevor 1992) but egg-capping has not been reported for any shorebird. Arnold (1992) found that egg-capping had little effect on the hatchability of American Coot (*Fulica americana*) eggs, but in this study it clearly had a detrimental effect because it killed three sandpiper chicks.

The rates of egg-capping I observed are similar to those reported for other birds (ca. 2% of nests, Derrickson and Warkentin 1991, Arnold 1992). It is possible that I could have underestimated the rates of egg-capping if parents had perceived a capped egg to be broken and removed it from the nest. This seems unlikely because rejection of broken eggs declines close to hatching in other birds (Kemal and Rothstein 1988) and because failed eggs were left in the nest. Although rates of egg-capping appear to be low, this phenomenon could act as a selective pressure because it directly affects parental fitness.

If the egg-capping hypothesis was the sole explanation for removal of eggshells, parents might move the shells just a short distance from the nestcup. Instead, shorebirds remove eggshells far from the nest (Whitfield and Brade 1991, Parmelee 1992, Sordahl 1994, this study), which is consistent with the predation hypothesis. Nonetheless, many ground-nesting birds that do not remove eggshells from their nests use the same habitats as shorebirds and are exposed to the same predators. For example, Willow Ptarmigan (*Lagopus lagopus*) nest sympatrically with Western and Semipalmated Sandpipers, and all of these birds can suffer high rates of nest depredation (e.g. Martin et al. 1989, Chapter II).

The predation hypothesis does not seem sufficient to explain why eggshell removal has evolved in shorebirds but not in other birds with nidifugous young. Predation risk increases close to nest departure in some birds (Redondo and Castro 1992), but usually as a function of increased begging by the young. It is unlikely that predation risk at hatching is higher for shorebirds. Shorebird young are similar to grouse and waterfowl young in that they usually remain in the nest for no more than 24 hours, and escape the risk of the site by leaving quickly. Like most precocial young, sandpiper chicks have a large cloacal yolk sac (B.K. Sandercock, pers. obs.) which probably minimizes their activity because they do not need to feed immediately. Further, although shorebirds generally react to humans as if they are a potential threat to their nest (Reid and Montgomerie 1985), some sandpipers have been observed to remove eggshells in the presence of an observer (Parmelee 1992, this study).

Risk of egg-capping could influence eggshell removal. If parents did not remove eggshells, the rate of egg-capping would presumably increase with clutch size and the degree of hatching asynchrony (Derrickson and Warkentin 1991). If the rate of egg-capping is a function of number of eggs, grouse and waterfowl would be more likely to remove eggshells because they lay larger clutches than shorebirds (Winkler and Walters 1983). In these three groups of birds, the young hatch

relatively synchronously (typically over 0.5-1 d) because incubation is usually initiated close to the completion of laying.

Shorebirds may be more susceptible to egg-capping because they differ from grouse and waterfowl in the shape of their eggs and mode of hatching. Grouse and waterfowl have eggs that are typically ovate. Their chicks hatch as follows: from a holepip the chick chips a lateral ring in the side of the shell by rotating its head, once it has broken about two-thirds of the shell the egg cap is pushed away (Bond et al. 1988). This mode of hatching has been termed symmetrical because the resulting eggshell fragments are round. In contrast, shorebirds have conical pyriform eggs, a shape that may be an adaption for incubation efficiency (Andersson 1978). Scolopacid chicks have egg teeth on both the upper and lower mandible (Jehl 1968). From a holepip, the chick does not rotate but produces a longitudinal slit which it rips by convulsing; the eggshell fragments are asymmetrical and irregular in shape (Wetherbee and Bartlett 1962, Bond et al. 1988).

I suggest that the risk of both egg-capping and predation have contributed to the evolution of eggshell removal in shorebirds. The large irregular-shaped eggshell fragments left from hatched shorebird eggs could pose a higher risk of interference than the small neatly pipped caps from grouse and waterfowl eggs. In this study, different portions of eggshell were responsible for hatching mortality in each of the capped sandpiper eggs. Risk of predation may contribute to eggshell removal by compelling the parents to carry the fragments far from the nest.

Additional reports of eggshell removal in other shorebirds and experimental manipulation of this behavior are necessary to further assess the relative importance of egg-capping and predation. Red-necked Phalaropes (*Phalaropus lobatus*) leave large eggshell fragments in the nest after hatching (B.K. Sandercock, pers. obs.); the risk of egg-capping could be lower if the mode of hatching is different. Moreover, Black Oystercatchers (*Haematopus bachmani*) remove eggshells only a short distance (<25 m) from the nest (Andres and Falxa 1995), in this species, the risk of predation may be low. To test the egg-capping and predation hypotheses in shorebirds, eggshells could be placed at varying distances from artificial nests and natural nests during hatching; control nests could be sham-visited. The predation hypothesis suggests that artifical nests with eggshells should be depredated more often than controls; the egg-capping hypothesis would be supported by no difference between treatments. If a shorebird's propensity to remove eggshells declined slowly with increasing distance (as a function of detection risk), the predation hypothesis would be strengthened. Alternately, the egg-capping hypothesis predicts that parents should quickly remove eggshells put in the nestcup but ignore those placed any distance from the nest.

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Chapter IV

Seasonal Declines in the Reproductive Effort of Arctic-Breeding Sandpipers: Different Tactics in Two Birds With an Invariant Clutch Size

Unpublished manuscript

Abstract. Clutch size, egg size and timing of clutch initiation were examined in Western and Semipalmated Sandpipers breeding at Nome, Alaska. Two features of the fecundity of these arctic-breeding shorebirds were unusual. First, despite the constraints of a short breeding season and a putatively invariant clutch size, there were seasonal declines in the reproductive effort of both sandpipers. Breeding was relatively synchronous (80% of the nests were initiated within 7-19 d), and four-eggs was the modal clutch size in all years. However, two and 3-egg clutches were also laid by both species (7.6-34.5% of all nests), and these clutches were initiated significantly later (6-8 d) and contained smaller eggs (2.9-3.5%) than 4-egg clutches. Small clutches were not renesting attempts, and were not caused by disturbance during laying or partial clutch loss. This is one of the first reports of a seasonal decline in the clutch size of a bird that usually lays an invariant number of eggs.

Second, the two sandpiper species tended to adjust different components of their reproductive effort. Western Sandpipers usually laid four eggs, and egg size in 4-egg clutches declined significantly with timing of laying in three of four years. In contrast, Semipalmated Sandpipers had a significantly smaller clutch size than Western Sandpipers, and there were no seasonal changes in the egg size of females laying 4-egg clutches. Semipalmated Sandpipers may reduce clutch size instead of egg size because their eggs are near the minimum size necessary to produce viable precocial young.

Four explanations for the seasonal declines in fecundity were tested. The data did not support the tradeoff or nutrient-reallocation hypotheses, and 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 weakly related to female age and familiarity with a mate, but not to female body condition.

Introduction

Reproductive effort has many components, but all animals are expected to evolve tactics which maximize their reproductive fitness. Important life-history traits in birds include: timing of breeding, breeding frequency, clutch size and egg size. In temperate or arctic regions, avian young produced early in the breeding season have higher survival and are more likely to recruit (Cooke et al. 1984, Daan et al. 1988, Perrins and McCleery 1989, Hochachka 1990). Furthermore, number of breeding attempts and clutch size should have a direct effect on the number of potential recruits. Residual egg size (controlling for parent quality) has a positive effect on offspring fitness in a range of bird species

(Bolton 1991, Amundsen et al. 1996, Dawson and Clark 1996), presumably because big eggs produce structurally larger young and/or young that have greater nutrient reserves (Williams 1994).

Variation in reproductive effort is usually considered to be an adaptation to variation in environmental conditions (Drent and Daan 1980). Experimental studies have shown that food supply often affects phenotypic variation in timing of breeding, and to a lesser extent, clutch and egg size (Rohwer 1992, Svensson 1995). Life-history theory predicts there should be genotypic interactions among the components of fecundity because of differential allocation of resources during reproduction (Roff 1992). For example, seasonal declines in clutch size are ubiquitous among birds (Klomp 1970, Rohwer 1992). Several hypotheses have been advanced to explain this phenomenon (Murphy 1986, Rohwer 1992), but the most widely accepted explanation is that seasonal declines in offspring survival outweigh the benefit of accumulating resources for additional eggs (Drent and Daan 1980). To better understand interactions among timing of laying, clutch size and egg size, it may be useful to examine birds where these aspects of fecundity are constrained.

Migratory shorebirds that breed in the arctic are a good example of a group with highly constrained reproductive effort. First, 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 may be necessary if migrants are to successfully reach distant wintering areas (Myers 1981, Reynolds and Székely 1997). Second, most arctic-breeding shorebirds lay a fixed clutch size of four eggs (Maclean 1972). The factors that determine shorebird clutch size are unclear, but appear to be unrelated to incubation capacity (Székely et al. 1994a, Chapter V). Birds that are unable to adjust reproductive effort by varying timing of laying or clutch size may be more likely to adjust egg size (e.g., Birkhead and Nettleship 1982). The heritability of egg size is high in many birds (Väisänen et al. 1972, Boag and van Noordwijk 1987), however, and genetic factors may account for most of the phenotypic variation in this trait. In this paper, I compared the reproductive effort of two arctic-breeding shorebirds: the Western Sandpiper (*Calidris mauri*) and the Semipalmated Sandpiper (*C. pusilla*). My objectives were: *i*) to examine the variation in timing of laying, egg and clutch size, *ii*) to measure the covariation among these three reproductive traits, and *iii*) to identify the factors that lead to seasonal variation in fecundity.

Methods

Study site and species

The nesting 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 see Baker 1992), but were easily distinguished during the breeding season by their plumage colouration 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). Nests were found on low, dry ridges close to shallow tundra ponds, and both species used the same habitats at my study site. Females laid eggs in a scrape on the ground, and both sexes incubated.

Estimation of reproductive parameters

Nests were located by searching the tundra and observing sandpiper behavior. Incubating birds flushed from the nest at short distances and used distraction displays to lead the observer away. If the clutch was not found immediately after a 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 stake 10 m from the nestcup. If a clutch contained less than four eggs when first discovered, field workers 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 buoyancy of the eggs was recorded. Nests were visited every 6-7 d during incubation and then daily close to the estimated hatching date. Clutch size was adjusted during incubation in some cases (Chapter V), but I used unmanipulated nests to estimate rates of partial clutch loss.

Laying rates of both species at Nome were 0.8 eggs/day. The duration of incubation averaged 20 and 21 days in Semipalmated and Western Sandpipers, respectively (Holmes 1972, Gratto-Trevor 1992, Chapter II). Date of clutch initiation was calculated by backdating from: *i*) the observed egg-laying schedule, *ii*) date of hatching, or *iii*) stage of incubation (determined from buoyancy of the eggs, Chapter II).

Egg length (L) and breadth (B) were measured by opening a pair of calipers until the egg passed between the tips. In a subsample of the eggs, egg volume was measured directly by water displacement in a volumeter (Székely et al. 1994b). The coefficient of egg shape (k, from k=V/LB² ,

Hoyt 1979) was determined to be 0.47 in both sandpiper species (B.K. Sandercock, unpubl data). I used these estimates of k to calculate volume from the egg length and breadth. A complication in studies of egg size is that eggs from one female are not independent observations, and repeatability of egg size was high in both species (B.K. Sandercock, unpubl.). To cope with this problem, all analyses were based on the mean egg volume of each clutch.

Handling of birds

Sandpipers were captured with walk-in traps placed over the clutch during incubation. Both parents were usually captured on every nest, and each bird was individually marked with combinations of coloured leg bands and a numbered metal band. I recorded the identity of mated pairs, and determined familiarity with a mate by comparing associations in consecutive years.

During handling of birds, field workers measured exposed culmen (tip of the bill to the edge of the shield), tarsus bone (notch behind the leg joint to the wrist of the foot) and flattened wing chord. I used Principal Component Analysis to calculate an index of body size from morphometrics recorded during the first handling occasion each year. The first principal component (PC1) explained 47.0-50.5% of the variation in females; the residuals of body mass on PC1 were used as size-independent measure of body condition (after Piersma and Davidson 1991).

Most Western Sandpipers were sexed by culmen length ($\male\male$ <24.2 mm, $\female\female$ >24.8 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 (<8% of possible cases, B.K. Sandercock unpubl.). Nonetheless, several additional criteria (courtship behaviour, palpitation of eggs, rates of breeding dispersal) indicate this approach is generally accurate for this species (Sandercock and Gratto-Trevor 1997, B.K. Sandercock unpubl.).

I attempted to age Western and Semipalmated Sandpipers with several techniques. It was impractical to use returns of banded young to age birds because few young were ever recaptured on the study area. Partial wing moult has been used to identify yearling Semipalmated Sandpipers in eastern North America (Gratto and Morrison 1981), but few birds were captured at Nome in this condition. In 1996, Western Sandpipers were aged by the colouration of the inner tertial and wing coverts. In yearlings, edges of these feathers are buff or chestnut whereas in adults the edges are white. This technique has been successfully used to age wintering Western Sandpipers (P.D. O'Hara,

unpubl.) and Dunlin (*C. alpina*, Page 1974, see also Prater et al. 1977). At Nome, 2/2 known yearlings and 6/6 known adults were correctly identified to the appropriate age class.

Data analysis

Rates of partial clutch loss were estimated using the Mayfield method (Mayfield 1975, Johnson 1979). All other statistics were calculated using the conventional procedures of SAS (SAS Institute 1990). Tests were two-tailed and considered significant at probability levels less than $\alpha=0.05$. 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 IV-1). One Western Sandpiper clutch of seven eggs was found in 1993; this unusual clutch was not considered further because two females may have used the same nestcup. There was no significant annual variation in clutch size within either species, but the annual variation was significant in a pooled analysis (Table IV-1). Female sandpipers produced more 2- and 3-egg clutches in 1994, and overall, Semipalmated Sandpipers had a significantly smaller clutch size than Western Sandpipers (Table IV-1).

Few renesting attempts were found during this study (Western 4 of 238 nests [1.7%], Semipalmated 1 of 208 [0.5%]). All renests were found close to the site of the first nest (mean distance: 77.0 m $\pm$27.2SD, n=5). Three Western Sandpiper females were captured on two nesting attempts: two females switched mates to renest and one remained with the same mate. The first nests of these females were depredated soon after the start of incubation (7.7 d $\pm$5.8SD, n=3) and the interval before renesting was short (6.6 d$\pm$3.4SD, n=3). Two females laid four eggs in both nesting attempts, and one female laid four and then three eggs. The renests were not included in the other analyses.

Clutches of fewer than four eggs might be expected if disturbance during laying caused females to deposit eggs outside of the nestbowl. Two and 3- egg clutches were found during laying more often (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).

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Table IV-1. Clutch size distributions of Western and Semipalmated Sandpipers breeding at Nome, Alaska[a]. 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	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
Statis-tics	Year $F_{3,220}=1.76$, P=0.16				Year $F_{3,201}=2.12$, P=0.10			

[a] Overall comparison with a two-way ANOVA: Species: $F_{1,421}=4.41$, P=0.04; Year: $F_{3,421}=3.74$, P=0.01; Species x Year: $F_{3,421}=0.17$, P=0.92.

Clutches of fewer than four eggs might also be expected if some eggs were partially 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 estimate of daily survival rate [d.s.r]=1). Most nests were found soon after incubation had started (Western 2.11±4.50SD d, n=214; Semipalmated 3.00±4.99SD d, n=195). Egg loss during incubation was rare (Western 4 losses in 1957.5 d of exposure, d.s.r.= 0.998± 0.001SE; Semipalmated 7 losses in 1728.5 d of exposure, d.s.r.= 0.996±0.002SE). I used these estimates to calculate the expected frequency of 2- and 3-egg nests (Western 1.0, Semipalmated 2.5). The observed number of 2- and 3-egg nests (Table IV-1) was significantly higher than these values (Western G_1=115.6, P<0.001, Semipalmated G_1=154.2, P<0.001), indicating that the variation in clutch size cannot be explained by partial clutch loss.

Variation in the timing of clutch initiation

Timing of laying was synchronous: 80% of the clutches were usually initiated within a two week period (range: Western 9-18 d; Semipalmated 7-19 d). In both sandpiper species, there was a highly significant difference between 2- or 3-egg and 4-egg clutches in laying date. Females that laid small clutches initiated their nests 6-8 days later than females that produced 4-egg clutches (Table IV-2). There was significant annual variation in the laying date of Western Sandpipers, but not Semipalmated Sandpipers (Table IV-2).

Variation in egg size

There was a significant difference between 2- or 3-egg and 4-egg clutches in mean egg volume (Table IV-3). Eggs in the 2- and 3-egg clutches were 2.9% (Western) and 3.5% (Semipalmated) smaller than eggs in 4-egg clutches. There was no annual variation in the egg volume of Western or Semipalmated Sandpipers (Table IV-3).

To further investigate the relationship between egg volume and laying date, I controlled for clutch size and limited the sample to 4-egg clutches (Figure IV-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, Figure IV-1). The egg volume of Semipalmated Sandpipers increased significantly in one year, but was otherwise unaffected by the timing of laying (Figure IV-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 x 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;

Table IV-2. Timing of clutch initiation in relation to the clutch size of Western and Semipalmated Sandpipers. Mean julian date [152=Jun 1]±1SD (*n* of nests).

Year	Western Sandpiper		Semipalmated Sandpiper	
	2-3 eggs	4 eggs	2-3 eggs	4 eggs
1993	151.5±0.7 (2)	143.9±2.9 (40)	151.9±6.0 (8)	144.6±4.2 (53)
1994	147.9±5.5 (8)	139.7±4.1 (48)	152.0±3.3 (19)	147.3±5.6 (36)
1995	153.8±9.3 (5)	143.7±6.6 (44)	155.5±6.4 (8)	146.5±6.0 (46)
1996	147.0±7.0 (3)	142.5±5.4 (59)	152.5±0.7 (2)	149.0±2.7 (22)
Total[a]	7.1±6.4 (18)	-0.7±5.0 (191)	4.8±5.0 (37)	-1.1±5.0 (157)
Statis	Clutch size $F_{1,201}$=27.7, P<0.0001		Clutch size $F_{1,186}$=26.7, P<0.0001	
-tics	Year $F_{3,201}$=3.83, P=0.01		Year $F_{3,186}$=1.55, P=0.20	
	Clutch size x Year $F_{3,201}$=0.69, P=0.57		Clutch size x Year $F_{3,186}$=1.46, P=0.23	

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

Table IV-3. Mean egg volume (mL) in relation to the clutch size of Western and Semipalmated Sandpipers. Mean±1SD (*n* of nests).

Year	Western Sandpiper		Semipalmated Sandpiper	
	2-3 eggs	4 eggs	2-3 eggs	4 eggs
1993	6.60±0.52 (4)	7.15±0.34 (44)	6.04±0.40 (10)	6.45±0.43 (55)
1994	7.08±0.61 (11)	7.27±0.41 (49)	6.14±0.40 (19)	6.17±0.39 (38)
1995	6.95±0.51 (5)	7.17±0.46 (45)	6.31±0.19 (8)	6.38±0.36 (49)
1996	7.08±0.40 (5)	7.09±0.43 (60)	6.16±0.01 (2)	6.49±0.35(23)
Total	6.96±0.55 (25)	7.17±0.41 (198)	6.15±0.36 (39)	6.37±0.40 (165)
Statis -tics	Clutch size $F_{1,215}$=7.14, P<0.01		Clutch size $F_{1,196}$=5.43, P=0.02	
	Year $F_{3,215}$=1.75, P=0.16		Year $F_{3,196}$=1.68, P=0.17	
	Clutch size x Year $F_{3,215}$=1.18, P=0.32		Clutch size x Year $F_{3,196}$=1.99, P=0.12	

Figure IV-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.

WESTERN SANDPIPERS · SEMIPALMATED SANDPIPERS

EGG VOLUME (mL) vs. DATE OF CLUTCH INITIATION

1993 — Western: b=-0.040 *, r^2=0.11, n=40; Semipalmated: b=+0.019 ns, r^2=0.04, n=53

1994 — Western: b=-0.038 **, r^2=0.15, n=48; Semipalmated: b=-0.004 ns, r^2<0.01, n=36

1995 — Western: b=-0.017 ns, r^2=0.06, n=44; Semipalmated: b=+0.016 *, r^2=0.09, n=46

1996 — Western: b=-0.028 **, r^2=0.12, n=58; Semipalmated: b=+0.001 ns, r^2<0.01, n=22
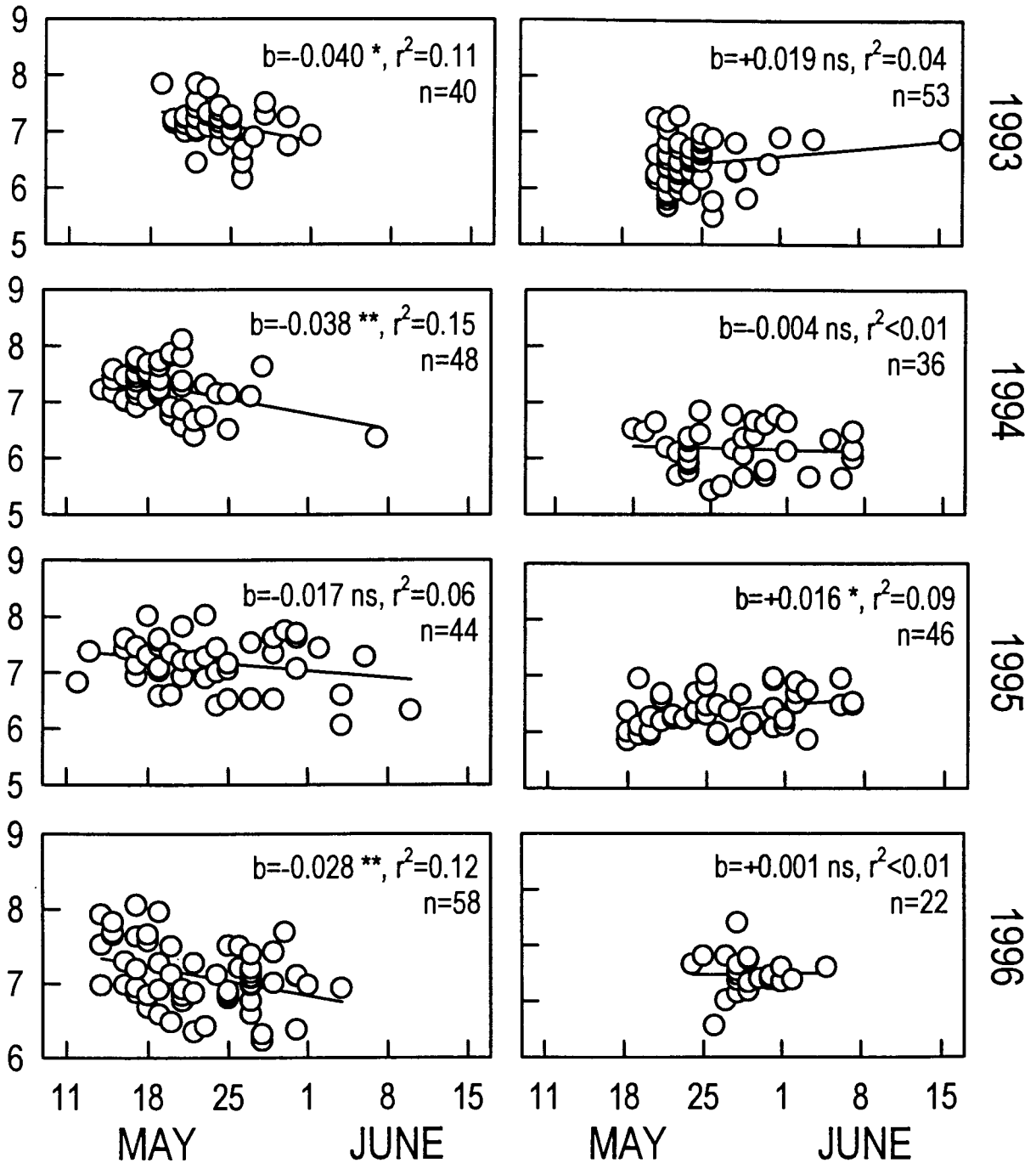
year: $F_{3,149}$=0.78, P=0.51; year x laying date: $F_{3,149}$=0.91, P=0.44). Egg size declined by 5-12% over the breeding season in Western Sandpipers.

Factors covarying with timing of clutch initiation

In Western Sandpipers, there was no significant difference between yearlings and newly settled adults in the timing of clutch initiation (Table IV-4), although yearlings nested two days later on average. Similarly, newly mated and reuniting pairs did not differ significantly in timing of clutch initiation (Table IV-4). New pairs of Western Sandpipers nested two days later than reuniting pairs but the opposite trend was observed in Semipalmated Sandpipers. Male experience with the study area had no effect on timing of clutch initiation (Table IV-4). Female Western and Semipalmated Sandpipers that had previously bred on the study area nested 4.5 and 3.5 days earlier, respectively, than birds that were captured for the first time. This difference was significant in Western Sandpipers (Table IV-4). Early breeding females did not have greater body reserves; less than 5% of variation in laying date was explained by body condition and the relationship between the two variables was not significant in any year (Table IV-5).

Discussion

The reproductive effort of Western Sandpipers and Semipalmated Sandpipers at Nome is unusual for two reasons. First, despite short and synchronous breeding seasons, there were seasonal declines in the reproductive effort 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 reproductive effort in response to the progression 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). I first consider whether the variation in clutch size is an artifact of my methodology, I then evaluate four possible explanations for the seasonal declines in fecundity, and finally, I consider the differences between the two species.

Clutch size variation in shorebirds as a methodological artifact

The clutch size variation that I observed in Western and Semipalmated Sandpipers (Table IV-1) is unusual. The frequency of 4-egg clutches ranges from 85-100% in most arctic (Mayfield 1978, Parmelee 1992, Lanctot and Laredo 1994) and temperate-breeding shorebirds (Miller 1979, Nethersole-Thompson and Nethersole-Thompson 1979, Berg 1992). Clutch size is generally four eggs in Western (Holmes 1972) and Semipalmated Sandpipers (Gratto et al. 1983, Gratto-Trevor 1992). The results of Tomkovich and Morosov (1983) are an exception: they found that only 63.4% (n=82) of Western Sandpiper nests contained four eggs at Uelen, Chukotska Peninsula, Russia.

Table IV-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 ±1SD *(n* of nests).

	Western Sandpiper	Semipalmated Sandpiper
Female age[b]		
Adult	0.8±5.5 (29)	
Yearling	2.8±2.6 (8)	
Statistics	$t_{15.8}$=-1.46, P=0.16	
Familiarity with a Mate[c]		
Remated pair	-3.9±2.9 (25)	-1.5±5.1 (33)
New pair	-1.7±5.2 (21)	-3.2±3.7 (12)
Statistics	$t_{30.5}$=1.78, P=0.09	t_{43}=-1.06, P=0.30
Familiarity with the Study Area[d]		

Female	Male		
Recapture	Recapture	-1.6±5.2 (21)	-3.2±3.7 (12)
Recapture	Band	-3.2±5.3 (18)	0.2±5.2 (5)
Band	Recapture	0.1±5.5 (25)	1.1±4.1 (16)
Band	Band	2.9±5.9 (54)	1.9±6.5 (25)
Statistics		Female $F_{1,114}$=12.5, P<0.001 Male $F_{1,114}$=0.33, P=0.57 Female x Male $F_{1,114}$=3.78, P=0.054	Female $F_{1,54}$=3.30, P=0.07 Male $F_{1,54}$=1.58, P=0.21 Female x Male $F_{1,54}$=0.59, P=0.44

[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.

Table IV-5. Timing of clutch initiation as a function of the body condition (residuals of body mass on body size [PC1]) of female sandpipers. Slope, t-test for H_o: **slope**=0, (n of females).

Year	Western Sandpiper	Semipalmated Sandpiper
1993	-0.26 ns, (41)	-0.04 ns, (52)
	r^2=0.02	r^2<0.01
1994	-0.33 ns, (51)	0.86 ns, (52)
	r^2=0.02	r^2=0.05
1995	-0.84 ns, (43)	-0.18 ns, (45)
	r^2=0.03	r^2<0.01
1996	-0.10 ns, (61)	-0.003 ns, (23)
	r^2<0.01	r^2<0.01
Statistics	Condition $F_{1,188}$=1.79, P=0.18	Condition $F_{1,164}$=0.23, P=0.63
	Year $F_{3,188}$=7.69, P<0.001	Year $F_{3,164}$=6.94, P<0.001
	Condition x Year $F_{3,188}$=0.56, P=0.64	Condition x Year $F_{3,164}$=0.82, P=0.48

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Researchers studying shorebirds often consider clutches of fewer than four eggs to be the result of partial nest predation. Sandpiper nests are sometimes left unattended during laying (Chapter II), and undetected egg predation should be highest at this stage. Females losing their first-laid eggs could be changing nest sites before laying a smaller clutch (Ganter and Cooke 1993). These explanations are unlikely in this study because there were no eggs lost from any of the nests that were monitored during laying. All egg losses occurred during incubation, and were presumably due to sandpipers removing broken eggs as part of nest-cup sanitation (Chapter III). Partial clutch loss was extremely rare in this study, and cannot explain the observed variation in clutch size. This is not the case at all sites: Semipalmated Sandpipers experience high rates of partial clutch loss in Manitoba (Gratto 1983).

The trend for more 2- and 3-egg clutches to be found during laying is consistent with the notion that disturbance leads to egg loss. Disturbance cannot explain, however, the differences in timing of laying and egg size that were related to clutch size. If clutches of fewer than four eggs had been produced by disturbance, the difference in clutch initiation should have been 0-1 d instead of 6-8 d. Small clutches may have been found during laying more often because they were produced late in the breeding season and field workers had become more efficient at locating newly initiated nests.

Clutch size variation in shorebirds has often been attributed to renesting (e.g., Pienkowski 1984) because renests sometimes contain fewer than four eggs (this study, Soikkeli 1967, Nethersole-Thompson and Nethersole-Thompson 1979, Gratto-Trevor 1992). Rates of renesting are high among shorebirds that breed at temperate latitudes (up to 2-4 times, Nol et al. 1984, Pienkowski 1984, Colwell and Oring 1988, Haig 1992), but are low among arctic-breeding species (Jehl 1973, Pienkowski 1984). The frequency of detected renests in this study (<2%) was low and is comparable to previous studies of Western (6.4%, n=78, Holmes 1971; 0%, n=82, Tomkovich and Morozov 1983) and Semipalmated Sandpipers (4.2%, n=520, C.L. Gratto-Trevor, unpubl.).

It is unlikely that renesting accounts for the seasonal decline in clutch size at Nome. The frequency of small clutches was high compared to the frequency of detected renests. Most nests were found during early incubation, and there was little opportunity for many first nesting attempts to have been completely depredated prior to discovery. Sandpipers (and other shorebirds, Berg 1992) only replaced clutches that were lost during early incubation, but the rates of total nest failure at Nome were low during the early breeding season (Chapter II). It would not have been possible to detect renesting if the birds nested unsuccessfully elsewhere and then moved onto the study area to lay a second clutch. Snowy Plovers (*Charadrius alexandrinus*) sometimes travel more than 50 km to breed a second time in one year (Stenzel et al. 1994). This species is polygamous, however, and both sexes disperse to find

new mates. Long-distance breeding dispersal has not been reported in any monogamous shorebird with a male-territorial breeding system. Renests should be more easily detected in Western and Semipalmated Sandpipers because the second nesting attempt is usually a short distance (<100 m) from the original nestcup (this study, C.L. Gratto-Trevor pers. comm., Holmes 1971).

The clutch size variation reported in this study is not likely to be the result of partial nest predation, disturbance during laying or renesting. I consider here four adaptive explanations for seasonal declines in reproductive effort.

Seasonal declines in the clutch size and egg size of shorebirds

Seasonal declines in clutch size are ubiquitous 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 (Chapter V), and Rohwer (1992) suggested that these birds should be an exception to the general pattern. For example, seabirds that lay one egg (Alcidae, Diomedeidae) obviously cannot reduce clutch size any further, although females may opt not to breed if conditions are unfavourable. The present study is one of the first to demonstrate that there can be a covariation between laying date and clutch size in a bird with a putatively invariant clutch size, and that the phenomenon of seasonal declines in clutch size is more widespread than previously thought. There are, to my knowledge, only three previous studies that have presented similar data. White-bellied Swiftlets (*Collocalia esculenta*) typically lay two eggs, but the frequency of 1-egg nests increases as their equatorial breeding season progresses (Francis 1987). Clutch size also apparently declines over the breeding season in Kentish Plovers (*Charadrius alexandrinus*, unpubl. data cited in Székely et al. 1994a), Spur-winged Plovers (*Vanellus spinosus,* Yogev et al. 1996) and Spotted Sandpipers (*Actitis macularia,* L.W. Oring, pers. comm.), although these authors did not rule out the alternate explanations considered above.

The factors leading to a maximum clutch size of four eggs in shorebirds are currently unknown (Chapter V), but this breeding tactic should restrict the ability of females to modify their reproductive effort. Several authors have suggested that birds with a fixed clutch size may cope with different environmental conditions by adjusting egg size (Miller 1979, Galbraith 1988, Grant 1991). The seasonal declines in the egg size of Western Sandpipers are consistent with this prediction. Seasonal declines in egg size have been observed in some shorebirds (Byrkjedal and Kålås 1985, Redmond 1986), and in seabirds that lay one egg (Harris 1980, Birkhead and Nettleship 1982). Many hypotheses have been offered to account for seasonal declines in clutch and egg size (Murphy 1986, Rohwer 1992), and I review here four explanations that are relevant to sandpipers.

H_1: The 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 may reduce the duration of breeding by laying fewer eggs and improve the survival of their young by laying larger eggs. That was not the case in this study, late-nesting sandpipers that produced 2- or 3-egg clutches laid smaller eggs than birds laying 4-egg clutches. Phenotypic correlations are a poor method for testing whether there are tradeoffs among the traits that contribute to reproductive success, and unfortunately, genotypic correlations are seldom available in field studies (Lessells et al. 1989). Fecundity traits may covary as a function of parental ability or territory quality, and several intraspecific studies of birds have found positive correlations between clutch and egg size (Galbraith 1988, Flint and Sedinger 1992, Wiebe and Bortolotti 1995).

H_2: 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, birds arrive on the breeding ground with limited endogenous resources. If laying is delayed, females may use nutrient reserves for body maintenance instead of egg formation. Clutch and/or egg size should decrease if environmental conditions prevent some individuals (or populations) from breeding. For example, Nol et al. (1997) reported that Semipalmated Plovers (*Charadrius semipalmatus*) showed a reduction in clutch size during a year of late spring phenology. The nutrient reallocation hypothesis was not supported in the present study, but my four years of data provide a relatively weak test of the idea. Western Sandpipers showed annual variation in laying date but there was no concomitant change in clutch size. Conversely, there was clutch size variation in Semipalmated Sandpipers, but it was not related to annual variation in the timing of laying.

The relative importance of endogenous and exogenous resources in shorebird reproduction remains unresolved. Erckmann (1983:128) argued that most shorebirds acquire all of the nutrients for egg production during the laying period. With the exception of Lapwings (*Vanellus vanellus*, Galbraith 1988, Blomqvist and Johansson 1995), however, natural food supply does not appear to have a strong effect on the egg size of most shorebirds (Nol 1989, Grant 1991). Correlations between fecundity and female body condition suggest that some shorebird species use stored, endogenous reserves for egg formation (Galbraith 1988, Blomqvist and Johansson 1995, and refs. therein, but see Nol et al. 1997). Timing of laying was not related to body condition in Western or Semipalmated Sandpipers. Residual mass could have been a poor indication of condition because birds were captured post-laying, and females may have depleted their reserves during egg production.

H_3: 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 (Chapter II), but the opposite trend has been reported in most other shorebird studies (Byrkjedal 1980, Pienkowski 1984, Reynolds 1987). Seasonal changes in the recruitment rates of shorebirds are almost impossible to assess because natal philopatry is weak (Oring and Lank 1984, Sandercock and Gratto-Trevor 1997), and return rates of young are usually low (<5%, Thompson et al. 1994). Western and Semipalmated Sandpipers are no exceptions; <3% of the nestlings banded in 1993-1995 were subsequently recaptured on the study area as breeding yearlings or adults (Chapter VII). However, Lank et al. (1985) found that the recruitment rates of Spotted Sandpipers (*Actitis macularia*) were not affected by seasonal timing. Further evaluation of this hypothesis requires the ability to track individual young for longer periods of time.

    H_4: The parent-quality hypothesis. Timing of arrival and laying are correlated in several migratory shorebird species (Soikkeli 1967, Hildén and Vuolanto 1972, Jönsson 1987), and in sandpipers (B.K. Sandercock and R.B. Lanctot, unpubl.). Western and Semipalmated Sandpipers that bred early in the breeding season laid larger clutches and bigger eggs. These results are consistent with the notion that birds of lower quality are nesting later in the breeding season. Three factors that may determine 'quality' of a breeding bird include age, experience with the breeding area and experience with a mate. Previous studies have tested these factors by using relative shorebird age (Hildén and Vuolanto 1972, Thompson and Hale 1991, Oring et al. 1994) and by comparing the fecundity of new and old pairs (e.g., Jönsson 1987). Age and experience are confounded in both instances, and I attempted to distinguish among these factors.

    In many birds, fecundity rates increase with parent age to some level (e.g., Robertson et al. 1994). These changes may be due to accumulated reproductive experience, or to age-specific breeding tactics that are based on the relative value of future reproduction (Rohwer 1992). Adult Semipalmated Sandpipers laid larger eggs and nested 2-3 days earlier than yearlings in Manitoba (Gratto et al. 1983). Gratto et al. (1983) identified yearlings by partial wing moult, but not all yearlings show this condition (Gratto and Morrison 1981). At Nome, only a few birds with partial wing moult were captured (breeding: 3 of 209 [1.4%]; migrating: 3 of 99 [3.0%]), and 3/3 known yearling Semipalmated Sandpipers were found to have replaced all of their wing feathers (B.K. Sandercock, unpubl.). Seasonal declines in the reproductive effort of Semipalmated Sandpiper could have been due to age-specific variation in fecundity, but only if yearlings were numerous and undetected. Plumage variation was a

reliable cue for identifying the age class of Western Sandpipers, and adults tended to breed earlier than yearlings. Some Western Sandpipers that were classed as adults (i.e., 2+ years of age) could have also been first-time breeders because young shorebirds sometimes remain in southern latitudes for one or more years before they make their first migration to the breeding grounds (Summers et al. 1995, Marks and Redmond 1996). Female age cannot explain all seasonal reductions in fecundity. Seasonal declines in clutch size have been documented within homogeneous age groups (Stutchbury and Robertson 1988, Rohwer 1992, Smith 1993), and it is clear that other factors are important.

Breeding site-fidelity is high among monogamous shorebirds with a male-territorial breeding system (including Western and Semipalmated Sandpipers, Sandercock and Gratto-Trevor 1997, Chapter VII). Birds returning to breed at the same site may gain two advantages: familiarity with a mate and familiarity with the local breeding area (Greenwood and Harvey 1982, Oring and Lank 1984). 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 could have included birds that were young and/or unfamiliar with the study area. When I controlled for these latter two factors, I found that experience with a partner had no effect on the timing of laying. However, the experience of female sandpipers with the study area had a significant effect on the timing of laying. I was unable to control for age in this analysis, but female Western Sandpipers bred 4.5 d earlier if they had nested on the study area before, whereas the difference between yearling and adult females was only 2 d. Therefore, experience with a local area appears to have a residual effect on female reproduction. Male experience with the study area may have had little effect on the timing of laying because clutch initiation is controlled by females.

In summary, seasonal declines in the clutch and egg size of Western and Semipalmated Sandpipers seem most consistent with variation in parent quality (H_4). Female age, experience with a mate and experience with the local area all appear to contribute to variation in timing of laying, and hence variation in clutch and egg size. The data do not support the notion that tradeoffs (H_1) or nutrient reallocation (H_2) are important. A critical test of the cost-of-delay idea (H_3) awaits development of technology that will allow researchers to follow young shorebirds as they disperse from their natal areas.

The different reproductive tactics of Western and Semipalmated Sandpipers

One question remains unresolved: why were there seasonal declines in the egg size of Western Sandpipers whereas clutch size changed in Semipalmated Sandpipers? Shorebirds, galliform birds and waterfowl all produce precocial young that leave the nest at hatching and secure their own food.

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Shorebirds include some of the smallest precocial birds (Rahn et al. 1975, Visser 1991), and calidrine sandpipers produce some of the smallest eggs of birds in this group (Sæther et al. 1986, Reynolds and Székely 1997). Surface-area to volume ratios could act as a lower boundary on the size of shorebird hatchlings because they are important in the development of homeothermy (Visser 1991). Semipalmated Sandpipers eggs were 12% smaller than Western Sandpiper eggs, and may be close to the minimum size necessary to produce 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.

Semipalmated Sandpipers nested later than Western Sandpipers, thus reductions in clutch size are consistent with the patterns of intraspecific variation in fecundity. Seasonal reductions in clutch size were surprising because Semipalmated Sandpipers at Nome start breeding a month earlier than other populations (Gratto and Cooke 1987). Birds at Nome could face greater time-constraints because they breed in the westernmost part of the species' breeding range (Gratto-Trevor 1992) and cope with longer migration distances. Although Western and Semipalmated Sandpipers have been well-studied in other areas, previous workers have not reported finding seasonal trends in either clutch or egg size. One explanation may be that the sandpipers at Nome are not closely related to other populations. There is a geographic cline in the bill morphology of Semipalmated Sandpipers, and birds breeding in western Alaska have shorter culmens than eastern birds (Harrington and Morrison 1979). Recent molecular work has also shown that populations of Western and Semipalmated Sandpipers at Nome are genetically distinct from those in other regions (Haig et al. 1997). The patterns of fecundity observed in Western and Semipalmated Sandpipers at Nome, Alaska may be best explained as adaptations to local conditions, and these factors require further examination.

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Chapter V

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.

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, 1993b). 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: *i*) energetic demands on females during egg-laying or gestation may influence the number of offspring they can produce, or *ii*) 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 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 often 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 than unmanipulated clutches, 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).

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 km² 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, Chapter II). Dates of clutch initiation and completion of laying were determined from egg-laying

schedules, or by backdating 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 if the damage occurred in early incubation.

It was difficult to match clutches of similar age because estimates of stage of incubation based on egg buoyancy were somewhat imprecise (±2 days, Chapter II). 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 (courtship displays, palpitation of eggs, rates of breeding dispersal) indicate this approach is generally accurate for this species (Sandercock and Gratto-Trevor 1997, B.K. Sandercock, unpubl.).

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: *i*) abandoned: eggs left pointing out by an observer were not rotated back into the nest for more than a week, and were consistently cold; *ii*) depredated (total nest failure): the eggs disappeared before the expected hatch date or there was signs of predator activity (fox urine, smashed eggshells); *iii*) partial clutch loss: an egg disappeared during incubation; or *iv*) successful: at least one chick was banded and left the nest. Partial clutch loss may have been caused by predators destroying eggs, but sandpipers will also remove any eggs with mechanical damage from the nest (Chapter III). 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. Sandercock, unpubl.), 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 Semipalmated Sandpipers, but Western Sandpipers deserted the experimental three-egg nests at a higher rate (Table V-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 V-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 V-1).

In both species, there was no significant difference among treatments in the rates of partial clutch loss, but losses were highest in the addition treatment (Table V-2). In Semipalmated Sandpipers, there was a significant difference among treatments in daily loss rates (Table V-2), but there was no difference between the addition and control treatments in loss rate ($\chi^2_1=0.07$, 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 V-2).

Table V-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=0.48		$\chi^2_2=0.10^a$, P=0.95		Sex: $F_{1,72}=0.13$, P=0.72; Trt: $F_{2,72}=0.23$, P=0.80			
					Sex x 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=0.044		$\chi^2_2=0.91^a$, P=0.64		Sex: $F_{1,88}=5.31$, P=0.02; Trt: $F_{2,88}=0.63$, P=0.54			
					Sex x Trt: $F_{2,88}=1.80$, P=0.17			

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

Table V-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=3.10, P=0.21	χ^2_2=6.02[a], P=0.049	G_2=0.68, P=0.71	χ^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=5.36, P=0.07	χ^2_2=2.18[a], P=0.34	G_2=1.17, P=0.56	χ^2_2=5.44[a], P=0.07

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

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 V-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 V-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 $G_2=5.16$, P=0.08; Semipalmated Sandpipers $G_2=0.38$, P=0.83). 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 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 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 (B.K. Sandercock, pers. obs.). 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 pers. comm., 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: 122) found that

Table V-3. Length of incubation, duration of hatch and hatchability 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)

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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 (ca. -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 potentially increase body reserves at a maximum rate of 1-2 g/day, R.W. Butler and T.D. Williams pers. comm.).

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 (Tab. 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 vs. 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 vs. 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 albatrosses (Rice and Kenyon 1962), some larids (Coulter 1973, Andersson 1976), 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 unsupported 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:

i) 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.

ii) 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 vs. 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 unpubl., 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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Chapter VI

Assortative Mating and Sexual Size Dimorphism in Western and Semipalmated Sandpipers

Abstract. Reverse sexual size dimorphism (females larger) is found in many shorebird species. Sexual selection could favour reverse dimorphism if: i) there is negative assortative mating for body size, and ii) reproductive effort covaries with body size but inversely for the two sexes. I tested this model in two small shorebirds that mate monogamously: Western and Semipalmated Sandpipers. Females were larger than males in both species, and the size difference between the sexes was greater in Western Sandpipers (3.6-16.3%, univariate morphometrics) than Semipalmated Sandpipers (2.0-9.0%). Mated pairs showed no correlation between female and male body size (PC1). Body size had a significant effect on timing of laying, but unexpectedly it was large males and small females that nested earlier. Large females laid larger eggs, and 9-15% of the variation in egg volume was explained by body size. The sexual size dimorphism of these two sandpiper species cannot be explained by assortative mating, and future work should examine the importance of intrasexual competition and ecological conditions during the non-breeding season.

Introduction

Sexual dimorphism is common among birds, and many hypotheses have been proposed to explain the evolution of avian body size (Jehl and Murray 1986). Shorebirds (suborder *Charadrii*) are a particularly diverse group, and the direction and magnitude of size dimorphism among these species has been shown to be related to mating system (Sæther et al. 1986) and the duration of parental care (Jönsson and Alerstam 1990). Sexual selection has presumably been important because males are larger in most polygynous species whereas females are larger in the few species with sex-role reversal. It is more difficult to explain the reverse sexual size dimorphism (females larger) that is found in monogamous shorebirds and other birds (Jehl and Murray 1986, Olsen and Cockburn 1993). Western and Semipalmated Sandpipers, for example, mate monogamously and are monomorphic in plumage but dimorphic in body size (Ouellet et al. 1973, Cartar 1984). Western Sandpipers are of particular interest because they have the greatest degree of reverse dimorphism among monogamous sandpipers (ca. 10-15%, Jehl and Murray 1986:50).

Reversed sexual size dimorphism may evolve in monogamous birds if natural or sexual selection acts such that fitness covaries positively with body size for females but negatively for males. In general, energy efficiency is negatively correlated with body size but the energy storage capacity of larger birds is greater (Erckmann 1981, Jönsson and Alerstam 1990). Males give complex display flights during courtship in several calidrine sandpipers (Miller 1979). Small body size may be advantagous for males if it increases agility (Jehl and Murray 1986), although males may be more susceptible to starvation because they are able to carry less energy stores. In contrast, large

body size should be advantagous for female sandpipers if it allows them to breed earlier or lay larger eggs (Erckmann 1981, Jehl and Murray 1986, Jönsson 1987, Jönsson and Alerstam 1990). The energy demands of sandpiper young are high because they are fast-growing and precocial, thus feeding conditions after hatching may determine the upper limit of female body size.

Negative assortative mating could increase selection on body size if birds pair with respect to morphology. Examples of negative assortative mating are rare, and are usually based on colour morph preferences in birds (Partridge 1983, Houtman and Falls 1994). Nonetheless, negative assortative mating with respect to body size has been reported in at least three species of monogamous sandpipers (Least Sandpiper *Calidris minutilla*, Stilt Sandpiper *Micropalma himantopus*; Jehl 1970, Dunlin *C. alpina*; Jönsson 1987). Furthermore, small males paired with large females appeared to nest earlier (Jehl 1970, Jönsson 1987), which would be an advantage if there is a seasonal decline in fledging success (Daan et al. 1988). In this paper, I examined whether there was evidence for: i) assortative mating, and/or ii) a relationship between fecundity and body size in Western (*C. mauri*) and Semipalmated Sandpipers (*C. pusilla*).

Methods

Field methods

Western and Semipalmated Sandpipers were studied at a 4 km² study site, 21 km east of Nome, Alaska (64°20'N, 164°56'W) during May-July in 1993-1995. Like most monogamous shorebirds, males are territorial and give display flights during courtship. Females lay a modal and maximum clutch size of four eggs, both sexes incubate the clutch, and males provide most of the parental care after hatching (Gratto-Trevor 1991, Chapter V, B.K. Sandercock, unpubl). Both species breed in the same habitat at this site, and nests are placed on low, dry ridges that are close to shallow tundra ponds.

Nests were located by observing sandpipers that flushed or gave distraction behaviour. Egg-laying rates were 1.25 days/egg, and duration of incubation was 20 (Semipalmated Sandpiper) or 21 days (Western Sandpiper, Chapter II). Date of clutch initiation was calculated by back-dating from egg-laying, stage of incubation (determined by floating eggs in water, Chapter II) or date of hatching. Clutch size was determined by revisiting nests found during laying until egg number was unchanged. Egg length and breadth were recorded with calipers, egg volume was estimated using $V=kLB^2$ (Hoyt 1979, where k=0.47, B.K. Sandercock, unpubl.).

Incubating birds were captured with walk-in traps placed over the clutch. Both parents were usually captured on every nest, and each bird was individually marked with combinations of coloured

leg bands and a numbered metal band. I recorded the following morphometrics during handling: exposed culmen, tarsus bone, and flattened wing chord. Most Western Sandpipers can be sexed by length of the culmen ($\male\male$ <24.5 mm, $\female\female$ >24.5 mm, Page and Fearis 1971, Cartar 1984), but Semipalmated Sandpipers could not be reliably sexed by external morphology alone. In both species, the larger of the two parents on a nest was assumed to be the female. Independent criteria (palpitated eggs, display flights, breeding dispersal) indicated this approach was 88% (Semipalmated) to 100% (Western) accurate.

Data analysis

Statistics were calculated using SAS (SAS Institute 1985); all tests were two-tailed and considered significant at probability levels less than $\propto$=0.05. Although univariate measures are often used to describe avian morphology, such variables may not be representative of overall body size (Freeman and Jackson 1990). I used Principal Component Analysis (PCA) to create an index of sandpiper body size based on culmen, tarsus and wing length (Rising and Somers 1989). I used the morphometrics from the first capture occasion, and treated each species separately. All the eigenvectors of principal component 1 (PC1) showed positive loadings, and PC1 explained 70.4% and 68.5% of the variation in body size of Western and Semipalmated Sandpipers, respectively.

Some birds and pairs were observed in more than one year, but I included reproductive data from only the first year that a bird was captured. In the analysis of assortative mating, each unique pair was included once. There was annual variation in the timing of clutch initiation, but not in egg volume or modal clutch size (Chapter IV). I adjusted clutch initiation dates by subtracting the mean laying date for a given year and species. I calculated a mean egg volume for each clutch, and pooled clutches of 2 and 3 eggs in the analysis of clutch size.

Results

Sexual size dimorphism

Female sandpipers were significantly larger than males in all univariate measures of body size (Table VI-1). The sexual size dimorphism of Western Sandpipers (culmen 16.3%, tarsus 6.2%, wing 3.6%) was greater than Semipalmated Sandpipers (culmen 9.0%, tarsus 3.4%, wing 2.0%).

Assortative mating

The univariate measures of body size were not significantly correlated among mated pairs of Western (culmen r=0.14, P=0.10; tarsus r=0.10, P=0.27; wing r=0.17, P=0.07, n=126) or Semipalmated Sandpipers (culmen r=-0.05, P=0.60; tarsus r=-0.14, P=0.11; wing r=-0.08, P=0.40, n=118).

Table VI-1. Univariate morphometrics (mean±1SD) of Western and Semipalmated Sandpipers. All lengths in mm.

	Western Sandpiper		Semipalmated Sandpiper	
	Females (*n*=98)	Males (*n*=98)	Females (*n*=106)	Males (*n*=95)
Culmen	26.4±1.0	22.4±1.0	18.7±0.9	17.1±0.8
	$F_{1,194}$=743.2, *P*<0.001		$F_{1,199}$=173.1, *P*<0.001	
Tarsus	23.7±0.8	22.2±0.8	22.4±0.8	21.6±0.8
	$F_{1,194}$=166.7, *P*<0.001		$F_{1,199}$=48.6, *P*<0.001	
Wing	101.1±2.6	97.5±2.5	99.0±2.7	97.1±2.5
	$F_{1,194}$=93.3, *P*<0.001		$F_{1,199}$=28.0, *P*<0.001	

Multivariate techniques gave the same result: female body size and male body size (PC1) were not correlated in either sandpiper species (Figure VI-1).

Body size and fecundity

There were significant relationships between male body size and date of clutch initiation in Semipalmated Sandpipers, and between female body size and date of clutch initiation in Western Sandpipers (Table VI-2). Large males and small females nest significantly earlier, trends contrary to the prediction that early nesting acts as a disruptive selective pressure on body size. Less than 7% of the variation in date of clutch initiation was explained by body size in either species. There was no difference in the body size of females that either laid 2-3 or 4 eggs (Table VI-2), thus large and small females did not differ in clutch size.

There was a weak but significant relationship between mean egg volume and female body size in both Western and Semipalmated Sandpipers (Table VI-2). Mean egg volume increased by 17% and 9% over the range of female body size in Western and Semipalmated Sandpipers, respectively (Figure VI-2). Female body size accounted for 9-15% of the variation in egg volume in both species.

Discussion

Western and Semipalmated Sandpipers were sexually dimorphic in body size, and the greatest degree of dimorphism was in culmen length. This is consistent with previous reports for these species (Ouellet et al. 1973, Cartar 1984) and for other shorebirds (Mueller 1989). The difference between female and male Western Sandpipers in culmen length (16.3%) is the greatest of all monogamous calidrine shorebirds (range 2-16%, Jehl and Murray 1986, Jönsson and Alerstam 1990). Despite this variation, I found no evidence for assortative mating in Western or in Semipalmated Sandpipers, although there was evidence that one component of reproductive effort (egg size) covaries with female body size. I contrast my results with previous studies of mating in shorebirds, and then consider alternate explanations for the evolution of reversed sexual size dimorphism.

Assortative mating in shorebirds

Assortative mating for body size can be produced by active mate choice, or by passive size-dependent variation in the availability of mates (Cooke and Davies 1983). Positive assortative mating for body size has been reported in Ringed Plovers (*Charadrius dubius*), but Hedenström (1987) concluded this may have been due to older birds being larger and pairing together. Negative assortative mating for body size has been reported in Dunlin, Least Sandpipers and Stilt Sandpipers (Jehl 1970, Jönsson 1987), shorebirds that are closely related to Western and Semipalmated Sandpipers.

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Figure VI-1. Relationship between male and female body size (PC1) in pairs of mated Western and Semipalmated Sandpipers.

WESTERN SANDPIPERS

N=126

r=0.13
P=0.16

SEMIPALMATED SANDPIPERS

N=118

r=-0.14
P=0.13

FEMALE SIZE (PC1)

MALE SIZE (PC1)

...87
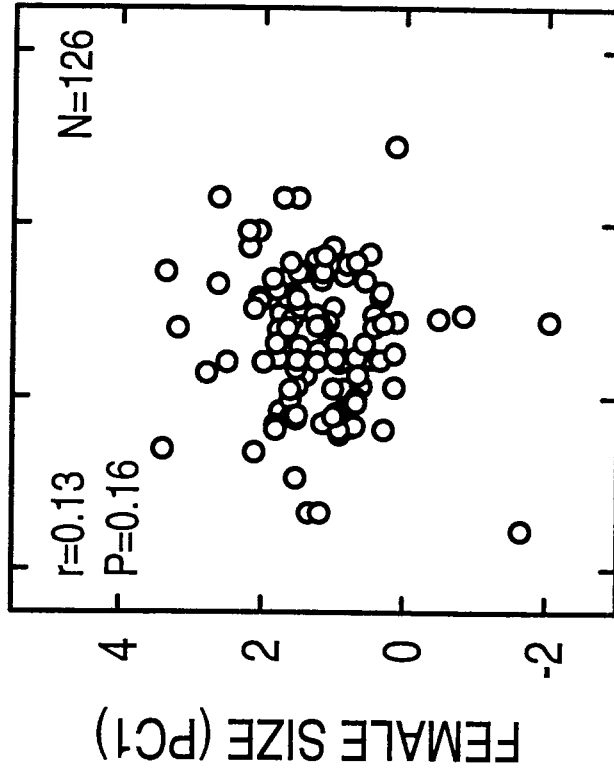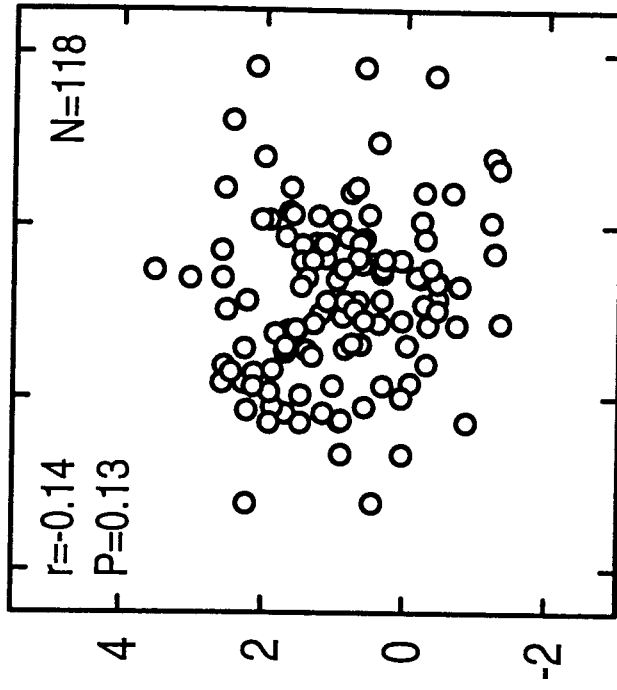
Table VI-2. Fecundity variables as a function of male body size and female body size (PC1). See Methods for details of analyses. Slope±1SE, *t*-test for H_o: slope=0.

	Western Sandpiper (♂♂ n=91, ♀♀ n=91)	Semipalmated Sandpiper (♂♂ n=94, ♀♀ n=103)
	Males	
Date of clutch initiation	0.54±0.71, *t*=0.77, *P*=0.45 r^2<0.01	-1.25±0.57, *t*=-2.19, *P*=0.03 r^2=0.04
	Females	
Date of clutch initiation	1.59±0.62, *t*=2.55, *P*=0.01 r^2=0.07	0.48±0.50, *t*=0.96, *P*=0.34 r^2<0.01
Clutch size	$F_{1,89}$=1.87, *P*=0.17	$F_{1,101}$=0.67, *P*=0.41
Mean egg volume	0.22±0.06, *t*=3.96, *P*<0.0005 r^2=0.15	0.11±0.04, t=3.21, P<0.005 r^2=0.09

Figure VI-2. Relationship between female body size (PC1) and mean egg volume in Western and Semipalmated Sandpipers.

WESTERN SANDPIPERS   SEMIPALMATED SANDPIPERS

N=91   N=103

EGG VOLUME (cm³)
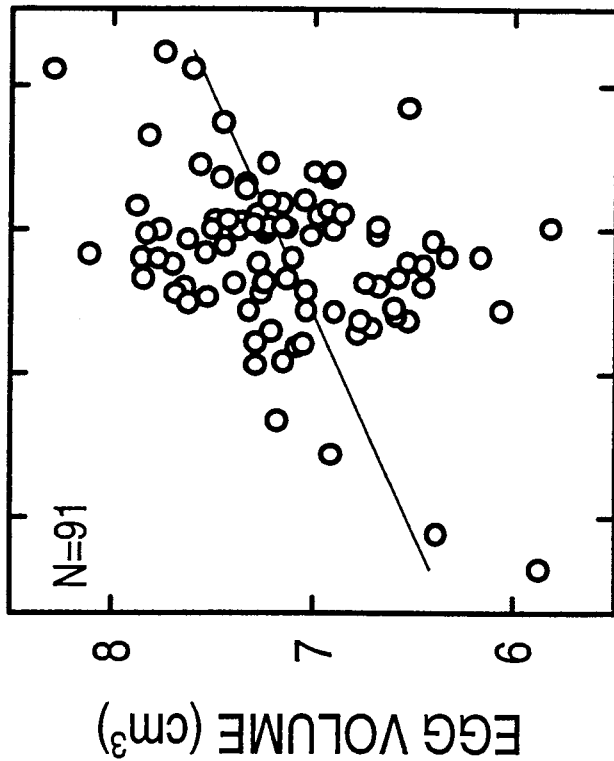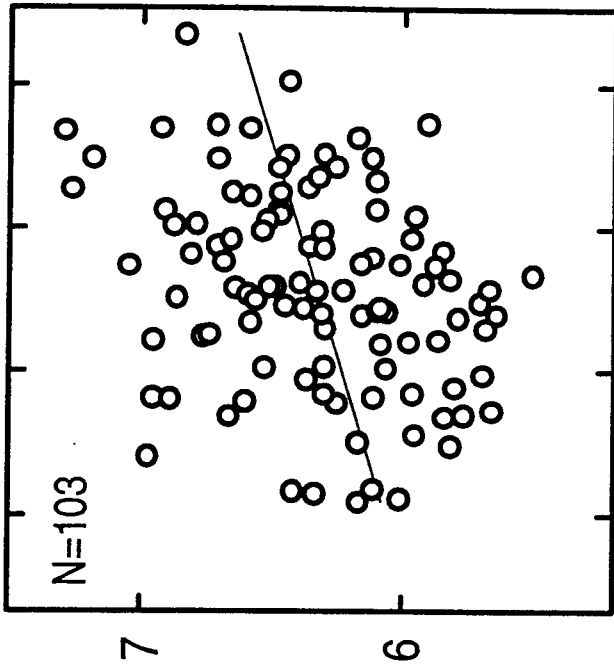
FEMALE BODY SIZE (PC1)

It is unlikely that differences in reproductive biology account for the discrepancy between the results of this and previous studies. All five of these latter species are small, monogamous shorebirds that breed in the arctic. Males are territorial and perform courtship display flights, and there is little difference among the species in the relative contribution of the sexes to parental care. My conclusions should also be robust because the sample size of this study (118-126 pairs) was greater than that of Jehl (1970, 29-41 pairs) or Jönsson (1987, 33 pairs). Rather, differences in methodology may have been important. Jehl (1970) and Jönsson (1987) calculated multiple correlations between univariate measures of body size and fecundity. Their results might have been nonsignificant if they had adjusted the degrees of freedom for the number of tests (Rice 1989) or if they had described body size with multivariate statistics (Rising and Somers 1989, Freeman and Jackson 1990). Moreover, neither Jehl (1970) or Jönsson (1987) compared the morphology of mated pairs directly. Both authors regressed an index of intrapair dimorphism (a difference or ratio between female and male body size) on timing of breeding (date of hatching or egg-laying), and found that early breeding pairs had greater dimorphism. However, a correlation between body size and timing in one sex could produce the same result without negative assortative mating. Therefore, in contrast to the generally held view, the evidence for negative assortative mating is weak. The random mating that I observed could be typical among monogamous sandpipers, but such results may be under-represented in the scientific literature if authors are less likely to publish null conclusions.

Reproductive effort and body size

Body size variation has been shown to affect fecundity and survival in many birds (reviewed by Choudhury et al. 1996, but see Cooch et al. 1992). In general, energy efficiency is negatively correlated with body size but the energy storage capacity of larger birds is greater (Erckmann 1981, Jönsson and Alerstam 1990).

The relationship between timing of breeding and body size was significant in this and in other studies of sandpipers (Jehl 1970, Erckmann 1981:228, Jönsson 1987). Unlike previous studies, however, I found no evidence that small males or large females nested earlier. My results therefore do not support the idea that size-dependent variation in timing of laying has lead to sexual size dimorphism. Early nesting appears to confer a reproductive advantage in sandpipers but the data are weak. Predation on shorebird nests is lowest during the early breeding season at Nome (Chapter II, but see Byrkjedal 1980), and Soikkeli (1967) found that early broods of Dunlin (*C. alpina*) had higher survival than late broods. Renesting potential may also be higher if the first clutch is initiated early. Survival of young until recruitment declines with timing of breeding in most birds (Daan et al.

1988, but see Lank et al. 1985), but this rate is difficult to examine in shorebirds because natal philopatry is low (Thompson et al. 1994). Sandpipers at Nome sometimes laid 2-3 eggs, but usually laid four eggs in their nests. The most parsimonious explanation for the lack of a relationship between body size and egg number is that the variation in clutch size was small.

Egg size has a residual positive effect (controlling for parent quality) on the growth and survival of young in most birds (e.g. Amundsen et al. 1996, Dawson and Clark 1996), and it should be advantageous for females to lay large eggs. Large females laid large eggs in this study, as do many other shorebird species (Väisänen et al. 1972, Miller 1979, Jönsson 1987, Blomqvist and Johansson 1995). These results support the notion that there is a fecundity advantage to large female size. In Semipalmated Sandpipers, yearlings lay smaller eggs than adults (Gratto et al. 1983). If females continue to grow after first breeding, the relationship between egg and body size could be confounded by female age (e.g. Cooch et al. 1992). This is an unlikely explanation here because yearling breeders seem rare at Nome; few banded nestlings have been recaptured as breeding birds on the study area (<3% of all banded nestlings, Chapter VII).

Two alternate explanations for size dimorphism

Intrasexual selection. I tested whether sandpipers mated assortatively, but sexual selection can also lead to size dimorphism through intrasexual competition for mates. The sex competing for mating opportunities is usually larger than the sex that provides parental care (Olsen and Cockburn 1993), and this is the case in most polygamous shorebirds (Jönsson and Alerstam 1990). Competition for mates is higher among male than female Western and Semipalmated Sandpipers, yet males are smaller in these and other monogamous shorebirds. Erckmann (1981) and Jehl and Murray (1986) have argued that males are the smaller sex because they give display flights during courtship; aerial agility is predicted to increase with small body size (Andersson and Norberg 1981). This model has not yet been empirically tested. Moreover, it still assumes that body size confers some fitness benefit. I found no evidence that body size affected reproductive success among mated males, but male sandpipers that are unable to obtain a mate (Gratto-Trevor 1991) could be larger birds. Aerial agility could also affect a male's risk of predation; male Least Sandpipers (*C. minutilla*) usually give display flights during still weather (Miller 1979), which may make them more vulnerable to avian predators.

Sex role specialization for ecological conditions. Sexual dimorphism may be an adaptation to ecological conditions encountered during the annual cycle. Body size could affect migratory flight efficiency or the reserves used during wintering. In several shorebird populations, birds from the

northern part of the wintering range are larger in body size, and may carry greater body reserves for coping with freezing events (Pienkowski et al. 1985, Castro et al. 1992). In Western Sandpipers, however, it is the smaller males that winter further north (Page and Fearis 1972, Naranjo et al. 1994, Harrington and Haase 1994). It seems unlikely that size dimorphism is an adaptation to wintering conditions; remaining in the north presumably facilitates early return of males to the breeding ground.

During migration, male Western and Semipalmated Sandpipers precede the females north during spring, and follow them south in the fall (Harrington 1982, Butler et al. 1987). Shorebird foraging depletes prey, causing temporal and spatial variation in the number of invertebrates at stopover sites (Schneider and Harrington 1981, Székely and Bamberger 1992). A longer bill may aid females to gather resources for egg-laying (Jönsson 1987, Jönsson and Alerstam 1990), in part by accessing prey that males missed during spring migration. Male sandpipers provide most of the parental care after hatching (e.g. Gratto-Trevor 1991); a short bill may be more efficient for gleaning prey in a terrestrial habitat (Jönsson 1987, Jönsson and Alerstam 1990). Future research should examine whether differences in bill morphology result in sex-dependent foraging rates or habitat preferences (*sensu* Rubega 1996). The latter may be the case in Semipalmated Sandpipers: long-billed birds forage in softer sediments than short-billed birds (Harrington 1982).

In their review of shorebird body size, Jehl and Murray (1986:50-51) argued that 'sexual dimorphism in the Western Sandpiper can be explained by sexual selection alone' and that there are 'no clues... to indicate that ecological factors have affected its degree of sexual dimorphism'. My findings refute the notion that assortative mating maintains sexual size dimorphism in this species or in the Semipalmated Sandpiper. I did find evidence that body size covaried with reproductive effort among females although not in males. Alternative explanations for the evolution of sexual size dimorphism, particularly intrasexual selection and ecological factors, deserve greater attention in the future.

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Chapter VII

Local Survival, Breeding Philopatry and Mate-fidelity in Western and Semipalmated Sandpipers

Unpublished manuscript

Abstract

Rates of local survival, recapture, breeding philopatry and mate-fidelity were examined in a 4-yr study of breeding Western (*Calidris mauri*) and Semipalmated Sandpipers (*C. pusilla*) at a site near Nome, Alaska. Natal philopatry was low (<3%), and returning young dispersed further than breeding adults. The local survival rate of Western Sandpipers was best described by a model with age- and time-dependence. The local survival rate of Semipalmated Sandpipers had significant time-dependent variation and was also higher in males than in females. The local survival rates of the two species were significantly different, presumably because there was an interaction among the different factors affecting this rate. The pooled rates of local survival were comparable (Western ϕ=0.59, Semipalmated ϕ=0.61), but the probability of recapture was higher in Western (p=0.82) than in Semipalmated Sandpipers (p=0.63). Breeding philopatry was strong in both species, although females that changed mates moved further (median distance, Western: 157 m, Semipalmated: 203 m) than reuniting pairs (34 m, 41 m) or males that changed mates (52 m, 38 m). Mate-fidelity was higher in Semipalmated Sandpipers (94.3% of returning pairs united) than Western Sandpipers (66.7% of pairs). Divorce was not the result of nesting failure, and mate change had no significant effect on breeding performance. The moderate survival, strong breeding philopatry and high mate-fidelity of sandpipers may be adaptations to the life-history strategy of long-distance migration.

Introduction

Migratory birds face two important decisions when returning to their breeding grounds: should an individual return to the same site as the previous year, and should an individual reunite with the same partner? Individuals that show breeding philopatry presumably benefit from prior knowledge of the distribution of local food resources, nest sites and/or predation risks. Similarly, there may be benefits to remaining with a mate: breeding performance may improve with the duration of the pair bond (Ens et al. 1996). On the other hand, birds that disperse may be able to increase reproductive output if they are able to find a better breeding site or another mate of higher quality. A theoretical framework for evaluating the mating decisions that lead to divorce in birds has not been available until relatively recently (Choudhury 1996, Ens et al. 1996), and avian breeding tactics appear to be affected by several factors.

First, rates of breeding philopatry may depend on an individual's ability to locate a mate. In birds, the natal and breeding dispersal of females is generally greater than that of males (Greenwood 1980, Greenwood and Harvey 1982). The factors leading to sex-biased dispersal rates are in birds are currently debated (Bollinger and Gavin 1989, Anderson et al. 1992), but the benefits of breeding

philopatry seem to be related to territoriality. For example, breeding philopatry is higher in the territorial sex of polyandrous shorebirds (Oring and Lank 1982), and in some monogamous species (Jackson 1994, but see Oring and Lank 1984). Second, an individual's ability to locate a mate may be related to survival or other characteristics of a species' life history. If survival rates are low, mate change may be frequent because the probability that both members of a pair will return is low (Rowley 1983). Pairing quickly should be especially important for migratory birds that travel to high latitudes and have a short breeding season (Chapter II). Mate-fidelity could be low because divorce is preferable to waiting for a previous partner to return (Williams 1996). Alternately, divorce rates may be high because there are more opportunities to change to a better mate (Ens et al. 1993).

A complication in measuring rates of survival and mate-fidelity is that a returning bird may be missed by an observer. The 'return rate' of birds to a study site in consecutive years is the product of three probabilities: *i*) the true survival rate, *ii*) the rate of breeding philopatry and *iii*) the rate of recapture (or resighting). Failure to consider all three of these rates can lead to biased interpretations. For example, return rates have often been used as an index of survival (Lebreton et al. 1992, Baker et al. 1995). A low return rate may be the result of low survival, but could also be explained by dispersal or a low rate of catchability (Sandercock and Gratto-Trevor 1997). Similarly, divorce rates have traditionally been calculated by considering pairs where both birds return the following year (Ens et al. 1996). A divorcing pair may be more difficult to detect than a reuniting pair because birds that change mates will be on separate nests and the rates of breeding philopatry could be different. New statistical techniques based on mark-recapture data (Burnham et al. 1987, Lebreton 1992) allow estimation of *iii*) the rate of recapture (p). The local survival rate (ϕ) is the product of rates *i*) and *ii*), and is an improvement over return rates as it is a more accurate measure of survival. My objective in this study was to obtain unbiased estimates of local survival, breeding philopatry and mate-fidelity in two migratory shorebirds: Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*C. pusilla*). I used improved mark-recapture techniques (programs RELEASE and SURGE) to measure local survival and recapture rates. Movements of banded birds were used to calculate rates of natal philopatry (young returning to breed in their natal area) and breeding philopatry (adults returning to breed in the same area). Finally, I used the estimates of breeding philopatry to evaluate the sex-specific variation in local survival and mate-fidelity.

Methods

Study species

Western and Semipalmated Sandpipers were studied at a 4 km² study site, 21 km east of Nome, Alaska (64°20'N, 164°56'W) during May-July in 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). The sandpipers are closely related (Haig et al. 1997, but see Baker 1992), but were easily distinguished during the breeding season by their plumage colouration and vocalizations. Females laid eggs in a scrape on the ground, and both sexes incubated.

Field methods

Nests were located by observing sandpipers that flushed or gave distraction behaviour. Egg-laying rates were 1.25 days/egg, and duration of incubation was 20 (Semipalmated Sandpiper) or 21 days (Western Sandpiper, Chapter II). Date of clutch initiation was calculated by back-dating from egg-laying, stage of incubation (determined by floating eggs in water, Chapter II) or date of hatching. Clutch size was determined by revisiting nests found during laying until egg number was unchanged. Egg length and breadth were recorded with calipers, egg volume was estimated using $V=kLB^2$ (Hoyt 1979, where $k=0.47$, B.K. Sandercock, unpubl.).

Nests were visited every 6-7 d during incubation and then daily around the expected date of hatching. Young were banded after all of the viable eggs had hatched, and their tarsi were large enough to accommodate the same bands that were used on adults. Nest fate was defined as one of two outcomes: (1) successful: at least one chick was banded and left the nest; or (2) unsuccessful: eggs were abandoned or disappeared before the expected hatching date, and/or there were signs of predator activity (Chapter II).

Incubating birds were captured with walk-in traps placed over the clutch. Each bird was individually marked with combinations of coloured leg bands and a numbered metal band. There was no loss of metal bands. Both parents were captured on most nests (86.8%), but occasionally a nest was depredated before both birds had been captured (neither: 2.0%, 1 bird: 11.2%, $n=446$ nests). Most Western Sandpipers can be sexed by length of the culmen (♂♂ <24.5 mm, ♀♀ >24.5 mm, Page and Fearis 1971, Cartar 1984), but Semipalmated Sandpipers could not be reliably sexed by external morphology alone. In both species, the larger of the two parents on a nest was assumed to be the female. Independent criteria (palpitated eggs, display flights) indicated this approach was 88-100% accurate.

The study area was a heterogeneous mixture of low tundra ridges, mudflats and shallow freshwater ponds. I used microtopographical features to plot nest locations on high resolution aerial photographs (scales: 1:1250-1:1600); the accuracy of this method was ±5 m. The study area was a small part of a much larger, continuous area of suitable habitat that surrounded Safety Sound, a brackish body of water formed by three river drainages. The study area was roughly circular and most sandpipers nested around the edges because there were lakes in the centre of the plot. The probability of detecting a dispersing bird likely varied within the study area because it was bounded to the west by scree slopes and to the south by ocean whereas there was suitable habitat to the east.

Data analysis

Local survival (ϕ) and recapture rates (p) were estimated in two steps, following the methodology outlined by Lebreton et al. (1992) and Cooch et al. (1996). This approach is relatively new but has been successfully applied to a variety of taxa, including several shorebirds (Paton 1994, Sandercock and Gratto-Trevor 1997, Warnock et al. in press). Program RELEASE (Burnham et al. 1987) was used to calculate the goodness-of-fit to a time-dependent model (ϕ_t, p_t). The component statistics of RELEASE are efficient for detecting heterogeneity in mark-capture data, and I included only estimable tests when calculating the overall significance of Tests 2 and 3. Next, I used program SURGE 4.1 to model local survival and resighting rates. Fit of a model was described by the deviance (DEV) and number of parameters (NP) of the model. The most parsimonious model was the one with the lowest value for Aikaike's Information Criterion (AIC=DEV+2*NP, Cooch et al. 1996). Likelihood ratio tests (LRT) were used to contrast nested models. The difference in deviances between two models was compared to a χ^2-distribution, and the difference in the number of parameters was used as the degrees of freedom. If the likelihood ratio test was nonsignificant, the reduced model was accepted and tested against models with fewer parameters.

The capture histories were based on the captures of breeding adults on the nests, and resightings were not included. Handling records of nestlings were discarded, thus the initial capture occasion was always the year a bird was first captured on a nest. Factors tested in the statistical models included sex (sex), year of study (t), and age class (ac). A two age-class model (2ac) was used to compare local survival in the year immediately following banding with subsequent years. In a sample of birds banded as adults, effects on local survival may be due to relative age, or to handling effects, transiency and/or heterogeneity of capture. The difference between age classes or sexes was sometimes constrained to be a constant difference with an additive model. Comparing an additive

model to a saturated model (e.g., ϕ_{2ac+t} vs. $\phi_{sex \cdot t}$) is similar to testing whether the interaction term is significant in a 2-way ANOVA.

All other statistics were calculated using the standard procedures of SAS (SAS Institute 1990); all tests were two-tailed and considered significant at probability levels less than $\propto=0.05$. There was annual variation in the timing of clutch initiation, but not in egg volume or modal clutch size (Chapter IV). To examine changes in breeding performance following mate change, I adjusted clutch initiation dates by subtracting the mean laying date for a given year and species. Analyses of egg size were based on the mean egg volume of each clutch.

Results

Natal philopatry

Few young were recaptured on the study area in years after they were banded: the overall return rates were <3% in both species (Table VII-1). Some of the recaptured nestlings were not found on nests and may have bred elsewhere. Fewer birds were captured as 1-year old breeders than was predicted by recapture rates, which suggests that the mean age of first breeding is greater than one year (Table VII-1). Returning young dispersed relatively long distances to their first breeding sites (median [range], Western 475 m [256-747, $n=5$], Semipalmated 697 m [481-907, $n=4$]) in comparison to breeding adults that dispersed.

Recapture and local survival rates

A total of 296 Western Sandpipers and 230 Semipalmated Sandpipers were captured as breeding adults during the four years of this study. There were insufficient data to calculate most of the goodness-of-fit tests from RELEASE (i.e., tests 3.Sm, 2.Ct, 2.Cm), but the estimable components of test 3.Sr were not significant in either Western ($\chi^2_4=9.08$, P=0.06) or Semipalmated Sandpipers ($\chi^2_4=5.29$, P=0.26). I did not use a variance inflation factor to adjust the likelihood ratio tests because the recapture data met the assumption of internal homogeneity (Lebreton et al. 1992). Local survival and recapture rates were modelled separately for the two species.

There was no significant difference between male and female Western Sandpipers in recapture rate (model 2a vs. 1a, Table VII-2). Moreover, there was no significant annual variation in the recapture rate of this species (model 3a vs. 2a). Similar results were found in Semipalmated Sandpipers (models 2b vs. 1b, 3b vs. 2b, Table VII-3), and recapture rate was best described as a constant in both sandpipers. Overall, Western Sandpipers had a significantly higher recapture rate than Semipalmated Sandpipers (model 2c vs. 1c, Table VII-4), and the mean recapture rate was 0.83 in Western Sandpipers and 0.67 in Semipalmated Sandpipers (Table VII-5).

Table VII-1. Return rates and age at first capture for nestlings that were banded and recaptured on the study area. Number of birds captured on nests, (number of birds captured as pre-breeding migrants and not found on a nest).

Year	Western Sandpiper				Semipalmated Sandpiper			
		Age at first capture (yr)				Age at first capture (yr)		
	No. banded	1	2	3	No. banded	1	2	3
1993	77	0	1 (1)	1	127	1	2 (1)	0
1994	111	1 (1)	2	---	44	0	0	---
1995	89	1	---	---	70	1	---	---
Pooled[a]	277	2 (1)	3 (1)	1	241	2	2 (1)	0

[a] If all birds first breed as yearlings, the expected distribution of age at first capture can be calculated from the probability of recapture. The distributions for Western (1: 4.98, 2: 0.85, 3+: 0.17, n=6) and Semipalmated Sandpipers (1: 2.68, 2: 0.88, 3+: 0.44, n=4) were based on constant probabilities of recapture (Western: p=0.83, Semipalmated: p=0.67, from Table VII-5). Statistics were not calculated because samples were small.

Table VII-2. Summary of model testing for Western Sandpipers (females: n=152, males: n=144). The fit of a model is described by the deviance (DEV) and the number of parameters (NP): a low value for Aikaike's information criterion (AIC) indicates a good model fit. Likelihood ratio tests (LRT) were used to compare nested models.

Model[a]	DEV	NP	AIC	Comparison of models
Modelling recapture probability (p)				
1a: $\phi_{2ac \cdot sex \cdot t},\ p_{sex \cdot t}$	492.8	14	520.8	
2a: $\phi_{2ac \cdot sex \cdot t},\ p_t$	492.8	12	516.8	sex effect on p,
				model 2a vs.1a: $\chi^2_2=0$, P=1.00
3a: $\phi_{2ac \cdot sex \cdot t},\ p_c$	492.8	11	514.8	year effect on p,
				model 3a vs. 2a: $\chi^2_1=0$, P=1.00
Modelling local survival (ϕ)				
4a: $\phi_{2ac \cdot t},\ p_c$	496.2	6	508.2	sex effect on ϕ,
				model 4a vs. 3a: $\chi^2_5=3.4$, P=0.64
5a: $\phi_{2ac+t},\ p_c$	497.4	5	**507.4**	interaction between age class and year on ϕ,
				model 5a vs. 4a: $\chi^2_1=1.2$, P=0.27
6a: $\phi_{2ac},\ p_c$	503.6	3	509.6	year effect on ϕ,
				model 6a vs. 5a: $\chi^2_2=6.2$, P=0.045
7a: $\phi_t,\ p_c$	504.7	4	512.7	age effect on ϕ,
				model 7a vs. 5a: $\chi^2_1=7.3$, P<0.01
Models used to derive estimates of ϕ and p				
8a: $\phi_{2ac \cdot sex},\ p_c$	502.1	5	512.1	
9a: $\phi_c,\ p_c$	509.2	2	513.2	

[a] Model subscripts: 2ac= two age classes, c=constant, sex=sex-dependent, t=time-dependent.

Table VII-3. Summary of model testing for Semipalmated Sandpipers (females: n=122, males: n=108). The fit of a model is described by the deviance (DEV) and the number of parameters (NP): a low value for Aikaike's information criterion (AIC) indicates a good model fit. Likelihood ratio tests (LRT) were used to compare nested models.

Model[a]	DEV	NP	AIC	Comparison of models
Modelling recapture probability (p)				
1b: $\phi_{2ac*sex*t}$, p_{sex*t}	535.4	14	563.4	
2b: $\phi_{2ac*sex*t}$, p_t	535.5	12	559.5	sex effect on p, model 2b vs. 1b: $\chi^2_2=0.1$, P=0.95
3b: $\phi_{2ac*sex*t}$, p_c	536.3	11	558.3	year effect on p, model 3b vs. 2b: $\chi^2_1=0.8$, P=0.37
Modelling local survival (ϕ)				
4b: ϕ_{sex*t}, p_c	540.9	7	554.9	age effect on ϕ, model 4b vs. 3b: $\chi^2_4=4.6$, P=0.33
5b: ϕ_{sex+t}, p_c	541.2	5	**551.2**	interaction between sex and year on ϕ, model 5b vs. 4b: $\chi^2_2=0.3$, P=0.86
6b: ϕ_{sex}, p_c	554.0	3	560.0	year effect on ϕ, model 6b vs. 5b: $\chi^2_2=12.8$, P<0.005
7b: ϕ_t, p_c	548.3	4	556.3	sex effect on ϕ, model 7b vs. 5b: $\chi^2_1=7.1$, P<0.001
Models used to derive estimates of ϕ and p				
8b: $\phi_{2ac*sex}$, p_c	552.9	5	562.9	
9b: ϕ_c, p_c	561.0	2	563.0	

[a] Model subscripts: 2ac= two age classes, c=constant, sex=sex-dependent, t=time-dependent.

Table VII-4. Overall estimates of local survival and probability of recapture for Western and Semipalmated Sandpipers breeding at Nome, Alaska[a]. Point estimate (95% CL).

Model	Parameter	Western Sandpiper	Semipalmated Sandpiper
8a, 8b: $\phi_{2ac*sex}$, p_c	Local survival rate		
	Females		
	Year after first capture	0.50 (0.39-0.61)	0.57 (0.42-0.71)
	Subsequent years	0.64 (0.49-0.77)	0.45 (0.30-0.61)
	Males		
	Year after first capture	0.56 (0.45-0.66)	0.68 (0.53-0.80)
	Subsequent years	0.73 (0.58-0.84)	0.70 (0.53-0.83)
	Recapture rate	0.84 (0.74-0.90)	0.63 (0.51-0.73)
9a, 9b: ϕ_c, p_c	Local survival rate	0.59 (0.53-0.66)	0.61 (0.53-0.68)
	Recapture rate	0.82 (0.71-0.89)	0.63 (0.52-0.74)

[a] Overall comparison of recapture rate: model 2c: $\phi_{2ac*t*species}$, p_c (DEV=1045.4, NP=11, AIC=1067.4) vs. model 1c: $\phi_{2ac*t*species}$, $p_{species}$ (DEV=1040.8, NP=12, AIC=1064.8), χ^2_1=4.6, P=0.032. Overall comparison of local survival rate: model 3c: ϕ_{2ac*t}, $p_{species}$ (DEV=1061.9, NP=7, AIC=1075.9) vs. model 1c, χ^2_5=21.1, P<0.001.

Table VII-5. Estimates of local survival and probability of recapture from the best-fit models for Western and Semipalmated Sandpipers breeding at Nome, Alaska. Point estimate (95% CL).

Model	Parameter	Western Sandpiper
5a: ϕ_{2ac+t}, p_c	Local survival rate	
	Year after first capture	
	1993-1994	0.60 (0.49-0.71)
	1994-1995	0.41 (0.29-0.53)
	1995-1996	0.56 (0.40-0.71)
	Subsequent years	
	1993-1994	—
	1994-1995	0.63 (0.50-0.74)
	1995-1996	0.76 (0.62-0.86)
	Recapture rate	0.83 (0.73-0.90)

Model	Parameter	Semipalmated Sandpiper
5b: ϕ_{sex+t}, p_c	Local survival rate	
	Females	
	1993-1994	0.54 (0.40-0.67)
	1994-1995	0.64 (0.47-0.78)
	1995-1996	0.30 (0.19-0.44)
	Males	
	1993-1994	0.70 (0.57-0.80)
	1994-1995	0.78 (0.63-0.88)
	1995-1996	0.46 (0.32-0.60)
	Recapture rate	0.67 (0.55-0.77)

In Western Sandpipers, there was no significant difference between the sexes in local survival rate (model 4a vs. 3a, Table VII-2). The most parsimonious model was one where ϕ was constrained to be a constant difference between the two age classes (model 5a). Further attempts to reduce this model (5a) were unsuccessful (6a vs. 5a, 7a vs. 5a) because there was significant annual and age-dependent variation in the local survival of Western Sandpipers. The local survival of Semipalmated Sandpipers was best explained by a different set of models. In this species, there was no significant difference between the age classes in local survival (model 4b vs. 3b, Table VII-3). There was no significant interaction between sex and time if local survival was constrained to be a constant difference between the sexes (model 5b vs. 4b). Model (5b) could not be reduced further (6b vs. 5b, 7b vs. 5b); it had the lowest AIC value of the tested models and was the best fit for Semipalmated Sandpipers.

The local survival rates of the two species were significantly different when compared with in a saturated model (model 3c vs. 1c, Table VII-4), which indicate there are significant interactions between age and sex that differ between the species. The overall estimates of local survival were comparable when calculated in a reduced model (Semipalmated ϕ=0.61, Western ϕ=0.59). The mean local survival rate of males was higher in both species, and the difference between the sexes ranged from 6-7 (Western) to 11-25 percentage points (Semipalmated). In Western Sandpipers, local survival rate was lower in the year after first capture and increased in subsequent years. Estimates of local survival from the best-fit models showed that the local survival rates of Western and Semipalmated Sandpipers were lowest in the 1994-1995 and 1995-1996 periods, respectively (Table VII-5).

Breeding philopatry

Distances moved were compared for sandpipers that reunited and those that changed mates. There was no annual variation in breeding philopatry, but there were differences between the sexes in both species. Females that changed mates moved significantly further than females that reunited with the same mate (Table VII-6, Figure VII-1). In contrast, males that changed mates did not move significantly further than reuniting males. Overall, there were no significant difference between the species in breeding philopatry (Table VII-6). Nonetheless, 14% of male Western Sandpipers that changed mates moved more than 200 m, whereas no male Semipalmated moved more than 150 m (Figure VII-1). Similarly, 11% of female Westerns that changed mates moved more than 600 m, and no female Semipalmated Sandpipers moved that distance.

Figure VII-1. Internest distances between nesting attempts in consecutive years for pairs that remated (shaded bars, Western n=24, Semipalmated n=33), males that changed mates (white bars, Western n=44, Semipalmated n=22), and females that changed mates (black bars, Western n=38, Semipalmated n=12).

WESTERN SANDPIPER

SEMIPALMATED SANDPIPER

PERCENTAGE

DISTANCE (m)

0   1-100   101-200   201-300   301-400   >400
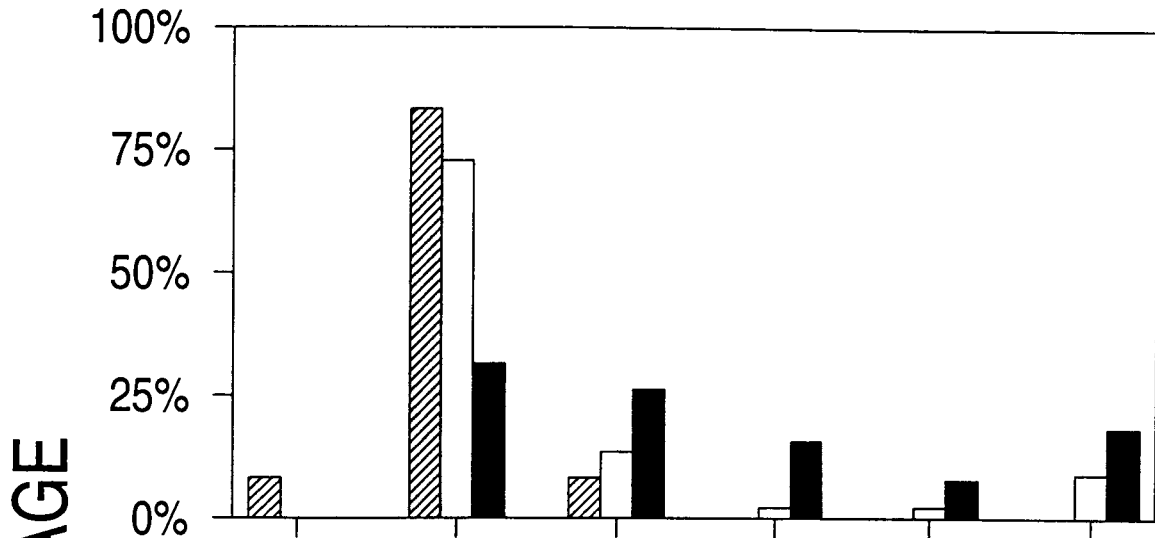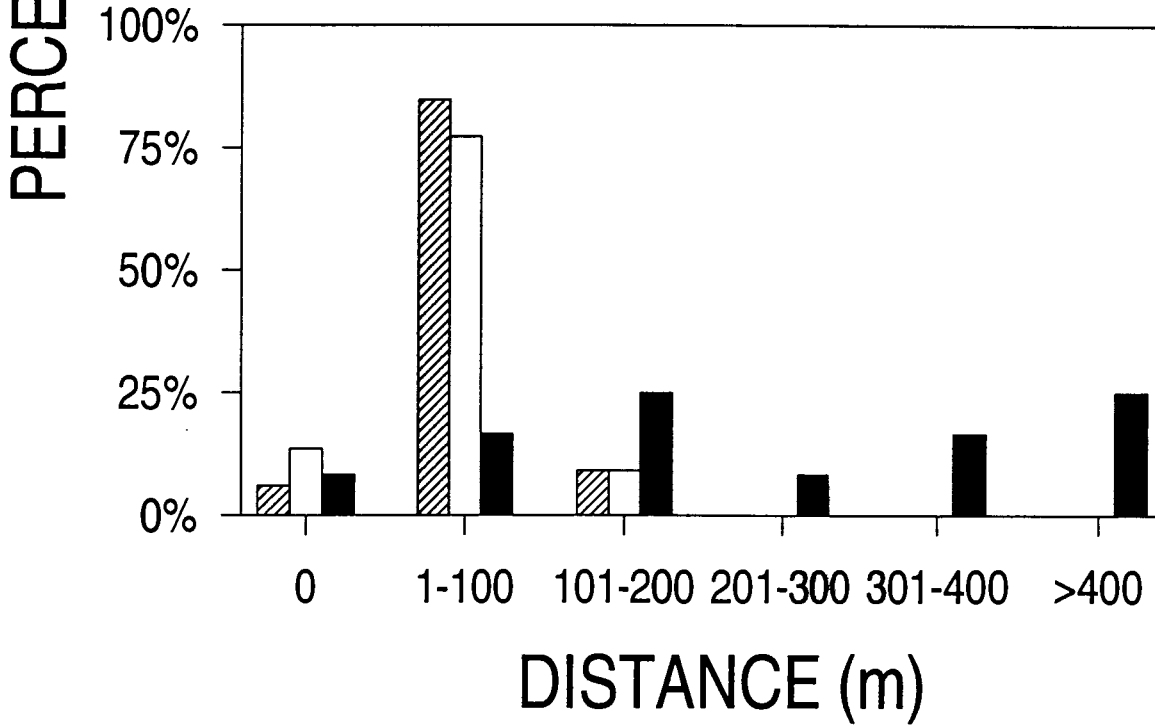
Table VII-6. Internest distances (in m) between nesting attempts in consecutive years. Analyses of variance were based on rank-transformed distances; years were pooled because there was no annual variation in breeding philopatry. Median, range (n of birds or pairs)

Pairing status[a]	Western Sandpiper	Semipalmated Sandpiper
i. Male changed mate	52, 3-803 (44)	38, 0-113 (22)
ii. Female changed mate	157, 16-947 (38)	203, 0-591 (12)
iii. Pair remated	34, 0-146 (24)	41, 0-113 (33)
Statistics	Group: $F_{2,97}$=13.8, P<0.0001	Group: $F_{2,58}$=6.6, P<0.001
	Year: $F_{2,97}$=0.7, P=0.51	Year: $F_{2,58}$=1.2, P=0.31
	Group x Year: $F_{4,97}$=0.4, P=0.84	Group x Year: $F_{4,58}$=1.1, P=0.37
Orthogonal contrasts	*i* vs. *iii*: $F_{1,103}$=2.3, P=0.13	*i* vs. *iii*: $F_{1,64}$=0.1, P=0.78
	ii vs. *iii*: $F_{1,103}$=23.3, P<0.0001	*ii* vs. *iii*: $F_{1,64}$=14.5, P<0.001

[a] There was no difference between the species in the internest distances of: males changing mates (Mann-Whitney U-test [χ^2 approximation], χ^2_1=2.7, P=0.10), females changing mates (χ^2_1=0.3, P=0.87), or remating pairs (χ^2_1<0.01, P=0.99).

Nestcup reuse was observed in both species, and reuse was usually by a remating pair or by a male returning in the following year (Figure VII-1). However, one male Semipalmated Sandpiper reused a nestcup two years later, and nested 70 m away during the interim year. Another Semipalmated male mated with three different females in three consecutive years, but reused the same nestcup each time. Eight nestcups were used by more than one pair, although it was usually by the same species (Western in a Western cup, n=4, Semipalmated in a Semipalmated cup, n=3, Western in a Semipalmated cup, n=1).

Mate-fidelity

Returning Western Sandpipers frequently changed mates, and only 36.6% of all birds remated with the same partner that they were associated with in the previous year (Table VII-7). Mate fidelity was significantly higher in Semipalmated Sandpipers: 62.9% of returning birds reunited with their previous mate (Table VII-7). There was no annual variation in the rates of mate fidelity of either species. Mate change may have been preceded by the death of a partner, but there were also divorces between returning pairs. To determine the divorce rate, I considered cases where both members of a mated pair were recaptured the following year. The rates of mate fidelity among returning pairs were significantly higher in Semipalmated Sandpipers (94.3%) than in Western Sandpipers (66.7%, Table VII-7).

Divorce was not the consequence of breeding failure in Western Sandpipers. Surprisingly, the nesting success of pairs that eventually divorced (90.9%, n=11) was higher than that of reuniting pairs (62.5%, n=24, Fisher's exact test, P=0.12). Birds that changed mates paired assortatively for breeding experience the following year. Birds that had previously bred on the study area (i.e., were banded) paired with similar birds, and birds that were first-time breeders (i.e., were unbanded) also paired with like birds. The frequencies were significantly different in both Western Sandpipers (newly mated pairs only, old ♀/old ♂: 17.8%, old ♀/new ♂: 15.3%, new ♀/old ♂: 21.2%, new ♀/new ♂: 45.8%, n=118, G_1=5.35, P=0.021) and Semipalmated Sandpipers (old ♀/old ♂: 20.7%, old ♀/new ♂: 8.6%, new ♀/old ♂: 27.6%, new ♀/new ♂: 43.1%, n=58, G_1=4.89, P=0.027).

Mate change had no measurable effect on the subsequent breeding performance of Western or Semipalmated Sandpipers (Table VII-8). The changes in laying date were not significantly different among groups, but remating pairs started their subsequent clutches earlier on average (Western: 2.9 d, Semipalmated: 1.5 d) than females (1.6 d, 1.3 d) or males that changed mates (0 d, -0.5 d). Overall, female Western Sandpipers had significantly earlier laying dates in the second year

Table VII-7. Mate fidelity of sandpipers captured on the study area in consecutive years. Percentage of birds or pairs that retained their mate(s) in year (i+1), (n of birds or pairs).

Year (i)	Western Sandpiper		Semipalmated Sandpiper	
	Returning birds[a]	Returning pairs[b]	Returning birds[a]	Returning pairs[b]
1993	36.4 (44)	53.3 (15)	68.3 (41)	93.3 (15)
1994	35.9 (39)	87.5 (8)	66.7 (42)	93.3 (15)
1995	37.5 (48)	69.2 (13)	45.5 (22)	100.0 (5)
Pooled	36.6 (131)	66.7 (36)	62.9 (105)	94.3 (35)
Statistics	G_2=0.03, P=0.99	G_2=3.0, P=0.22	G_2=3.5, P=0.17	G_2=0.6, P=0.73

[a] Mate change resulted from an undetected divorce or from the absence (and presumably the death) of a mate. The rates of mate fidelity among returning birds were significantly different between species (G_1=16.2, P<0.001).

[b] Both members of the pairs returned; mate change was by divorce only. The rates of mate fidelity among returning pairs were significantly different between species (G_1=9.3, P<0.005).

Table VII-8. The effect of mate change on the breeding performance of sandpipers. Fecundity data in consecutive years were treated as paired observations in a repeated-measures ANOVA. Mean ±1SD.

	Western Sandpiper			Semipalmated Sandpiper		
	Residual timing of laying[a]					
Pairing status	Year (i)	Year ($i+1$)	n	Year (i)	Year ($i+1$)	n
Male changed mate	-0.7 ±5.0	-0.7 ±5.7	41	-1.2 ±4.6	-0.7 ±3.9	24
Female changed mate	-1.4 ±5.7	-3.0 ±4.9	36	-0.2 ±7.1	-1.5 ±5.1	12
Pair remated	-0.9 ±5.2	-3.8 ±2.9	24	-0.1 ±5.4	-1.6 ±5.2	30
Statistics	Pairing status: $F_{2,98}$=2.0, P=0.14 Time: $F_{1,98}$=5.1, P=0.03 Status x Time: $F_{2,98}$=1.56, P=0.21			Pairing status: $F_{2,63}$<0.01, P>0.99 Time: $F_{1,63}$=1.15, P=0.29 Status x Time: $F_{2,63}$=0.97, P=0.38		
	Clutch size					
Pairing status	Year (i)	Year ($i+1$)	n	Year (i)	Year ($i+1$)	n
Male changed mate	3.91 ±0.29	3.95 ±0.21	44	3.88 ±0.33	3.60 ±0.76	25
Female changed mate	3.90 ±0.31	3.92 ±0.27	39	3.71 ±0.47	3.71 ±0.61	14
Pair remated	3.96 ±0.20	4.00 ±0	24	3.76 ±0.50	3.85 ±0.36	33
Statistics	Pairing status: $F_{2,104}$=0.93, P=0.40 Time: $F_{1,104}$=1.49, P=0.22 Status x Time: $F_{2,104}$=0.05, P=0.96			Pairing status: $F_{2,69}$=0.36, P=0.70 Time: $F_{1,69}$=0.49, P=0.49 Status x Time: $F_{2,69}$=1.94, P=0.15		
	Mean egg size (cm^3)					
Pairing status	Year (i)	Year ($i+1$)	n	Year (i)	Year ($i+1$)	n
Male changed mate	7.23 ±0.44	7.23 ±0.40	44	6.43 ±0.41	6.24 ±0.41	25
Female changed mate	7.22 ±0.41	7.22 ±0.31	39	6.29 ±0.39	6.30 ±0.41	14
Pair remated	7.20 ±0.34	7.28 ±0.42	24	6.23 ±0.47	6.20 ±0.43	33
Statistics	Pairing status: $F_{2,104}$=0.03, P=0.98 Time: $F_{1,104}$=0.44, P=0.51 Status x Time: $F_{2,104}$=0.35, P=0.71			Pairing status: $F_{2,69}$=0.74, P=0.48 Time: $F_{1,69}$=1.53, P=0.22 Status x Time: $F_{2,69}$=1.26, P=0.29		

[a] Timing of laying was corrected for annual variation by subtracting the mean date of laying; negative values indicate dates before the mean. Clutch and egg size were not adjusted because there was no annual variation in these aspects of fecundity (Chapter IV).

(Table VII-8). There was little indication otherwise that female fecundity improved between consecutive years, or that female quality changed for males that switched mates.

Discussion

Natal philopatry and age of first breeding

Return rates of sandpiper young to the study area were low (<3%), as they are in Semipalmated Sandpipers breeding in Manitoba (Gratto 1988, Sandercock and Gratto-Trevor 1997) and most other shorebirds (Oring and Lank 1984, Thompson et al. 1994). Low return rates may be partially explained by poor survival in the year after hatching, but natal dispersal was higher than breeding dispersal in both sandpipers. The nestlings that were recaptured as breeders on the study area moved 5-10 times further than site-tenacious adults. Natal philopatry may be weak in shorebirds (Oring and Lank 1984, Sandercock and Gratto-Trevor 1997), because migrating young have already absorbed the costs of dispersal (Weatherhead and Forbes 1992). The nests of some returning young were not found, and these birds could have dispersed off the study area. Recaptures of young sandpipers before laying may indicate that some birds are prospecting for breeding sites near their natal area. Reconaissance for breeding sites has been reported in Spotted Sandpipers (*Actitis macularia*, Reed and Oring 1992).

Yearling Western and Semipalmated Sandpipers can sometimes be identified by plumage characteristics (Prater et al. 1977, Gratto and Morrison 1981), and yearling Western Sandpipers were present as breeders at Nome (Chapter IV). Not all philopatric young were recaptured as yearlings, however (see also Gratto 1988). Small sandpipers are thought to start breeding as yearlings (Thompson et al. 1994, Hitchcock and Gratto-Trevor 1997), but more birds were recaptured as older birds than was predicted by the recapture rates. Studies on the wintering grounds have shown that yearlings of several shorebird species delay their first breeding attempt and do not migrate north during their first summer (Summers et al. 1995, Marks and Redmond 1996). This appears to be the case in Western (P.D. O'Hara, pers. comm.) and Semipalmated Sandpipers as well (Gratto and Morrison 1981, Spaans 1984, Gratto-Trevor 1992). The causes of variation in the age of first breeding require further study on the wintering grounds.

Recapture and local survival rates

There was little variation in the recapture rates of sandpipers. There may have been little annual variation because nest searching effort was high in all years. I suspect that most nests were found because few broods of unknown origin were encountered on the study area. There may have been no difference between the sexes in recapture rate because males and females jointly incubated the clutch

(Ashkenazie and Safriel 1979, Chapter II), and birds were captured in pairs. Western Sandpipers had a recapture rate that was about 20 percentage points higher than Semipalmated Sandpipers. The two species nested close to each other, and it seems unlikely that habitat differences could have affected detectability. Semipalmated Sandpipers nested later in the breeding season than Western Sandpipers (Chapter IV), and suffered higher nest predation as a result (Chapter II). Recapture rates may have been lower in Semipalmated Sandpipers because more nests were destroyed before both birds in a pair could be captured. In Lesser Snow Geese (*Anser caerulescens*, Viallefont et al. 1995), age of first breeding affects the probability of breeding in the subsequent year. If a similar process is operating in Semipalmated Sandpipers, the lower recapture rate could also indicate that there is temporary emigration and that adults are opting not to breed some years (see also Gratto-Trevor 1991).

In Western Sandpipers, local survival was significantly lower in the year after first capture than in subsequent years. This difference could be explained by age-dependent variation in survival (*sensu* Loery et al. 1987), especially if a large percentage of the newly-marked individuals were young birds breeding for the first time. Band recoveries have shown that mortality is usually higher in young shorebirds (Boyd 1962, Peach et al. 1994), possibly because young birds are inexperienced at coping with migration, foraging and predators (Evans and Pienkowski 1984, Kus et al. 1984). Handling effects could not explain the difference between groups, because birds were captured every year. The lack of an age-class effect in Semipalmated Sandpipers may indicate that young birds of this species were uncommon at Nome.

Male sandpipers had higher local survival than females, and this sexual difference could be the result of variation in breeding philopatry or mortality. Estimates of dispersal distance from finite study areas are usually biased because of edge effects (Jackson 1994, Baker et al. 1995, Koenig et al. 1996). This problem was relatively unimportant in this study because males and reuniting pairs usually moved only short distances (< 200 m) relative to the size of the study area (4 km²). Females that changed mates moved considerably further, however, and the range of distances observed suggest that females could have easily moved off of the study area. Thus, the lower local survival rate of females may have been partly due to permanent emigration. Inferential evidence suggests that the sex-dependent variation in local survival is not completely explained by sex-biased breeding dispersal. The difference between the sexes in local survival was greater in Semipalmated (11-25 percentage points) than in Western Sandpipers (6-7 points). Nonetheless, there were no significant differences between the species in breeding philopatry, and if individuals of either species moved

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further, they were more likely to be Western Sandpipers. Differences in local survival between the sexes are also consistent with variation in mortality rates. Gratto-Trevor (1991) reported that 12 of 15 known Semipalmated Sandpipers killed during breeding were females.

It is unclear what the survival rates of Western and Semipalmated Sandpipers should be. Shorebirds are thought to have high survivorship (Evans and Pienkowski 1984, Evans 1991), and survival may be high for phylogenetic reasons. Alternately, survival may be low in small sandpipers because survival covaries with body size (Gaillard et al. 1989). Estimates of local survival in Western (ϕ=0.59) and Semipalmated Sandpipers at Nome, Alaska (ϕ=0.61) were similar to another population of Semipalmated Sandpipers in northern Manitoba (ϕ=0.59, Sandercock and Gratto-Trevor 1997). The mark-recapture statistics used in this study are relatively new, and there are few comparative estimates for calidrine sandpipers or for other shorebirds that have been calculated with similar methods. Dunlin (*C. alpina*) in California had high rates of local survival once they were established on the wintering site (ϕ=0.74, Warnock et al., in press). Return rates of >0.70 (a minimum estimate of survival), have also been reported in Temminck's Stints (*Calidris temminckii*, Hildén 1978) and Dunlin (Jönsson 1991). Local survival has been estimated to be 0.66 in Piping Plovers (*Charadrius melodus*, Root et al. 1992), 0.69 in Snowy Plovers (*C. alexandrinus*, Paton 1994), and 0.70 in Redshanks (*Tringa totanus*, Thompson and Hale 1993). Thus, local survival in shorebirds seems to be intermediate to that of temperate passerines (Loery et al. 1987, Clobert et al. 1988, Blondel et al. 1992) and seabirds (Chastel et al. 1993, Harris et al. 1994).

Breeding philopatry

Female-biased breeding dispersal is common among monogamous, male-territorial birds (Greenwood 1980). Both of the sandpiper species that I investigated showed female biases in the distance moved between breeding attempts in consecutive years. Breeding philopatry was strongest among male sandpipers, and this is consistent with several other monogamous shorebirds (Soikkeli 1967, Thompson et al. 1988, Jackson 1994). The most obvious advantage of returning to a previous breeding site is familiarity with the local conditions, particularly the distribution of food resources and/or predation risks. Sandpipers do not maintain the pair-bond during winter, and breeding philopatry may also facilitate locating a previous mate after migration. Male-biased breeding philopatry in sandpipers is presumably a consequence of male territoriality. The advantages of familiarity with the site should be greatest for males because they make nestcups (Chapter V) and perform aerial displays during courtship (Miller 1983, Chapter VI).

Breeding philopatry varies among shorebirds as a function of mating system and environmental factors (Oring and Lank 1984). Breeding dispersal is higher among species that are polygamous and/or breed in ephemeral habitats (e.g. phalaropes, Colwell et al. 1988, Piping Plovers *Charadrius melodus*, Haig and Oring 1988, Snowy Plovers *C. alexandrinus*, Stenzel et al. 1994), presumably because breeding philopatry is less of an advantage for obtaining mates and resources. Breeding philopatry may be high among arctic-breeding sandpipers (this study, Soikkeli 1967, Tomkovich and Soloviev 1994), because most are monogamous and depend on tundra habitats that are relatively stable. Dispersal may also be limited if patches of habitat act as islands (Weatherhead and Forbes 1992). Semipalmated Sandpipers near Churchill, Manitoba bred in a relatively discrete area: the delta of the Mast River (Gratto et al. 1985). Semipalmated Sandpipers at Nome may have moved greater distances than birds in this other population because the suitable habitat was more continuous at my study site.

Reuse of nestcups was observed in both Western and Semipalmated Sandpipers (see also Holmes 1971, Gratto et al. 1985), and has been reported in several shorebirds (Thompson et al. 1988, Johnson et al. 1993). Nestcup reuse can be viewed as an example of particularly strong breeding philopatry, and is remarkable among birds that travel between the arctic circle and the equator during their annual cycle. There is growing evidence that migratory shorebirds also show fidelity to stopover sites (Smith and Houghton 1984, Harrington et al. 1988) and to wintering areas (Smith and Stiles 1979, Myers et al. 1988, Warnock and Takekawa 1996, P.D. O'Hara, unpubl. data). These patterns of resource use make shorebirds particularly vulnerable to environmental degradation, and provide a strong argument for the conservation of their habitats.

Mate-fidelity

Mate-fidelity has usually been calculated by examining the divorce rates of returning pairs (Ens et al. 1996). This approach underestimates the true divorce rate because the probability of capturing both members of a divorcing pair is lower than capturing a reuniting pair. The two birds of a divorcing pair will be on separate nests, and as I have shown above, females may disperse further to find new mates. In contrast, the two birds of a reuniting pair will be on one nest, and may show stronger breeding philopatry. Therefore, rates of breeding philopatry must be considered when interpreting patterns of mate-fidelity. For example, Ens et al. (1996) summarized the divorce rates of 76 species of birds but were surprised not to detect a relationship between divorce and mortality. One obvious possible explanation is that species-specific variation in breeding philopatry confounded the estimates of both divorce and mortality.

Rates of mate-fidelity were high among Semipalmated Sandpipers at Nome: 95% of all returning pairs remated, and 63% of returning birds retained their mate. Rates of fidelity were lower among Western Sandpipers (67% of pairs, 37% of birds). These estimates are comparable to Semipalmated Sandpipers in northern Manitoba (81% of pairs, 49% of birds, Gratto et al. 1985), and Western Sandpipers at Kolomak River, Alaska (62% of pairs, 31% of birds, Holmes 1971). The difference in mate-fidelity between the two species was not an artifact of breeding philopatry. If the lower divorce rate of Semipalmated Sandpipers was due to undetected breeding dispersal, the rates of breeding philopatry should have been different, but the distances moved were the same in both species. Moreover, the availability of alternate mates should have been similar because the local survival rate was about the same in both species. The factors leading to the difference in mate-fidelity between the two species are unknown.

Nesting failure was not the proximate cause of divorce in Western Sandpipers. Several hypotheses aimed at explaining divorce can be rejected (Choudhury 1995) because sandpipers did not improve reproductive success after changing mates. Indeed, the high levels of mate-fidelity in Semipalmated Sandpipers are somewhat surprising because breeding performance was unaffected by the duration of the pair-bond. Reuniting pairs bred earlier on average than birds that changed mates, but the difference was small and timing of laying was variable. Overall, the lack of an effect on reproductive performance suggests that nonadaptive hypotheses may be more important. For example, male Western Sandpipers winter at higher latitudes than females (Harrington and Haase 1994, Naranjo et al. 1994), and precede females north during spring migration (Butler et al. 1987). Most pair formation probably occurs on the breeding grounds, although there may be some activity during spring passage as well (Frodin et al. 1994, Tomkovich and Soloviev 1994). Divorce may occur as a side-effect of the differential arrival of the two sexes or as the result of accidental separation of the pair during migration (Choudhury 1995). It was beyond the scope of this study to conduct focal behavioural observations to determine whether divorce is due to desertion, usurpation or pre-emption (Ens et al. 1996), and these questions deserve further study.

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Chapter VIII

General Discussion

'The restlessness of shorebirds, their kinship with the distance and swift seasons, the wistful signal of their voices down the long coastlines of the world make them, for me, the most affecting of wild creatures.' (Matthiessen 1967:21).

Introduction

Human activity has had a detrimental effect on the shorebird populations of North America for at least 150 years. Unregulated market-hunting in the late 1800s significantly reduced the populations of many of the larger shorebirds. Passage of the Migratory Bird Treaty Act in 1918 mitigated some of these effects, but some species have never returned to their former abundance (Page and Gill 1994). A century later, shorebird populations are still threatened, but by a potentially more damaging factor: habitat alteration. Migratory shorebirds rely on coastal and interior wetlands as stopover sites (e.g., Western Sandpiper, Iverson et al. 1996, Semipalmated Sandpiper, Hicklin 1987), and many of these habitats have been lost to agricultural production, or urban and industrial development (Myers et al. 1987, Gill et al. 1994, Page and Gill 1994). Pollution from pesticides and oil is an added concern in these areas (Rattner et al. 1995). Wintering areas in the tropics are also being degraded as mangrove habitats are converted into shrimp production (Delgado 1986), and only the arctic-breeding grounds have not been heavily impacted by human exploitation. The development of conservation strategies for shorebirds is challenging because the migration routes of shorebirds usually straddle the political boundaries of multiple countries. International cooperation appears to be the only viable solution. To this end, the Western Hemisphere Shorebird Reserve Network has identified more than 90 sites in North and South America that support large numbers of shorebirds (Myers et al. 1987).

The effectiveness of the Reserve Network has not yet been determined. Counts of migrating shorebirds at these sites provide a relatively coarse index of population status, mainly because turnover times are difficult to determine (Butler et al. 1987, Iverson et al. 1996). Population viability analysis (PVA, Beissinger 1997) may be a more powerful approach with a greater predictive ability for estimating the population persistence of shorebirds (Ryan et al. 1993, Hitchcock and Gratto-Trevor 1997). The drawback of PVA is that it requires detailed demographic information, and these data can be difficult to obtain. I initiated this study of Western (*Calidris mauri*) and Semipalmated Sandpipers (*C. pusilla*) with the aim of obtaining accurate estimates of fecundity, survival and other demographic parameters. I have been successful in most regards, although some questions remain unanswered.

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Summary

Reproductive rates were low in Western and Semipalmated Sandpipers: females usually laid only one clutch, and both species had a modal clutch size of four eggs (Chapter IV, see also Gratto-Trevor 1992, Wilson 1994). Similar reproductive rates have been reported in other arctic-breeding sandpipers (Jehl 1973, Parmelee 1992, Lanctot and Laredo 1994). A new finding, however, was that there can be seasonal variation in sandpiper reproductive rates. Late-breeding Western Sandpipers tended to lay smaller eggs, whereas clutch size was reduced in late-nesting Semipalmated Sandpipers (Chapter IV). Seasonal declines in the reproductive effort of sandpipers were surprising; this phenomena has rarely been described for birds with a putatively invariant clutch size. In general, the variation in fecundity appeared to be related to bird quality. Large females laid larger eggs, but not large clutches (Chapter VI). Females that were familiar with the study area (Chapter IV), and pairs that reunited (Chapter VII) tended to breed earlier.

Most aspects of sandpiper fecundity appeared to be an adaptation to long-distance migration. I found that about 80% of all nests were usually initiated within a 2-week period (Chapter IV), and other arctic-breeding sandpipers also have compressed breeding seasons at high latitudes (Miller 1983, Pienkowski 1984). A short breeding season may be a consequence of the suitability of the local nesting conditions, or it may be a tactic that facilitates early departure on migration. Northern populations of sandpipers usually have faster egg laying rates (e.g., Dunlin *C. alpina*, Holmes 1966, Soikkeli 1967), but egg-laying rates (1 egg / 36 h) were slower at Nome than in southern populations of the same species (Chapter II). Slow laying-rates and the unusual seasonal variation in reproductive effort may indicate nutritional stress at this site. Enlargements of clutch size had a significant effect on the length of incubation (Chapter V). A small clutch size could be an adaptation to reduce the overall length of breeding because it reduces the duration of both egg-laying and incubation.

Several factors had no effect on sandpiper reproductive rates. Clutch size was not related to female body size (Chapter VI), or to the duration of the pairbond (Chapter VII). In the past, clutch size in sandpipers was thought to determined by the incubation capacity of the parents. Anecdotal evidence supported this notion: the conical eggs of shorebirds fit tightly together, and parents rotate displaced eggs so that the narrow ends are in the centre of the clutch. I challenged this conventional view with experimental manipulations of clutch size. Sandpipers were able to incubate clutches of three and five eggs with no changes in parental behaviour, and only minor effects on nest success

(Chapter V). The factors that determine clutch size in shorebirds are unresolved and await further investigation.

Overall, I had good success in measuring fecundity and identifying some of the causal factors that explain variation in reproductive rates. I was not able, however, to determine the effect that timing of laying, egg size and clutch size had upon the survival of young. Early nesting, large eggs and big clutches increase the reproductive success of other birds (Chapter IV), but two aspects of sandpiper biology prevented me from testing this important assumption. First, sandpiper young were cryptic and highly mobile after leaving the nest. It was sometimes possible to detect young broods if the attending parent(s) gave distraction displays, but not after the parents had abandoned their young (Gratto-Trevor 1991). Second, philopatry rates were low (Chapter VII) and few young were recaptured as recruits. Determination of survival rates among young sandpipers in their first year of life awaits a technological innovation that allows extended monitoring of shorebird young.

Survival is more difficult to measure than fecundity because the timing and causes of mortality in free-living birds are usually unknown (Lebreton et al. 1992). Shorebirds are thought to have high survivorship (Evans and Pienkowski 1984, Evans 1991), but empirical estimates of these rates are limited for most species (Thompson and Thompson 1991). My estimates of survival and other demographic parameters have important implications for the conservation of arctic-breeding sandpipers. First, I used statistical techniques based on mark-recapture data to correct for the probability of recapture, and found that local survival increased with relative age in Western Sandpipers (Chapter VII). There was little evidence of age-dependent variation in fecundity (Chapter IV), but variation in the age of first breeding (Chapter VII) would affect entry into the breeding population. Second, natal dispersal in sandpipers was high (Thompson et al. 1994, Chapter VII), and immigration should reduce the extinction risks of local populations (Höglund 1996). Dispersal of young shorebirds leads to gene flow and reduced population differentiation (Haig et al. 1997), which could buffer small populations against the risk of genetic bottlenecks. Last, levels of local survival in Western and Semipalmated Sandpipers were moderately high (ca. $\phi=0.60$, Sandercock and Gratto-Trevor 1997, Chapter VII). Hitchcock and Gratto-Trevor (1997) used stochastic models to simulate population size and found that sandpiper numbers are most sensitive to changes in adult survival rates and that variation in productivity is less important. In conclusion, conservation efforts should be directed at reducing sources of mortality for adult birds. The site-fidelity of adult sandpipers was strong on the breeding grounds (Chapter VII) and in other areas (P.D. O'Hara, unpubl.). Thus,

preservation of the habitats used by migratory sandpipers during their annual cycle may be the best tactic for assuring that these species are protected in the future.

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<u>Master of Science</u> University of Alberta   1991
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<u>Ph.D. Research on Sandpipers</u> Simon Fraser University   1993 - 1996
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● Graduate Fellowship, Simon Fraser University (4)	SFU	1994 - 1996
● Northern Science Training Grant, DIAND (3)	SFU	1994 - 1996
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● Frank M. Chapman Research Grant, American Museum of Natural History (2)	Queen's	1993 - 1994
● Dean's Grant for Doctoral Field Travel, Queen's University	Queen's	1993
● Student Membership Award, Cooper Ornithological Society	Queen's	1993
● Graduate Award, Queen's University	Queen's	1992
● Dean's Travel Assistance Award, University of Alberta	U of A	1991
● Northern Science Training Grant, DIAND (2)	U of A	1989 - 1990
● Boreal Alberta Research Grant, Canadian Circumpolar Institute	U of A	1989
● Graduate Scholarship, Province of Alberta	U of A	1989
● Max and Marjorie Ward Scholarship, University of Alberta	U of A	1989
● Advanced Education and Job Training Scholarship, Province of British Columbia	UBC	1987
● Mary and Joseph Bryant Scholarship, University of British Columbia	UBC	1987
● Excellence in Education Scholarship, Province of British Columbia (2)	UBC	1985 - 1986
● Provincial Entrance Exam Scholarship, Province of British Columbia	UBC	1984
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5. Publications

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6. Presentations and Posters

- Evolution of sexual size dimorphism in two calidrine sandpipers. 18th Pacific Ecology Conference (PEC), 22 Feb 1997.
- Patterns of fecundity in two arctic-breeding sandpipers. Simon Fraser University, 21 Mar 1996; Canadian Wildlife Service, 26 Mar 1996.
- Survival estimates for Dunlin. 2nd CWS/NSERC Research Colloquium, 15 Mar 96.
- Incubation ability in calidrine shorebirds: a test of the four-egg threshold. 17th PEC, 10 Feb 1996.
- Survival estimates for Semipalmated Sandpipers. 16th PEC, 25 Mar 1995; 1st CWS/NSERC Research Colloquium, 10 Mar 1995; SFU/UBC Retreat, 31 Oct 1995.
- The adaptive significance of clutch size in precocial birds. 5th Alaska Bird Conference and Workshop, 4 May 1994; 15th PEC, 5 Mar 1994.
- Breeding biology of Western and Semipalmated Sandpipers. SFU Western Sandpiper Workshop, 3 Nov 1993, 20 Nov 1994, 12 Nov 1995, 9 Nov 1996; SFU/UBC Retreat, 25 Nov 1994.
- Brood defence in Willow Ptarmigan: tests of parental investment theory. Queen's University, 1 Oct 1992; University of Alberta, 10 Nov 1991.
- Effect of past investment and future benefit on brood defence of Willow Ptarmigan. 109th Meeting of the American Ornithologists' Union, 15 Aug 1991.
- Brood defence tactics in Willow Ptarmigan. 11th PEC, 10 Mar 1990; 24th Prairie Universities Biological Seminars (PUBS), 16 Feb 1990; 23rd PUBS, 18 Feb 1989.

7. Academic Accomplishments

- Reviewed submissions to Auk (16 Jul 1996), Condor (21 Dec 1995, 13 Apr 1994, 24 Mar 1993), J. Field Ornith. (19 Jun 1996) and NERC (Nat. Environmental Research Council - UK, 19 Feb 1996).
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