# Breeding biology of the Least Sandpiper (*Calidris minutilla*) on the Queen Charlotte Islands, British Columbia

by

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## ABSTRACT

The breeding biology of the Least Sandpiper was studied on the Queen Charlotte Islands, British Columbia, in a newly discovered, and relatively dense, population. Climatic conditions were milder, and the breeding season longer, than in other parts of the species' range. The purposes of the study were: (a) to obtain longterm data on breeding, which were lacking for this species, and (b) to investigate whether the species' conservative breeding strategy differed on the Queen Charlotte Islands because of the high breeding density and the mild climate.

Many nests were found and many breeding adults and chicks were banded over the years 1984-88. Data were obtained on: timing of egg laying, hatching, and fledging; return rates of yearlings and older birds; adult measurements; egg measurements; philopatry and site fidelity; mate fidelity; chick growth; and rates and causes of depredation on nests.

Relative size of mates was not related to nesting date. Older and more experienced birds nested earlier than yearlings or experienced but divorced pairs. Older females hatched more eggs than yearlings, but both fledged similar numbers of chicks per egg hatched. Mean egg volume was positively related to female body weight, and older females laid larger eggs because they were heavier than yearling females. Mean egg volume for the same females was highly constant in successive years. Mean egg volume was not related to hatching success, fledging success, or return rates of yearlings.

Length of parental care of broods was inversely related to date for both sexes. Very late-nesting females abandoned clutches before eggs hatched, with some males successfully incubating the last few days alone and then tending the brood alone. Most of these males abandoned their brood before fledging but, even so, many chicks fledged. When both members of a pair were alive, mate fidelity was almost 100% for the population. The age at first breeding for new breeders was one year. Yearlings constituted about 20% of the breeding population.

Predation caused significant nest mortality early each season. Replacement clutches usually were laid if a first clutch was lost before mid June. Replacement clutches and first clutches fledged young at similar rates. The long nesting season allowed more opportunity for laying of replacement clutches and fledging of chicks late in the season.

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## TABLE OF CONTENTS

## LIST OF TABLES

## LIST OF FIGURES

## LIST OF APPENDICES

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Margo Hearne, the heart and soul of Delkatla Wildlife Sanctuary, has fought many battles on behalf of wildlife habitat on the Queen Charlotte Islands. Margo also jointly discovered the first Least Sandpiper nest in Delkatla and helped me search for nests on many occasions during the following years. I deeply appreciate the friendship, hospitality, and encouragement given to me and my family over the years from this remarkable woman.

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# DEDICATION

This thesis is dedicated to my parents, John (Jack) K. Cooper (1909-1982) and Louise V. Cooper, who gave me a wonderful array of unique experiences with the natural world. These experiences gave me great enjoyment, a diversity of perspectives on how to live life, and provided motivation for me to pursue my career path.

# INTRODUCTION

It is widely held that natural selection molds individual behaviour which maximizes the reproduction of genes through offspring and other relatives (Emlen and Oring 1977; Wittenberger 1979); the major contribution to an individual's fitness is the production of its own offspring, in most cases (Wittenberger 1981). Therefore, an appropriate approach to explore the evolution of a species' mating system is to analyze: (a) the reproductive biology of individuals; and (b) the interacting reproductive features of individuals of the sexes.

Birds have long served as valuable models for studies of life-history strategies. Shorebirds, especially sandpipers and their kin (Scolopacidae), offer many advantages for the study of reproductive strategies. The group exhibits a diversity of mating systems and patterns of parental investment (Pitelka et al. 1974). Mating systems include monogamy, lek polygyny, and polyandry; with the ancestral mating system of shorebirds being likely monogamy with shared parental care (Jenni 1974; Pitelka et al. 1974). Roughly 75% of the 86 species of Scolopacidae are monogamous with incubation shared between the sexes. Relative investment by the sexes in parental care, however, varies widely both within and among monogamous species.

Almost all species of Scolopacidae lay a determinate clutch of four eggs, unlike most other bird taxa, which are more variable (MacLean 1972). Variable clutch size is an important means of varying reproductive investment in most bird species, so scolopacids clearly are constrained in this regard. Individual scolopacids can increase their investment in egg production only by altering the composition, size or shape of eggs, or by attempting to produce more than one brood per season. Shorebirds, like most other taxa with precocial young, make relatively heavy investments in eggs compared to most other bird taxa, with total clutch mass ranging between 40-115% of adult female body mass (Schönwetter 1967). Caloric density of shorebird eggs is also relatively high (Sotherland and Rahn 1987).

The Calidridinae is a large (24 species) and diverse subfamily of the Scolopacidae (Hayman et al. 1986). The breeding ecology of several members of the Calidridinae have been studied extensively: Western Sandpiper (*Calidris mauri*; Holmes 1971a,1973), Semipalmated Sandpiper (*C. pusilla*; Ashkenazie and Safriel 1979; Gratto 1988; Gratto et al. 1983, 1985), Dunlin (*C. alpina*; Holmes 1966a,1971b; Soikkeli 1966,1967; Jönsson 1987), Temminck's Stint (*C. temminckii*; Hildén 1975, 1978); and Stilt Sandpiper (*C. himantopus*; Jehl 1973).

The Least Sandpiper (*C. minutilla*) is the smallest member of the Calidridinae (Hayman et al. 1986). Its breeding range extends in a broad band from the Pribilof Islands across the low- and sub-arctic of North America from western Alaska to Newfoundland and south to northwestern British Columbia, northern Manitoba, James Bay, and Nova Scotia (American Ornithologists' Union 1983); and occasionally Massachusetts (Anderson 1980). Its breeding range extends farther south than any other calidridine species, except possibly Dunlin (Hayman et al. 1986).

The Least Sandpiper is a "typical" calidridine. It is monogamous and single-brooded, males are smaller than females, the sexes share incubation, and females desert broods before males. Its breeding biology has been studied in northern Manitoba (Jehl 1970, 1971) and on Sable Island, Nova Scotia (Miller 1977, 1979, 1983a, 1985), but no information is available from western parts of its range.

The diversity of mating systems within the Scolopacidae contrasts with the ubiquity of fixed clutch size and biparental care in monogamous species of the family. The relatively conservative features of monogamous breeding systems suggest that variation in reproductive success and strategies within populations must be low. There are several levels at which breeding success of individuals can be evaluated including: mate acquisition; egg production;

hatching of eggs; fledging of young; and return of young to breed in following years. Previous studies have shown that reproductive success in shorebirds, and many other avian taxa, is influenced by age, experience, mate fidelity, and geographic location (e.g., Coulson 1966; Davis 1975; Oring et al. 1983; Hannon and Smith 1984; Gratto and Cooke 1987; Thompson and Hale 1991; Croxall et al. 1992).

In this study, I examine components of breeding and reproductive success of Least Sandpipers breeding at an extremely southern geographic location in their range, on the Queen Charlotte Islands, British Columbia. The study population was unusually dense for this species, and had been established for fewer than 20 years due to a human-induced change in habitat. In addition, the study area had a less severe climate than in most of the species' breeding range.

The relationships between age, experience, and pair status on reproductive success are the central themes of the study. I tested the hypotheses that older and more experienced birds would have higher reproductive success than younger, less experienced birds. I anticipated also that early nesting and an extended breeding season would occur because of the relatively mild climate. Divergences from the conservative monogamous breeding strategy that Least Sandpipers follow (polygyny, laying of more than one replacement clutch, or extended parental care) were also anticipated given the relatively long breeding season and high densities of breeding birds. In addition, I expected to provide further documentation of disassortative mating based on intra-pair size differences. Because of the nature of the study I also anticipated obtaining data on fledging success, the return of young to breed, and age of first breeding; all of these being data that were lacking for Least Sandpipers.

# STUDY AREA

This study was conducted at Masset, British Columbia, Canada in Delkatla Inlet (54° 02′ N 132° 06′ W) and surrounding areas during 1984-1988. Masset is located on the northeast corner of Graham Island, the largest island in the Queen Charlotte Island archipelago (Figure 1). The Delkatla Wildlife Sanctuary (hereafter Delkatla), which contains all of Delkatla Inlet inland of a road causeway, was the focus of the research (Figure 2). Delkatla contains 111 ha of mudflats and marshlands and 111 ha of meadowlands (Crippen Consultants Ltd. 1986). Delkatla is bordered to the north, east and south by coniferous forest and, to the west, by the Village of Masset (Figure 2).

Historically, Delkatla Inlet was an intertidal estuary with significant amounts of marine mudflats exposed at low tide. The inlet was used extensively as a feeding and staging area by migratory waterfowl and shorebirds. During 1964, a solid causeway was built across Delkatla Inlet to provide road access to Masset. Two culverts were installed to allow discharge of excess water from the inlet, but inflow of saltwater was prevented. During 1977, two-way culverts were installed to allow flow of saltwater into Delkatla. However, because of the limited amount of discharge, the effects on salinity were negligible (Crippen

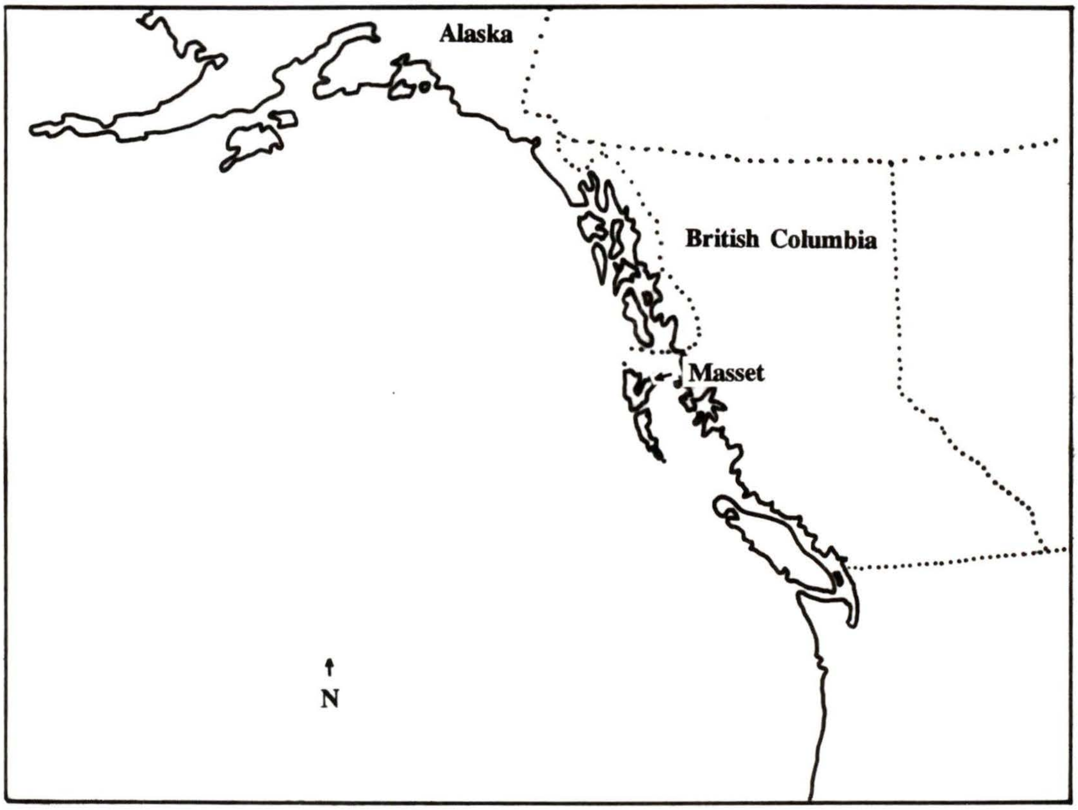


Figure 1. The study area was located at Masset, on the northeastern tip of Graham Island. The Queen Charlotte Islands archipelago is about 80 km west of the British Columbia mainland.

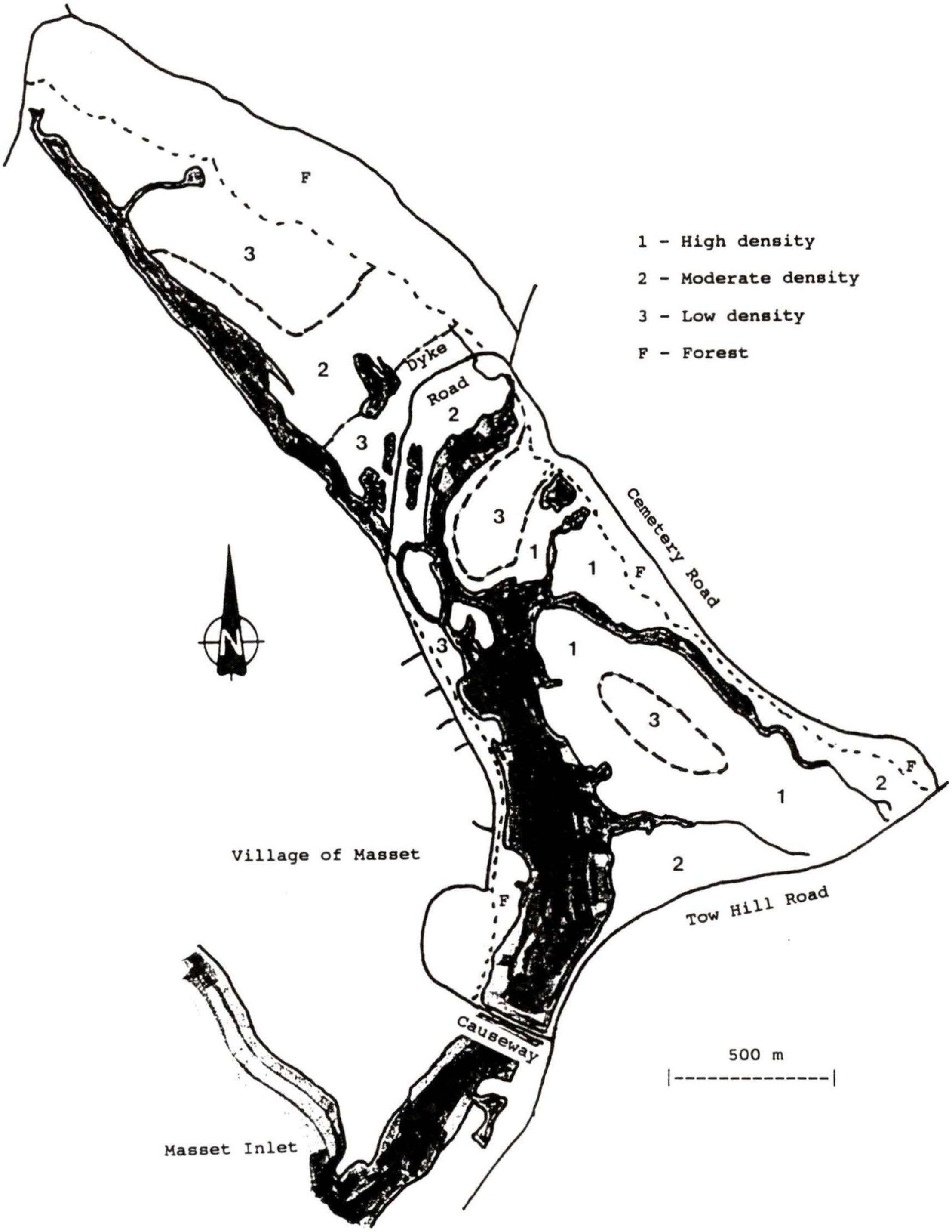


Figure 2. Areas of high, moderate and low densities of Least Sandpiper nests in Delkatla Inlet, 1984-1988.

Consultants Ltd. 1986). As a result, Delkatla began to gradually change from an estuarine intertidal habitat to a freshwater marsh habitat.

Since 1964, Delkatla has reverted to a freshwater, acidic environment with freshwater aquatic species occurring in the permanent water. Exposed mudflats occur when low tides drain the inlet. Upland areas are generally open with grasses, sedges, rushes, herbs and mosses occurring in elevational bands above the high tide line (Appendix 1). Sitka spruce (*Picea sitchensis*) and red alder (*Alnus rubra*) are encroaching rapidly along the open upland edges near the surrounding forest and on drier sites farther out in the marsh, while the rush *Juncus effusus* is invading much of the moister upland and crowding out grasses and sedges.

Least Sandpipers were first confirmed as breeding at Delkatla during 1983 (P. Hamel pers. comm.; Miller 1985), although they likely had been established for several years prior to discovery. Research during 1984 suggested that the density of the Delkatla breeding population was unusually high for the species.

Additional observations were made at: a golf course complex 3 km east of Masset where a few pairs of Least Sandpipers occurred along the edges of drainage ditches;

along sand-dune beaches northeast of Delkatla where Least Sandpipers occurred near temporary freshwater pools; and Delkatla Inlet outside the causeway where Least Sandpipers foraged in intertidal areas.

## METHODS

During 1984 and 1985 observations were made almost daily from late May to late June. Delkatla was visited almost daily from early May to late July during 1986 and from early May to early August during 1987-1988. Nests were searched for from the beginning of egg laying in mid May to early July; searches during 1984-1985 were less systematic and began in late May. Nest searches were mainly conducted by teams of two people dragging a 30-m length of rope between them. Searches were conducted so that the entire study area was systematically searched four or five times per year. Most nests were discovered by flushing incubating birds and some nests were found by spotting the nest cup as an observer walked along. Nest locations were marked by stakes placed 7 m to the north of the nest cup, and were mapped on base maps during 1986-1988. Each nest was visited every day, or every second day, after being found.

Adult birds were caught on the nest with a simple drop trap (Miller 1977). Chicks were caught as nestlings or, in a few cases, shortly after they had left the nest during 1986-1988. All adult birds were banded with one United States Fish and Wildlife Service (USFWS) aluminum leg band and a unique combination of coloured plastic leg bands during 1984-1988. All chicks were banded with one USFWS aluminum band during 1986 and both an aluminum and coloured bands during 1987-1988. Thereafter, all positive identifications of known individuals were recorded.

Because coloured bands faded somewhat between years, all colour bands were replaced each year a bird was captured. Some positive identifications of birds that were not captured in a year subsequent to its year of banding were made by reading the band number through a 20-45X spotting scope or by determining the combination of recognizable (but faded) coloured bands. Some birds that were identified only by old colour band combinations were accepted as returning birds (two or more "positive" identifications were required).

Three measurements were taken on most adults: length of exposed culmen (bill length) and wing chord were measured to the nearest 0.1 mm with dial calipers; and body mass was weighed to the nearest 0.1 g with a Pesola spring balance. Mass was measured during incubation, usually the first time a bird was captured. Gender was determined by a combination of behavioural observations and measurements (Miller 1983a,b, 1985; Hayman et al. 1986).

The date the first egg was laid was taken to be the "start of breeding" for a pair. Clutch-initiation dates were determined by direct observation during the laying period or by back dating (26 days) from the date of hatching. The laying of definitive four-egg clutches was considered to require five days (Miller 1983a), while the incubation period was determined to be 21 days (Miller 1983a; this study). Eggs of known egg-laying sequence were marked with indelible ink to allow identification of specific eggs throughout the incubation period. Eggs were considered to have hatched if the chick had completely extricated itself from the shell. A clutch was considered to have hatched successfully if at least one egg hatched.

Replacement clutches were clutches known to be the second clutch produced by a pair in one season. To minimize the inclusion of replacement clutches in analyses related to the start of breeding (which would give later dates for start of breeding), I excluded clutches initiated later than 25 days after the laying of the first egg each year for most analyses of first clutches (following Jönsson 1987).

Egg length (EL) and breadth (EB) were measured to the nearest 0.1 mm with dial calipers. Egg volume (EV) was estimated as an index of volume: $EV = (EL)(EB)^2$ (Väisänen et al. 1972).

Broods were located on a daily basis, by searching the area where they were last observed, to confirm their survival during 1987-1988. Broods were considered to be alive if one or two adults were present and they exhibited protective parental behaviour (Miller 1985), or if one or more young were found. Adults exhibiting protective parental behaviour were considered to be attending their broods [see Cooper and Miller (1992) for possible confounding behaviours], and were tracked daily until parental behaviour ceased.

Chicks were considered to have fledged if they were capable of sustained flight (17-20 days of age) and were positively identified (sighting confirmed by myself, or observed at least twice by other observers). A great effort was made to identify all fledged chicks. Although it is possible that some chicks fledged but were not observed, and thus not counted as having fledged, I believe this possibility to be extremely low. A brood was considered to have fledged successfully if at least one chick fledged.

The precise age of older birds was known for relatively few individuals whereas minimum ages were known for all others. This occurred because most breeding adults were captured for the first time at an unknown age. Age classes for adults were, therefore, divided into older birds (2 years old and older) and yearlings (1 year old) for purposes of comparing age effects.

Foraging areas in and near Delkatla Inlet were searched periodically throughout the season to document the occurrence of fledged young and previously banded adults that were not captured at nests. Adults and fledglings were deemed to have departed the study area on the day after they were last observed.

Data were collected for each nesting attempt but were often incomplete for various reasons. Therefore, sample sizes for various analyses reported below often differ. Statistical analyses were performed with Systat (5.0). A probability level of $p \leq 0.05$ was considered to be statistically significant.

# RESULTS

## Summary of birds captured and banded

In this study 227 adult and 599 chick Least Sandpipers were captured and banded (Table 1). Of 468 captures of breeding birds (not including recaptures during a single year), 227 (48.5%) were initially captured as unbanded adults on nests, 173 (40.0%) had been captured and banded as adults in previous years, 62 (13.2%) were recaptured as yearlings in the year after they were banded as chicks, and 6 (1.3%) were recaptured 2 or more years after being banded as chicks. Banding effort increased each year from 1984-1987 and was most intensive in 1987 and 1988. By 1988, I estimated that approximately 80% of the breeding population on the study area was composed of banded birds. The breeding population at Delkatla was estimated to be about 90 pairs.

## Breeding Cycle

The breeding cycle of this population is summarized in Figure 3. Date of arrival of individuals could not be

| | Year | | | | | |
|---|---|---|---|---|---|---|
| | 1984 | 1985 | 1986 | 1987 | 1988 | Total |
| No. new adults banded | 46 | 33 | 55 | 62 | 31 | 227 |
| No. previously banded adults recaptured or seen | N/A | 12 | 33 | 42 | 86 | 173 |
| No. yearlings captured, banded as chicks in preceding year | N/A | 1 | 4 | 26 | 31 | 62 |
| No. adults captured, banded as chicks 2 or more years previously | N/A | N/A | 1 | 1 | 4 | 6 |
| Total no. breeders captured | 46 | 46 | 93 | 131 | 152 | 468 |
| Chicks banded | 37 | 49 | 143 | 191 | 179 | 599 |

**Table 1. Summary of banding data and resightings for Least Sandpipers each year.**

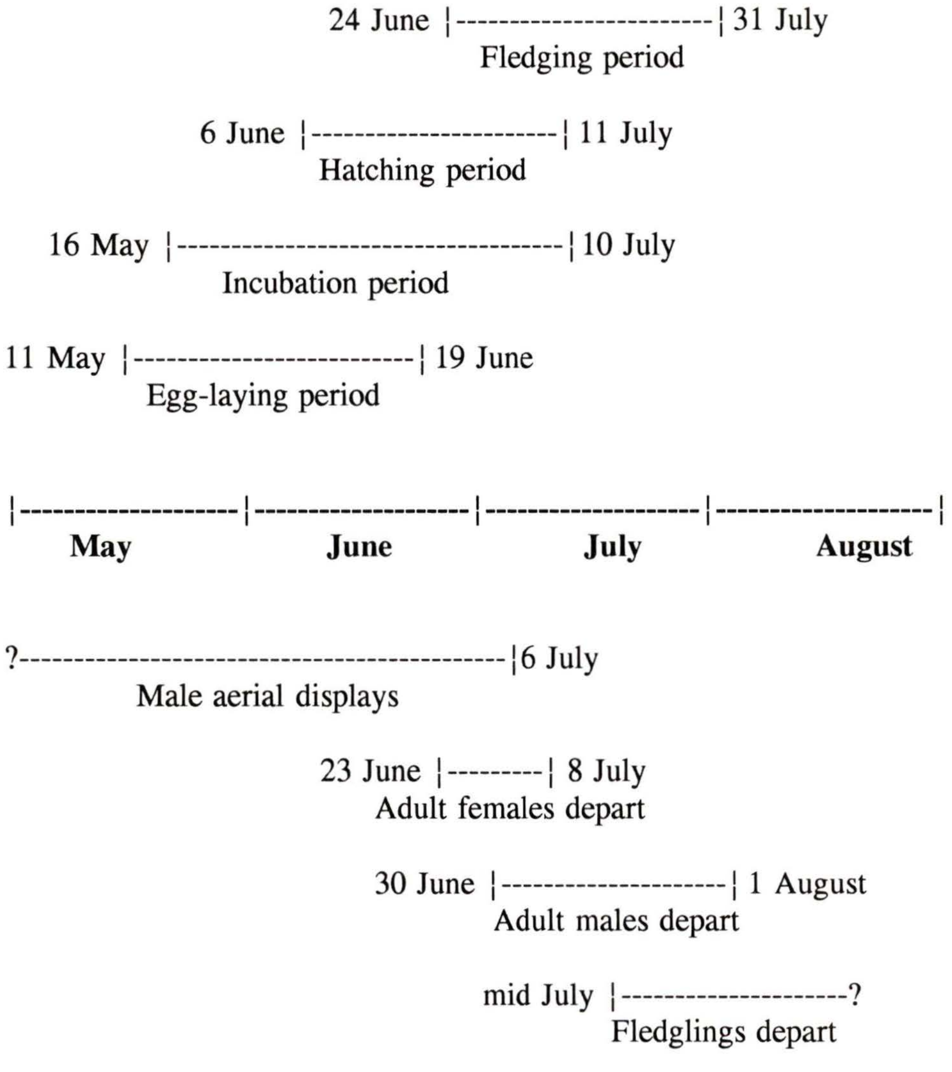


**Figure 3. Schematic summary of the breeding cycle of Least Sandpipers at Delkatla Inlet, Queen Charlotte Islands, 1984-1988.**

determined reliably, although males began arriving in late April each year (M. Hearne pers. comm.) and some were displaying when I arrived on the study site during early May. Males arrive before females and perform aerial displays over ephemeral territories in order to attract a mate (Miller 1983b). Relatively few displaying males were observed during the first week of May, but numbers increased through the end of May and early June, before declining through the remainder of June. A very few late-nesting males continued displaying until early July. Early in the season (May), nests were spaced farther apart than later (June), when new nests began to appear between established nests. Egg laying commenced in mid May (earliest date for the first egg laid was 11 May) and continued to mid June (latest date for the last egg laid was 19 June). Incubation of eggs occurred from 16 May to 10 July. Chicks hatched between 6 June and 11 July. Fledging of young occurred from 24 June to early August. Breeding females left Delkatla (presumably on the southward migration) between 23 June and 8 July while breeding males left between 30 June and 1 August. No adults were observed after the latter dates. With few exceptions, adults were not seen on the study site after they abandoned their brood, or after their final nesting attempt. Most fledglings departed between late July and mid August. By mid August only the extremely late-hatched fledglings remained on the study site.

## Body Measurements

Body measurements for each sex and age class are summarized in Table 2. Females had longer culmens and wing chords, and were heavier than males. Older females had significantly longer wing chords and were significantly heavier than yearling females, while older males had significantly longer wing chords than yearling males.

Regressions of relationships between culmen, wing chord and weight were done for each sex and age class. There were no significant relationships between weight, culmen or wing chord and age of females or older males. Weight was significantly positively related to culmen ($r^2$=0.281, p=0.020, n=19) and to wing chord ($r^2$=0.498, p=0.002, n=16) for yearling males.

Although culmen and wing chord are often used as indicators of "size" in the literature on shorebirds (e.g., Jehl and Murray 1986), I found no significant relationships between these two morphological features for any sex or age class. For yearling males, however, the relationship of culmen to wing chord was just nonsignificant ($r^2$=0.142, p=0.069).

|  | Sex | Age | N | Mean | SD | Range | p* | M:F ratio |
|---|---|---|---|---|---|---|---|---|
| **Culmen (mm)** | F | All | 135 | 18.7 | 0.74 | 17.0 - 20.4 | <0.001 | 0.92 |
|  | M | All | 148 | 17.2 | 0.59 | 15.5 - 18.8 |  |  |
|  | F | 1 | 20 | 18.7 | 0.68 | 17.4 - 19.7 | 0.001 |  |
|  | M | 1 | 28 | 17.3 | 0.62 | 16.3 - 18.8 |  |  |
|  | F | 2+ | 73 | 18.7 | 0.82 | 17.0 - 20.4 | <0.001 |  |
|  | M | 2+ | 80 | 17.2 | 0.50 | 16.1 - 18.5 |  |  |
|  | F | 1 | 20 | 18.7 | 0.68 | 17.4 - 19.7 | ns |  |
|  | F | 2+ | 73 | 18.7 | 0.82 | 17.0 - 19.7 |  |  |
|  | M | 1 | 28 | 17.3 | 0.62 | 16.3 - 18.8 | ns |  |
|  | M | 2+ | 80 | 17.2 | 0.50 | 16.1 - 18.5 |  |  |
| **Wing chord (mm)** | F | All | 89 | 86.6 | 1.87 | 81.8 - 90.7 | <0.001 | 0.97 |
|  | M | All | 89 | 84.0 | 2.06 | 79.9 - 92.5 |  |  |
|  | F | 1 | 19 | 85.6 | 1.46 | 82.5 - 88.0 | <0.001 |  |
|  | M | 1 | 20 | 83.7 | 2.36 | 79.9 - 88.6 |  |  |
|  | F | 2+ | 58 | 87.0 | 1.90 | 81.8 - 90.6 | <0.001 |  |
|  | M | 2+ | 62 | 84.9 | 2.09 | 81.4 - 92.5 |  |  |

**Table 2. Summary of data on body measurements of Least Sandpipers, and on age and sex differences. M/F ratio is provided for each measurement to show relative sizes.**

*** Differences were tested with Student's t-test**

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | F | 1 | 19 | 85.6 | 1.46 | 82.5 - 88.0 | 0.003 | |
| | F | 2+ | 58 | 87.0 | 1.90 | 81.8 - 92.5 | | |
| | M | 1 | 20 | 83.7 | 2.36 | 79.9 - 88.6 | 0.03 | |
| | M | 2+ | 62 | 84.9 | 2.09 | 81.4 - 92.5 | | |
| **Weight (g)** | F | All | 85 | 23.7 | 1.54 | 19.8 - 29.0 | <0.001 | 0.94 |
| | M | All | 74 | 22.2 | 1.90 | 18.8 - 28.5 | | |
| | F | 1 | 19 | 22.8 | 1.24 | 19.9 - 24.7 | 0.018 | |
| | M | 1 | 16 | 21.3 | 1.51 | 18.7 - 24.8 | | |
| | F | 2+ | 50 | 23.8 | 1.35 | 20.9 - 26.4 | 0.003 | |
| | M | 2+ | 42 | 22.0 | 1.40 | 19.7 - 26.4 | | |
| | F | 1 | 19 | 22.8 | 1.24 | 19.9 - 24.7 | 0.005 | |
| | F | 2+ | 50 | 23.8 | 1.35 | 20.9 - 26.4 | | |
| | M | 1 | 16 | 21.3 | 1.51 | 18.7 - 24.8 | ns | |
| | M | 2+ | 42 | 22.0 | 1.40 | 19.7 - 26.4 | | |

**Table 2 cont. Summary of data on body measurements of Least Sandpipers, and on age and sex differences. M/F ratio is provided for each measurement to show relative sizes.**

*** Differences were tested with Student's t-test**

## Eggs and Clutches

Most complete first clutches contained four eggs (5 eggs-1; 4 eggs-247 (92%); 3 eggs-20; 2 eggs-2). Two-egg clutches are not normal definitive clutches in northern-breeding scolopacids, while three-egg clutches may typify one species and occur occasionally in others (MacLean 1972). Clutches with fewer than four eggs may have been found after damaged eggs had been removed by the parents or after the clutch had been partially depredated. The removal of a damaged egg was witnessed at one nest, and presumed at several other nests, from which damaged eggs disappeared. The single clutch of five eggs was thought to have been laid by a single female because colours and pigment patterns were similar on all eggs. Replacement nests included 22 clutches (79%) with four eggs and six (21%) with three eggs.

Measurements of EL, EB, and EV are summarized in Table 3. Mean EV per clutch for the population was highly constant across years (ANOVA, F=0.050, df=4, p=0.995), as was EL

| | Mean | SD | Range | n |
|---|---|---|---|---|
| Length (mm) | 28.5 | 0.93 | 25.3 - 32.1 | 1131 |
| Breadth (mm) | 20.7 | 0.45 | 19.1 - 23.3 | 1131 |
| Mean egg volume (cc) | 12.2 | 0.60 | 10.47 - 14.26 | 298 (clutches) |

**Table 3. Measurements of Least Sandpiper eggs.**

(ANOVA, F=0.405, df=4, p=0.805) and EB (F=0.138, df=4, p=0.968). Mean EV per clutch for early and late clutches (median = day no. 15) during 1986-1988 was also similar (ANOVA, F=0.152, df=1, p=0.697, n=191 clutches).

Mean EV varied positively with female weight for older ($r^2$=0.101, p=0.018, n=55) and yearling females ($r^2$=0.219, p=0.028, n=22; Figure 4). The slopes of the regression lines did not differ significantly, nor were Y-intercepts significantly different. Both age classes of females laid eggs with similar mean EVs [12.25 cc (n=79 clutches) vs. 12.10 cc (n=23 clutches); ANOVA F=1.162, df=1, p=0.284]. There were no significant relationships of mean egg volume to female culmen or wing chord.

Mean EVs for all females in consecutive years were highly correlated (Pearson $r$=0.866, p<0.001, n=38; Figure 5). Correlations for yearlings (first and second breeding years) and older females were $r$=0.998 (p<0.001, n=5) and $r$=0.851 (p<0.001, n=33), respectively.

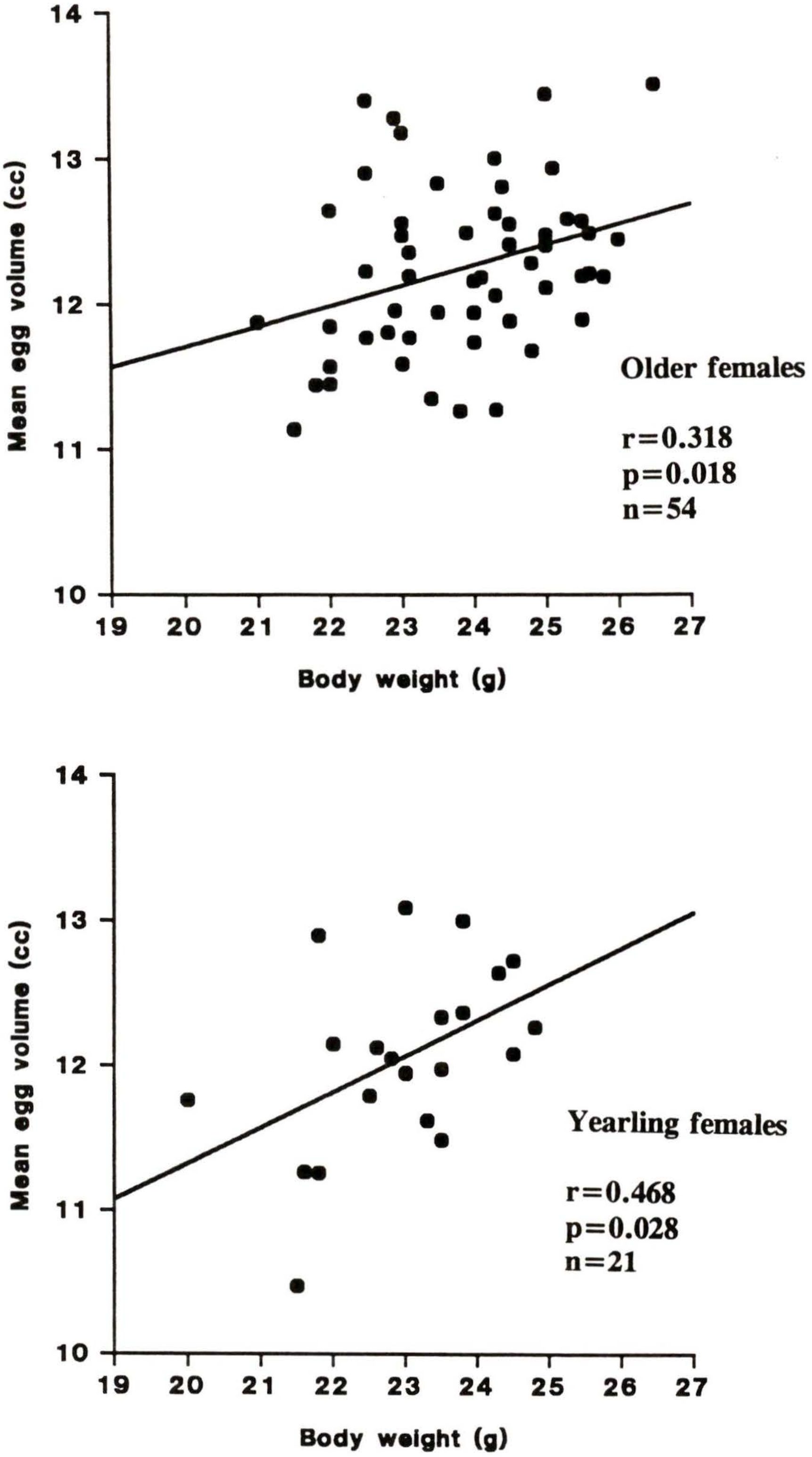


Figure 4. Relationship of mean egg volume per clutch to body weight for older (2+ year old) and yearling (1 year old) females. Data for the same females in different years are included.

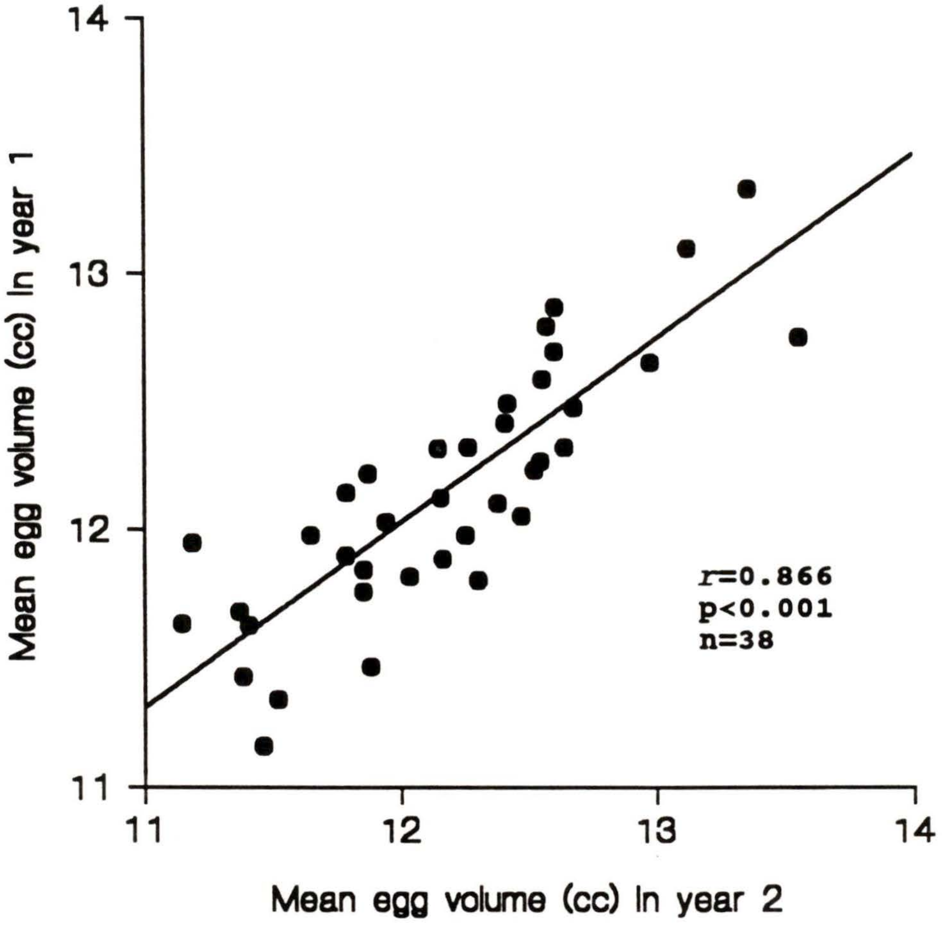


Figure 5. Mean egg volume per clutch of initial clutches for the same females during consecutive years. Data includes only the first two consecutive years for females with data for more than two years.

### Date of Clutch Initiation

Clutches were initiated between 11 May and 15 June (including first and replacement clutches), a range of about 5 weeks (Figure 6). Most first clutches were begun during the first 3 weeks of the egg-laying period.

Clutch initiations peaked rapidly during the first 1 to 2 weeks of the egg-laying season each year (Figure 6). Peak 3-day blocks of clutch initiations varied between years: days 10-12 in 1986; days 4-6 in 1987; and days 7-9 in 1988. A second peak occurred during 1986, 1988 and, overall, during the middle of the clutch-initiation period (days 16-24). This represents clutch initiations by pairs with yearling birds, plus replacement clutches of experienced pairs that had lost their first clutch relatively early during incubation. A third peak occurred during the last 6 days of the clutch-initiation period during all years. This peak likely comprises replacement clutches only, of early-nesting pairs that had lost their initial clutches late in incubation, plus late-nesting pairs that had lost their first clutches in early to mid incubation.

The date on which the first egg was laid by any individual in the population during 1984-1988 varied from 11 to 15 May (Table 4). Median dates for first clutch

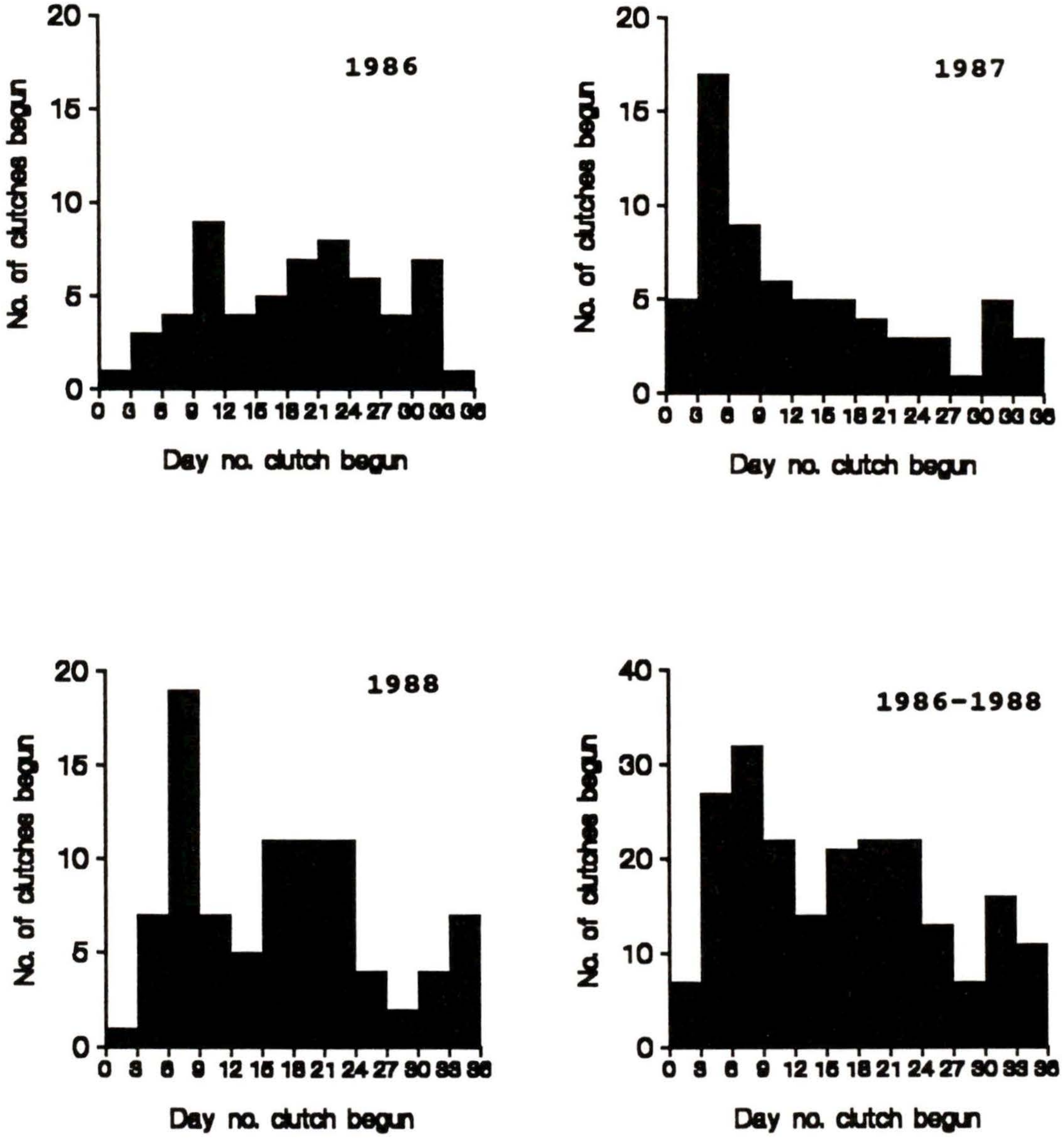


Figure 6. Seasonal trends in egg laying. Frequency histograms are shown for the number of clutches started in 3-day intervals (initial and replacement clutches).

| Year | Mean | SD (days) | Median | Earliest | n |
|---|---|---|---|---|---|
| | | First clutches | | | |
| 1984 | 26 May | 7.21 | 24 May | 15 May | 14 |
| 1985 | 21 May | 6.00 | 18 May | 13 May | 16 |
| 1986 | 25 May | 6.67 | 26 May | 11 May | 44 |
| 1987 | 20 May | 6.27 | 18 May | 12 May | 52 |
| 1988 | 23 May | 6.51 | 23 May | 11 May | 69 |
| | | Replacement clutches | | | |
| 1987 | 6 June | 6.39 | 3 June | 28 May | 8 |
| 1988 | 4 June | 9.02 | 1 June | 15 May | 11 |

**Table 4. Data on dates of clutch initiation for first and replacement clutches.**

initiation ranged from 18 to 26 May in different years (Table 4). Median clutch-initiation date for first clutches was significantly earlier during 1987 than 1986 (8 days earlier) and 1988 (5 days earlier; Table 4; Tukey HSD test, $p<0.005$). The median date for replacement clutch initiation of 2 June was about 13 days later than the median date of 20 May for initial clutches during 1987-1988.

There was no significant correlation ($r=0.359$, $p=0.120$, $n=20$) in clutch-initiation date for experienced females over successive years. One experienced female, however, laid the first egg of the year for the population during both 1987 and 1988. The only yearling female for which complete data are available laid eggs 3 days earlier in her second breeding season than in her first.

Data on clutch initiations for pairs with different breeding experience and age are summarized in Figure 7. During the first 25 days of the egg-laying period of 1987-1988, reunited pairs began laying initial clutches on average 4.5 days earlier than experienced but divorced pairs (18 May vs. 22-23 May). Although this difference was just nonsignificant statistically (Student's $t=2.027$, $df=31$, $p=0.051$), the trend probably reflects a genuine pattern for the following reasons. If I include data on all clutches for reunited and divorced experienced

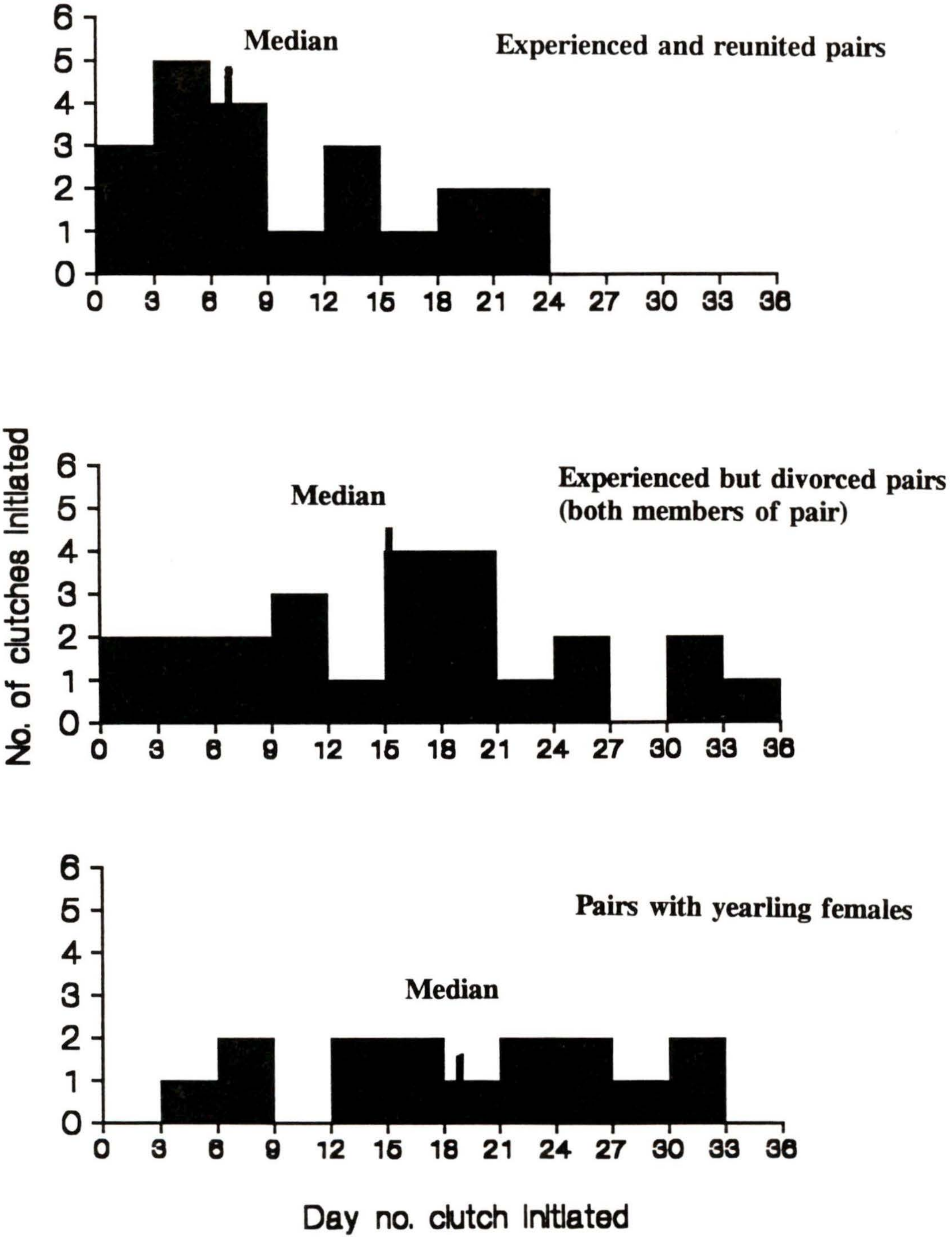
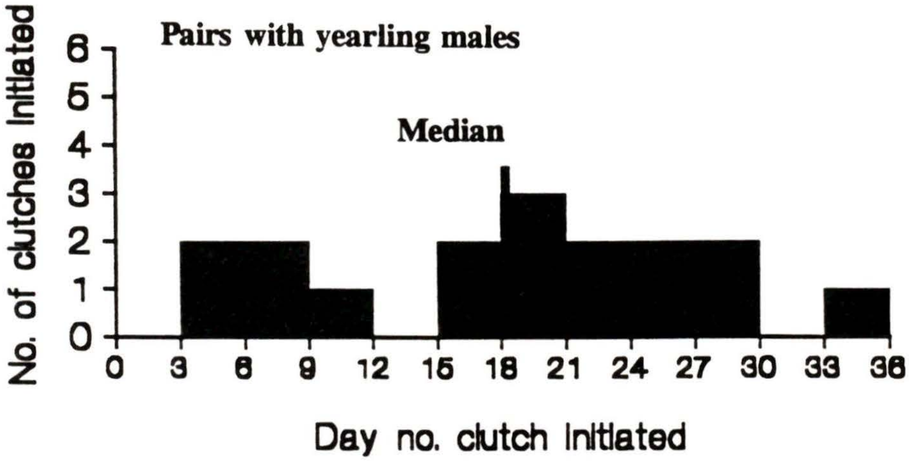


Figure 7. Relationship of nesting date to breeding experience and age.



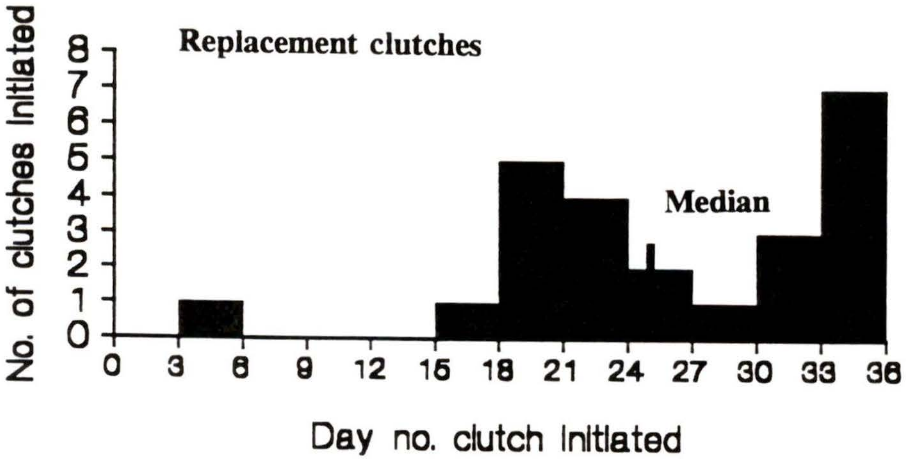


Figure 7. (Continued).

pairs, not known to be replacement clutches, but including those begun after the first 25 days of the egg-laying period, the mean difference is then 6.7 days and is statistically significant (Student's *t*=2.774, df=48, p=0.008). Although this analysis includes clutches that may have been misidentified as first clutches (see Methods), if I assume that I would have made the same error equally for both reunited and divorced pairs, then experienced reunited pairs nested significantly earlier than experienced but divorced pairs.

When I combined all pairs of birds with previous breeding experience (reunited and divorced pairs), experienced pairs began laying first clutches (mean = 19 May) 6 days earlier than pairs with yearling females or yearling males (mean = 25 May; Student's *t*=2.577, df=60, p=0.012). Pairs in which both members were yearlings (n=5) began laying first clutches later than all other pairs (mean = 29 May, Student's *t*=-2.719, p=0.026, df=46).

### Intra-pair Size Differences and Date of Clutch Initiation

I excluded reunited pairs from analyses of the effects of intra-pair size differences on date of clutch initiation because of the likely strong influence of familiarity in speed of pair formation. For experienced pairs in which both sexes were divorced there were no significant relationships between date of clutch initiation and culmen, wing chord or weight for either sex (Table 5). Also, there were no significant relationships in regressions between clutch-initiation date and intra-pair differences for culmen ($r^2$=0.001, p=0.871, n=34), wing chord ($r^2$=0.069, p=0.308, n=17) or weight ($r^2$=0.018, p=0.664, n=13).

For pairs with yearling males, date of clutch initiation was significantly related to male culmen (Table 5), meaning that shorter-billed yearling males nested earlier than longer-billed yearling males. For pairs with yearling females there were no significant relationships between date of clutch initiation and female culmen, however (Table 5). Nor were intra-pair size differences in culmen, wing chord, or weight significantly related to clutch-initiation date for pairs with yearling females or with yearling males. The slope of the regression between intra-pair difference in culmen length for pairs with yearling females and date of clutch initiation was negative, but insignificant (Figure 8).

|  | r | p | n | r | p | n |
|---|---|---|---|---|---|---|
|  | Experienced Females |  |  | Experienced Males |  |  |
| Culmen (mm) | 0.098 | ns | 48 | 0.120 | ns | 54 |
| Wing Chord (mm) | 0.229 | ns | 38 | 0.196 | ns | 40 |
| Weight (g) | -0.010 | ns | 37 | 0.057 | ns | 27 |
|  | Yearling Females |  |  | Yearling Males |  |  |
| Culmen (mm) | -0.369 | ns | 10 | 0.537 | 0.026 | 17 |
| Wing Chord (mm) | 0.192 | ns | 10 | -0.404 | ns | 13 |
| Weight (g) | -0.440 | ns | 10 | -0.422 | ns | 10 |

**Table 5. Relationship of date of clutch initiation to body measurements for experienced and yearling breeders, 1986-1988.**

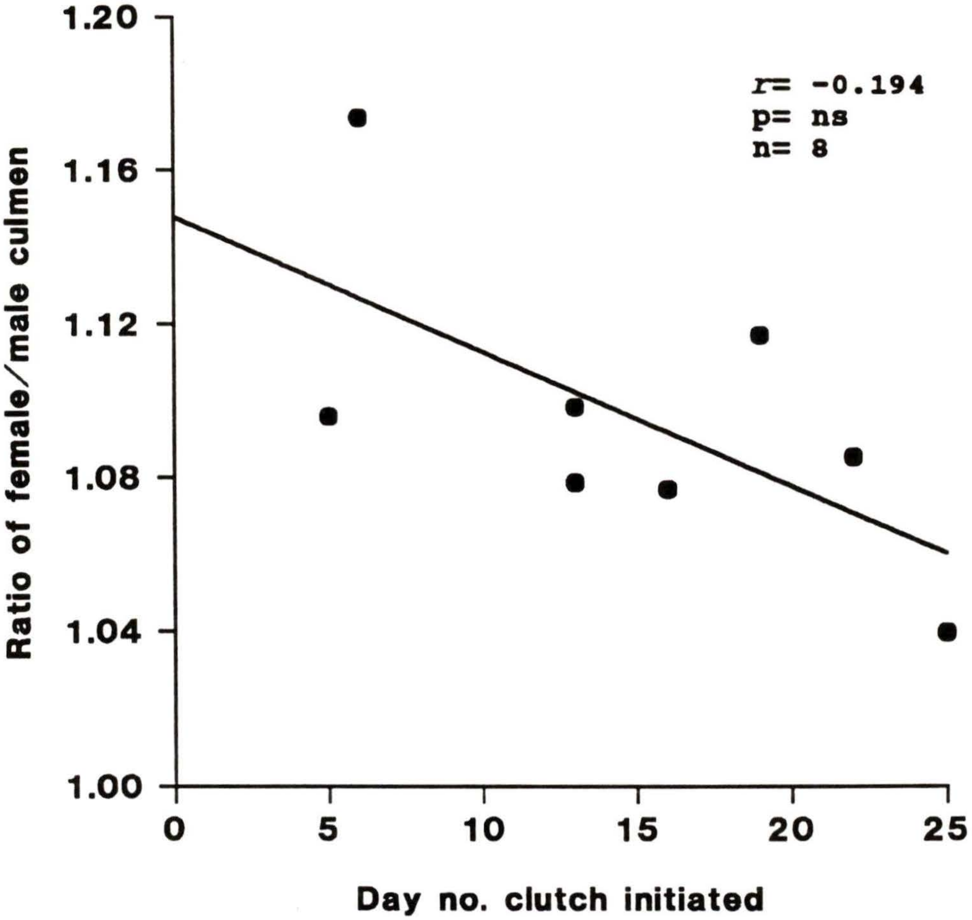


Figure 8. Relationship of laying date to sexual size dimorphism within pairs, for pairs that included yearling females.

**Hatching of Eggs**

Of 298 clutches found during 1984-1988, including clutches that were depredated or abandoned before incubation commenced, 169 (56.7%) hatched successfully. The numbers of clutches, numbers of eggs laid, and numbers of eggs hatched for clutches that hatched successfully are summarized in Table 6. Hatchability (proportion of eggs hatched in successful nests) of eggs in these clutches did not vary from 1984 to 1988 (ANOVA, F=0.450, df=4, p=0.772, n=169 clutches). The mean number of eggs that hatched in successful nests was 3.37 and the median was 4. In most cases, all eggs that were remaining in the nest at the time of hatching, hatched successfully. Frequencies of numbers of eggs hatched per clutch are summarized in Table 7.

For all clutches during 1986-1988, there was no significant relationship between date of clutch initiation and hatching success. After partitioning first-clutch initiation dates into early (day no. 1-12) or late (day no. 13-25 days) there was no significant difference in the probability of a first clutch hatching between early and late clutch-initiation dates (Chi-squared=0.32, df=1, p=0.573).

Experienced females that reunited with their previous

| Year | No. clutches | No. eggs laid | No. eggs hatched | Mean no. eggs hatched/clutch | % |
|---|---|---|---|---|---|
| 1984 | 10 | 40 | 37 | 3.70 | 92.5 |
| 1985 | 15 | 56 | 50 | 3.33 | 89.3 |
| 1986 | 41 | 159 | 136 | 3.32 | 85.5 |
| 1987 | 51 | 201 | 174 | 3.41 | 86.6 |
| 1988 | 52 | 205 | 172 | 3.31 | 83.9 |
| Total | 169 | 661 | 569 | 3.37 | 86.1 |

**Table 6. Annual summary of number of clutches found, eggs laid, and eggs hatched in nests that hatched successfully.**

| | Frequency | | | | |
|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | 4 |
| No. eggs hatched/clutch | 47 | 4 | 15 | 24 | 60 |
| No. fledglings/brood | 25 | 23 | 15 | 30 | 10 |
| No. yearlings returned/ fledged brood | 27 | 13 | 5 | 1 | 0 |

**Table 7. Data summary for frequencies of survivorship of eggs, fledglings, and yearlings. (Data for eggs and fledglings are from 1987-88 and include only clutches for which the number of eggs hatched was known precisely. Data for yearlings are from the 1987 brood-year only).**

year's mate were no more likely to lay clutches that hatched than experienced females that paired with a new mate (Chi-squared=0.08, df=1, p=0.771). However, experienced females were significantly more likely to lay clutches that hatched than yearling females (Chi-squared=15.16, df=1, p=0.023). This difference likely was due to a higher rate of predation by ravens on yearling female nests (40%) than on older female nests (19%).

There was no statistically significant relationship between mean EV per clutch and hatching success (Table 8).

## Replacement Clutches

Replacement clutches were laid by some, and possibly most, pairs if the first clutch laid was lost before eggs hatched or before 15 June. Replacement clutches were initiated on average 5.5 days after the loss of the first clutch (Table 9, Fig. 9). Initiation dates for replacement clutches were, obviously, significantly later than for initial clutches (Table 4). There was a weak, but nosignificant, negative trend for the interval to shorten as the nesting season progressed ($r^2$=-0.072, p=0.177). There was no significant difference in intervals between pairs with older or yearling females. There were insufficient

| | n | Mean egg volume (cc) | SD | p* |
|---|---|---|---|---|
| Clutches: | | | | |
| Hatched | 132 | 12.2 | 0.64 | |
| Failed | 111 | 12.2 | 0.59 | ns |
| Chicks: | | | | |
| Fledged | 84 | 12.2 | 0.63 | |
| Perished | 48 | 12.1 | 0.65 | ns |
| Yearlings: | | | | |
| Returned | 15 | 12.2 | 0.64 | |
| Did not return | 21 | 12.2 | 0.43 | ns |

**Table 8. Comparison of mean egg volume for clutches that hatched (1986-1988), fledged (1987-88), and returned yearlings (1987) with those clutches that did not.**

*** Differences were tested with Student's t-test**

| | Interval between first and second clutches (days | No.days first clutch incubated | Day no. first clutch was lost | Inter-nest distance (m) |
|---|---|---|---|---|
| Mean | 5.5 | 5.6 | 19.3 | 53 |
| SD | 1.93 | 5.20 | 5.99 | 37 |
| Median | 5 | 4 | 18 | 45 |
| Minimum | 2 | 0 | 10 | 6 |
| Maximum | 10 | 19 | 30 | 163 |
| n | 27 | 19 | 27 | 23 |

Table 9. Summary of data on timing and location of replacement clutches.

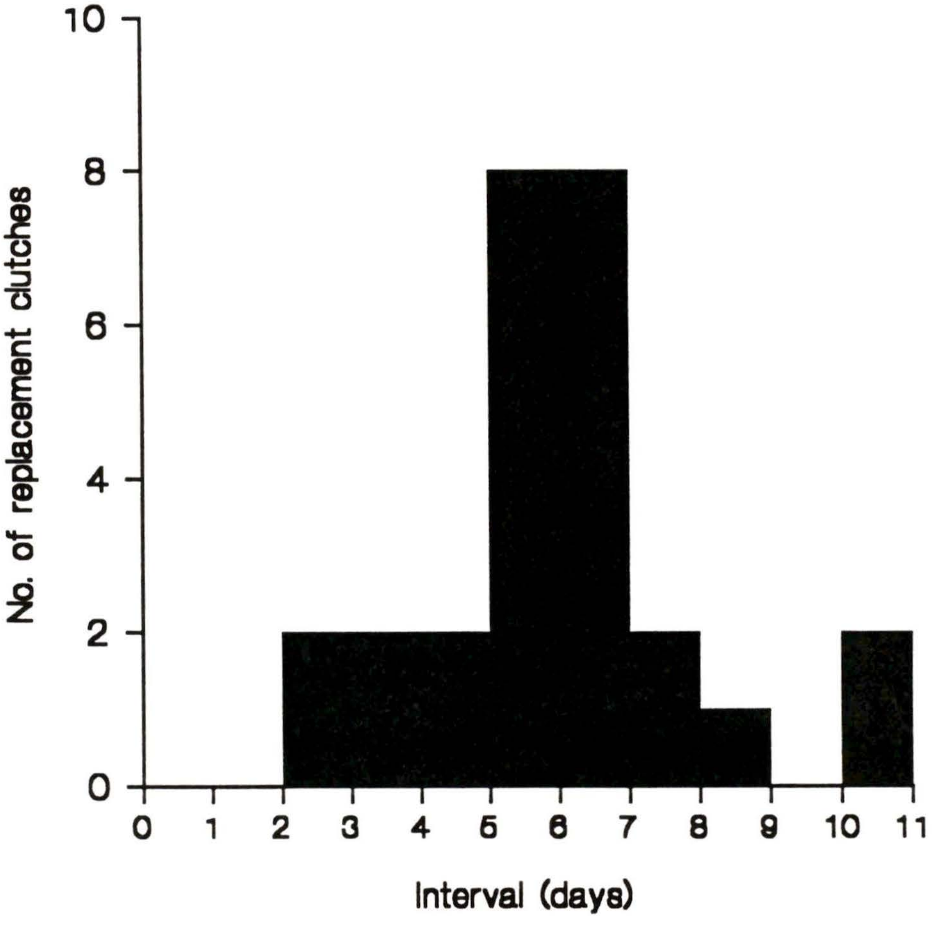


**Figure 9.** Frequency distribution of the interval between the loss of the first clutch and beginning of the replacement clutch.

data to compare reunited pairs with experienced, but divorced, pairs.

Replacement clutches were more likely to contain three eggs than initial clutches (mean=3.77 vs. 3.94; Student's *t*=2.219, df=16, p=0.041), although median clutch sizes for initial and replacement clutches were the same (i.e., four eggs). Mean EV per clutch of replacement (12.30 cc) and initial clutches (12.16 cc) were similar (Student's *t*-test, p=0.375).

From 1986 to 1988, 16 of 27 (59%) replacement clutches hatched, an almost identical hatching success as in first clutches [144 of 254 (58%)]. There was no significant difference in hatching success between replacement and initial clutches (Chi-squared=1.08, df=1, p=0.293). During 1987-1988, 10 of 14 (71%) replacement clutches that hatched, fledged young. This fledging success was slightly higher than the 64% (96 of 150) of hatched first clutches that produced fledged chicks. There was no significant difference between: (a) hatched and unhatched replacement clutches relative to date of clutch initiation; (b) interval between loss of the first clutch and initiation of the second clutch; (c) number of days the first clutch was incubated; (d) female age; or (e) male age. As with many very late clutches (those that would hatch in the first week of July), females tended to abandon very late replacement clutches before eggs hatched.

Of 27 cases, pair bonds were known to remain intact for 11 replacement clutches, were thought to remain intact for six clutches, and were unknown for 10 clutches. The unknown cases included nests for which only one member of a pair was identified for the initial or replacement clutches. Although data are lacking I believe that pair bonds remained intact for virtually all replacement clutches provided that both members of a pair were still present. Older females were no more likely to lay replacement clutches than yearlings (Chi-squared=0.040, df=1, p=0.848).

Two very unusual cases involving replacement clutches occurred. On 8 June 1986, a male of unknown age was trapped while incubating four eggs. This nest hatched four chicks on 22 June. Although the female was observed regularly with this brood, the male was not seen with her after the young hatched. On 25 June this same male was trapped while incubating four eggs on another nest, 126 m from his first nest. This second nest hatched three young on 1 July and the male attended the brood until at least 10 July. Because there were only nine days between the hatching of these two clutches, the male either: (a) abandoned his first clutch and mate during the middle of the incubation stage and mated with a second female; (b) abandoned his first clutch and mate after the eggs hatched and then paired with another female and helped incubate her clutch; or (c) mated with both females and incubated both clutches simultaneously, staying with the second clutch after the first one hatched.

During 1987, four chicks hatched from one nest on 8 June, but were thought to perish on 11-12 June. Neither banded adult from this nest was seen again from 12 to 18 June. Beginning on 18 June, first the female and then the male were found regularly in the vicinity of the first nest. On 10 July, the male was found with four young that were estimated to have hatched on 7-8 July. All four young fledged subsequently. The female was not seen with the young and likely had abandoned the brood after the eggs hatched, although she was present in the area during what would have been the incubation period. This was the only known case of a replacement clutch being laid after the loss of a brood.

## Fledging of Young

During 1987 and 1988, broods were monitored very closely so that confirmation of fledging could be made (Figure 10). During 1987, 107 banded chicks fledged.

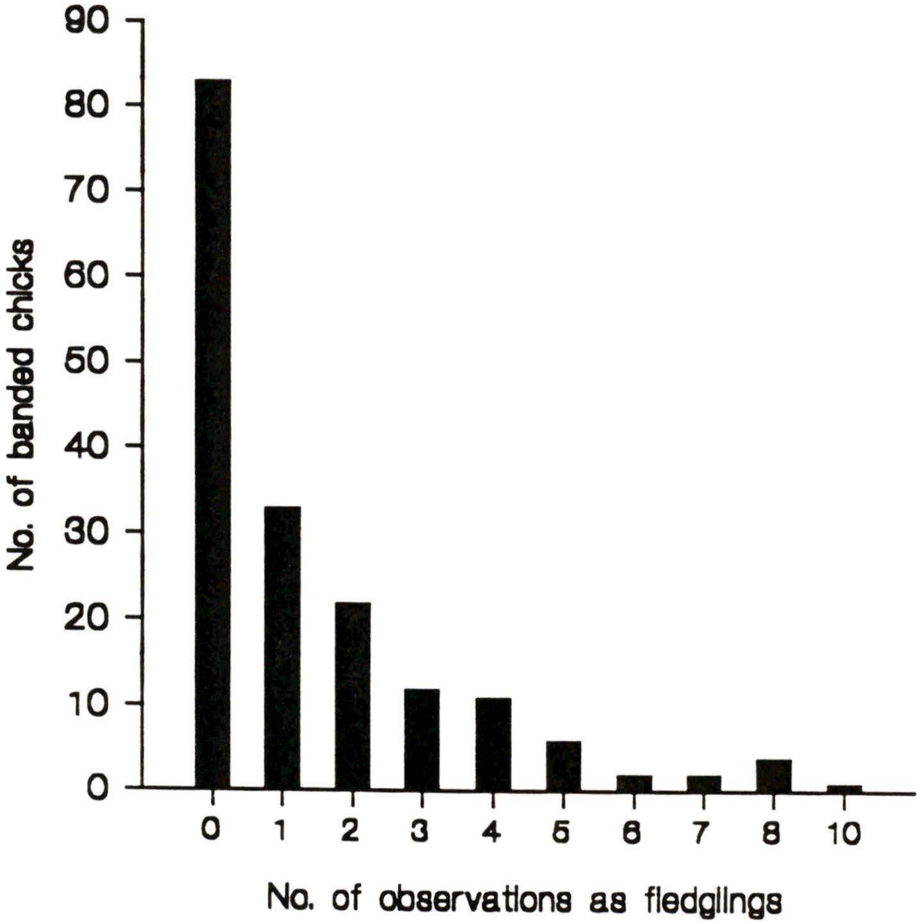


Figure 10. Frequency distribution of the number of banded chicks that were seen as fledglings (1988 data).

During 1988, 89 banded chicks fledged. Of these 196 fledglings, 13 were captured as mobile young from unknown nests and were, therefore, discounted from further analysis. The remaining 183 fledglings were banded as 1-day-old chicks, and each was confirmed as a fledgling capable of strong flight.

From the 79 known clutches that produced fledglings, 274 of 310 (88.4%) eggs hatched, and 183 of 274 (66.8%) chicks fledged. A summary of data on numbers of fledglings per brood is provided in Table 7. Although the number of clutches that produced fledglings was similar between 1987 and 1988, fledging success varied slightly between years (Table 10). The mean difference in fledglings per brood of 0.41 fledglings was not statistically significant, however (Student's $t$=1.857, p=0.067). Over the two years, a mean of 2.32 chicks fledged per nest in which eggs hatched.

For initial clutches that hatched successfully during 1987-1988 (n=79), there were no differences in fledging success (fledging of at least one chick) between early (days 1-12) and late (days 13-25) clutch initiations (Chi-squared=0.005, df=1, p=0.943).

For nests that hatched (including replacement clutches), the number of chicks per nest that survived to

| Year | No. clutches | No. eggs hatched | No. fledglings | Mean fledglings/ clutch | SD | % Fledglings/ hatched eggs |
|---|---|---|---|---|---|---|
| 1987 | 39 | 138 | 98 | 2.5 | 1.02 | 71.0 |
| 1988 | 40 | 136 | 85 | 2.1 | 1.01 | 62.5 |

**Table 10. Data summary on fledglings, from nests that produced fledglings.**

fledge was slightly inversely related to date, but the regression was nonsignificant ($r$=-0.039, p=0.207, n=107). Of special interest is the last clutch to hatch during 1988 (7 July): all four young fledged after the female abandoned the nest 3 days before hatching and the male abandoned the brood after 8 days. The successful fledging of this brood, with relatively little parental care, suggests that the length of the breeding season at Delkatla is not constrained by the ability of chicks to fledge in mid summer.

Replacement clutches (n=10) fledged more young per nest than initial clutches (n=69), but the difference was just statistically nonsignificant (ANOVA, F=3.337, df=1, p=0.072).

Pairs with experienced females fledged at least one young (28 of 50 clutches) significantly more often than pairs with yearling females (7 of 21 clutches; Chi-squared=15.52, df=2, p<0.001), mainly because of higher hatching success. However, when considering only clutches that hatched, then fledging success for yearling and older female was similar (ANOVA, F=0.329, df=1, p=0.570).

Clutch-initiation dates for pairs with older females were similar (< 1 day difference) for pairs that fledged or did not fledge chicks (Student's $t$=0.326, p=0.746).

Although yearling females that fledged broods nested on average 3.8 days earlier than yearling females that did not fledge broods, the mean difference was, again, nonsignificant (p=0.453).

Reunited pairs fledged more young per nest from initial clutches (median=3) than experienced but divorced pairs (median=2); however the mean difference was statistically nonsignificant (Table 11; ANOVA, F=1.973, df=1, p=0.170).

There was no significant relationship between the duration of female brood attendance and number of chicks fledged ($r^2$=0.026, p=0.182, n=71). However, there was a significant positive relationship for males ($r^2$=0.067,p=0.025, n=74).

Fledging of young was not significantly related to mean EV per clutch (Table 8).

## Duration of Parental Care

Parents typically shared incubation until eggs hatched, then tended their young for varying lengths of time. Data on brood attendance for broods that fledged are summarized in Table 12. Data for adults from broods that were adopted

| | Mean fledglings/ clutch | SD | Median | n |
|---|---|---|---|---|
| Reunited pairs | 2.4 | 1.00 | 3 | 12 |
| New pairs | 1.8 | 0.83 | 2 | 16 |

**Table 11. Fledging success of experienced pairs that were reunited or newly formed.**

| | Female attendance | Male attendance | CID |
|---|---|---|---|
| Mean | 7.9 | 17.5 | 14.3 |
| SD | 4.9 | 5.2 | 9.3 |
| Median | 8.0 | 18.5 | 14.0 |
| Minimum | -3.0 | -1.0 | 1.0 |
| Maximum | 18.0 | 25.0 | 35.0 |

**Table 12. Duration of parental care of broods and mean clutch initiation day no. (CID) for pairs that fledged chicks, 1987-1988.**

by other adults were not used [see Cooper and Miller (1992)]. The mean difference between females and males was 9.6 days; and brood attendance between the sexes differed significantly (Student's $t$=-11.944, df=69, p<0.001). Brood attendance was highly negatively correlated with date of clutch initiation for females and moderately negatively correlated for males (Figure 11; $r$=-0.750, p<0.001, n=68 for females and $r$=-0.548, p<0.001, n=73 for males).

Males typically tended early-hatching broods until the chicks fledged or perished, whereas females abandoned early-hatching broods several days before chicks fledged. Many males from early-hatching nests exhibited protective parental behaviour several days beyond the date their chicks fledged (see Miller 1985). Male brood attendance was less highly correlated with date than female brood attendance, because male attendance remained more constant over the season, while females from very late nests (still being incubated in early July) tended to accelerate abandonment of their nests, often leaving before their eggs hatched. In fact, several males completed the last 1-4 days of incubation alone. Two clutches, abandoned by the females 3 and 4 days before hatching, hatched successfully but did not produce fledglings. One clutch abandoned by the female 2 days before eggs were due to hatch, hatched and fledged chicks. Of two clutches abandoned by the female 1 day before hatching, one hatched and fledged chicks while the other hatched but did not fledge chicks. All four clutches that were abandoned by the female on the day of hatching produced fledged chicks. Late in the season, broods were able to fledge without any attendance by females and with males abandoning a few days before fledging.

Mean duration of brood attendance of broods that fledged for yearling females (mean=7.3 days), compared with older females (mean=7.6 days), did not differ significantly (Student's $t$=0.131, p=0.897). The effect of length of pairbond on duration of parental care was nonsignificant for experienced females for pairbonds of one versus two or more years (Student's $t$=1.785, p=0.083).

Conversely, yearling males (mean=14.5 days) attended broods for a significantly shorter duration than older males (mean=18.9 days; Student's $t$=-2.792, df=45, p<0.01). This effect is likely due to yearling males nesting 4.5 days later than older males (p=0.008) and, since brood attendance is negatively correlated with date, later-nesting birds abandoned their broods earlier.

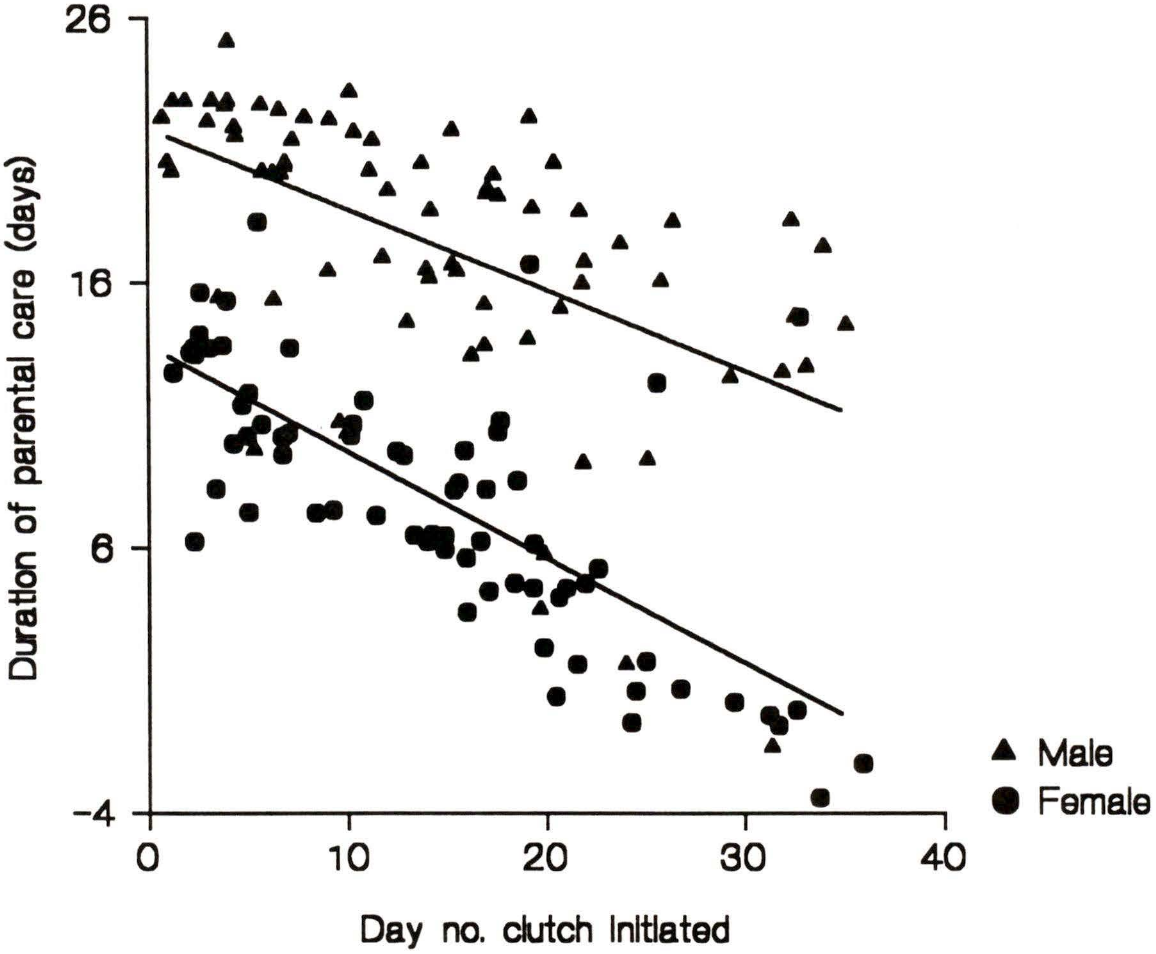


Figure 11. Relationship of the length of brood attendance to clutch initiation.

## Age of First Breeding

Of the 68 breeders recaptured after being originally banded as chicks, 62 (91.2%) were captured as yearlings. The remainder (8.8%) were captured at 2-3 years of age. Because not all birds were captured each year, and because over 90% of the breeding birds that were banded as chicks were initially captured as yearlings, it is possible that those breeders recaptured for the first time at 2 or 3 years of age, after being originally banded as chicks, may have bred at Delkatla during their first year and were simply not captured. In any case, because over 90% of the fledglings that were captured were captured as breeding yearlings, it is reasonable to conclude that the age of first breeding for the majority of this population of Least Sandpipers is 1 year.

Yearlings composed a large proportion of the breeding population at Delkatla. During 1987-1988, yearlings banded as chicks the previous year comprised 19.8% and 19.1%, respectively, of all breeding birds captured.

## Return of Young To Breed

During 1985-1988, 62 yearling birds were captured at nests. Thirty-five of 60 birds that were positively sexed were males and 25 were females, a ratio that does not differ significantly from unity (Chi-squared=1.66, df=1, $0.05<p<0.10$).

The sex ratio of yearlings captured during 1987 (12 males:13 females) was significantly different than during 1988 (18 males:11 females; Table 13; Chi-squared=3.308, df=1, $p<0.05$).

During 1988, 31 of 107 (29.0%) young that fledged in 1987 returned to breed as yearlings: 18 males; 11 females; and two birds of unknown sex. Complete data (number of chicks fledged and number of yearlings returning the following year) are available for 1987 only. Of 44 broods in which the number of young fledged was known during 1987, 17 broods (n=43 fledglings) were known to have produced yearlings (n=24) that returned to nest during 1988. The other seven yearlings originated from broods in which the

| Year | No. yearlings captured | No. males | CID |  |  | No. females | CID |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  | Mean | SD | Median |  | Mean | SD | Median |
| 1985 | 1 | 1 | N/A | N/A | N/A | 0 | N/A | N/A | N/A |
| 1986 | 4 | 3 | N/A | N/A | N/A | 1 | N/A | N/A | N/A |
| 1987 | 26 | 12 | 17.3 | 5.03 | 16.5 | 13 | 18.0 | 6.12 | 20.0 |
| 1988 | 31 | 18 | 9.6 | 9.96 | 5.0 | 11 | 10.9 | 9.06 | 7.0 |
|  | 62 | 34 | 12.8 | 9.70 | 11.5 | 25 | 14.9 | 8.19 | 18.0 |

Table 13. Data summary on the number of yearlings captured and clutch initiation dates (CID) for clutches that produced yearlings.

number of fledglings per brood in the previous year was not known. Yearlings were not captured from the remaining 27 broods that fledged young during 1987.

The return rate for yearlings during 1988, from broods that produced yearlings, was 55.8% (24/43). The minimum return rate during 1988, for all fledglings banded during 1987, was 29.0% (31/107). Comparisons of return rates for fledglings between years cannot be made because data on return of known fledglings are available for one year only. However, 136 day-old chicks banded during 1986 produced 26 captured yearlings during 1987 (19.1%), whereas 174 day-old chicks banded during 1987 produced 31 captured yearlings during 1988 (17.8%).

A comparison of data on fledglings per brood, numbers of yearlings returned, and clutch-initiation dates for 1987 nests that produced yearlings vs. nests that did not are summarized in Table 14. There were no significant relationships between production of yearlings that returned to breed and: (a) age class of parent; (b) experience of parent birds; or (c) parent body size.

Mean clutch-initiation dates for clutches that produced fledglings that returned to breed the following year were significantly earlier in 1987 than 1986 (Table 13; Student's

|  | No. Broods | No. Fledglings | Mean fledglings/brood | SD | Median fledglings/brood | Mean yearlings returned/brood | SD | Median yearlings returned/brood | Median CID |
|---|---|---|---|---|---|---|---|---|---|
| Broods that produced yearlings | 17 | 43 | 2.53 | 0.940 | 3 | 1.41 | 0.620 | 1 | 5.5 |
| Broods that did not produce yearlings | 27 | 64 | 2.37 | 1.120 | 2 | 0 | 0.000 | 0 | 10.0 |
| Total | 44 | 107 | 2.43 | 1.043 | 3 | 0.57 | 0.779 | 0 | 7.0 |

**Table 14. Data summary on fledging success and overwinter survival, for broods that fledged chicks during 1987.**

*t*=2.243, df=21, p=0.036 for females and Student's *t*=2.288, df=26, p=0.030 for males).

For broods during 1987 that were known to produce fledglings, mean clutch-initiation date was slightly earlier for clutches that produced fledglings that returned as yearlings during 1988 (19 May) than for clutches that produced fledglings that did not return as yearlings (24 May). However, this difference of 5 days was statistically nonsignificant (Student's *t*=1.532, df=38, p=0.134).

Mean EVs did not differ between clutches that produced fledglings that returned to breed and those that produced fledglings that did not return to breed (Table 9).

## Mate Fidelity

Mate fidelity in this population was extremely high. During 1986-1988, 31 pairs were known to retain the same mates from the previous year and many more were suspected of having done so. Only one pair failed to reunite when both members were known to be alive and nesting on the study site. Therefore, mate fidelity between years when both adults were present was 96.9%. Three of the 31 pairs were known to have remained paired for 3 consecutive years.

Reunited pairs nested in the vicinity of their nest from the previous year. Similarly, experienced males that mated with new females nested near their previous year's nest. Experienced females that paired with new males tended to nest farther from their previous year's nest compared with experienced males.

## Predation, Abandonment, and Observer Effects

Predation of Least Sandpiper nests by Common Raven (*Corvus corax*; hereafter raven) had a major impact on nesting success. All predation by ravens originated from one pair that nested in a nearby forest at the southern end of Delkatla. During 1987 and 1988 this pair foraged daily in Delkatla from May to mid June. During 1987, three fledged young foraged with their parents for several days before they all moved to the Masset dump. During 1988, the family moved to the dump after the fledgling ravens left the nest, without the family spending any time in Delkatla.

Ravens routinely searched for food in Delkatla by soaring low over the marsh or by landing and walking about, pecking at the ground. Depredation of two nests was witnessed. When nests were found, eggs were either eaten on site or carried away intact towards their nest, presumably to feed their young. Depredated nests were often visibly disturbed, but some were left intact. Although other potential predators [e.g., Northwestern Crow (*Corvus caurinus*), Sandhill Crane (*Grus canadensis*), raccoon (*Procyon lotor*), marten (*Martes americana*), red squirrel (*Tamiasciurus hudsonicus*) and ermine (*Mustela erminea*)] were known to occur in or near Delkatla, I attributed all predation to ravens due to lack of evidence to the contrary. Support for this conclusion was gained during both years when losses of nests to predators ceased after the ravens left Delkatla.

During 1986-1988, 74 of 257 (28.8%) nests were depredated by ravens (Table 15). The proportion of nests depredated increased each year: 1986 - 14.9%; 1987 - 30.2%; and 1988 - 38.1%. Daily predation rates on Least Sandpiper nests by ravens were calculated for 1988 (Table 16). Predation rates were relatively high for incomplete clutches of one to three eggs, and relatively low for four-egg clutches. Ravens were apparently able to locate uncovered nests more readily than nests being incubated. Early in the

| Year | No. clutches | No. hatched | No. depredated by ravens | No. destroyed by cattle | No. abandoned | Other |
|---|---|---|---|---|---|---|
| 1986 | 74 | 39 (52.7%) | 11 (14.9%) | 8 (10.8%) | 16 (21.6%) | 0 |
| 1987 | 86 | 45 (52.3%) | 26 (30.2%) | 10 (11.6%) | 4 (4.7%) | (1.2% |
| 1988 | 97 | 49 (50.5%) | 37 (38.1%) | 0 | 5 (5.2%) | (7.0% |
| Totals | 257 | 133 (51.8%) | 74 (28.8%) | 18 (7.0%) | 25 (9.7%) | (2.7% |

**Table 15. Fate of Least Sandpiper nests, 1986-1988.**

| | No. eggs in clutch | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | Source |
| No. of nests | 16 | 23 | 28 | 50 | This study |
| Queen Charlotte Islands | 0.25 | 0.33 | 0.24 | 0.03 | " |
| Sable Island, Nova Scotia | 0.45 | 0.12 | 0.07 | 0.04 | Miller 1983 |

**Table 16. Estimated predation rate (nests/day) of Least Sandpiper nests, 1988.**

season, uncovered nests were more visible, when viewed from above, than later in the season when growth of vegetation around nests tended to obscure visibility.

Ravens appeared to forage more often near their own nest than farther away. During 1988, survival of Least Sandpiper nests was significantly lower for those nests within 1 km of the raven nest than for those more than 1 km distant (Table 17). However, during 1987, there was no significant difference. Considering all causes of nest mortality (predation, abandonment, destruction), nest survival during 1988 was significantly higher for nests over 1 km distant from the raven nest than for those nests within 1 km (Table 17). Again, during 1987, there was no significant difference in nest survival relative to distance from the raven nest.

Trampling of nests by domestic cattle (*Bos taurus*) was an important cause of nest mortality during 1986 and 1987 (11.3% of 160 nests), but not during 1988 when cattle were absent (Table 15). Eggs were crushed underfoot as animals walked along, or when a cow lay down. One nest containing four newly hatched young was found flattened, with all young crushed to death. The eggs from another nest appeared to have been consumed when the tuft of grass the nest was concealed in was grazed to ground level.

| | 1988* | | 1987** | |
|---|---|---|---|---|
| **Distance (m)** | **No. nests** | **Mean survival (days)** | **No. nests** | **Mean survival (days)** |
| < 500 | 18 | 12.4 | 12 | 19.4 |
| 500-1000 | 29 | 12.9 | 28 | 20.4 |
| 1000-1500 | 13 | 21.8 | 13 | 21.8 |
| >1500 | 16 | 23.9 | 13 | 20.7 |

**Table 17. Nest survival relative to the distance from the Common Raven nest.**

* 1988 Chi-squared = 17.36 $p<0.01$

** 1987 Chi-squared = 0.61 ns

Abandonment of nests occurred more frequently during 1986 than during 1987-1988 (Table 15). Abandonment resulted in the loss of 9.7% of nests during 1986-1988. Abandonment occurred for several reasons including: (a) accidental breaking of eggs during the flush, when approached by a human observer, which fouled the nest; (b) the disappearance of one member of a pair; and (c) the presumed mishandling of trapped birds. One male was thought to abandon its nest immediately after being severely entangled in the nest trap.

During 1988, I tested the effect of type of nest check by observers on nest survival, by estimating nest survival between nest checks, relative to the degree of disturbance during the previous nest check (Table 18). Three levels of nest checks were considered. There was no significant differences in nest survival among the various types of nest checks (Chi-squared=1.35, p>0.05, df=2). Of course, it was not possible to determine the effect on nest survival of finding a nest versus not finding a nest.

| Method | No. visits | No. depredated | No. not depredated | Per cent survival |
|---|---|---|---|---|
| Flushed incubator | 222 | 16 | 206 | 93 |
| Flushed incubator and handled eggs | 277 | 17 | 260 | 94 |
| Trapped or attempted to trap incubator | 142 | 6 | 136 | 96 |

**Table 18. Survival of nests between nest checks relative to the type of disturbance during the nest check, 1988 (nests 88-01 through 88-69)*.**

* Chi-squared = 1.35 $p>0.05$

# DISCUSSION

## Breeding Cycle

The timing of spring arrival to breeding areas in the Scolopacidae is believed to be adapted to average conditions there (Holmes 1966a; Perrins 1970). It is thought that species that breed at high latitudes will respond to local conditions and breed as early as possible because of the relatively brief nesting season (Soikkeli 1967); in this way chicks hatch when food is abundant (mainly small terrestrial arthropods - Holmes 1966b; Holmes and Pitelka 1968; Nettleship 1973). Least Sandpipers at Delkatla began laying eggs about 2 weeks earlier than on Sable Island, Nova Scotia (Miller 1983a) and about 3 weeks earlier than in northern Manitoba (Jehl 1970) and extreme northwestern British Columbia (J.M. Cooper unpub. data). However, production of fledglings was not influenced by date of nesting.

The Queen Charlotte Islands, although about 10° latitude farther north than Sable Island, are warmer and wetter during spring (Appendix 2; Miller 1983a). Conditions for breeding are likely more favourable at Delkatla at an earlier date in the spring, compared with Sable Island, because of the relatively mild Pacific maritime climate.

Conditions favourable for breeding also occur earlier at Delkatla than in more northern breeding areas such as mountainous areas of northwestern British Columbia (J.M. Cooper unpub. data) and northern Manitoba (Jehl 1970) where the climate is colder.

Some populations of northern scolopacids are known to breed earlier in warmer springs than in colder springs (Hildén and Vuolanto 1972; Green et al. 1977; Miller 1983a); while one population of Red Phalaropes did not breed at all during phenologically very late summers (Mayfield 1978). Timing of breeding at high latitudes is largely determined by the melting of snow cover, which determines the timing of emergence of prey (Holmes 1970; MacLean 1975). Snow is not a factor on the Queen Charlotte Islands because it occurs very rarely, and only during winter. I expected that the trend of delayed nesting during colder (later) springs would apply to all populations of northern scolopacids, including the population at Delkatla. During this study, breeding occurred earlier, on average, during 1987 than during 1988 or 1986, although the date on which the first egg of the year was laid varied by only 1 day between among years. Spring temperatures, however, were similar during 1987-1988. Although rainfall was about 50% greater during the spring of 1987 than during the spring of 1988 (weather data are not available for 1986), I do not believe that rainfall influences the onset of egg laying. The cause of the variation in the average beginning of egg laying between 1987 and 1988 remains unknown.

The egg-laying period at Delkatla was 40 days long (36 days for clutch initiations), about 1.3 times as long as for Least Sandpipers on Sable Island (Miller 1983a) and about 2.4 times as long as in northern Manitoba (Jehl 1970). This egg-laying period is longer than for most calidridine populations, which is usually about a month (Holmes 1971b, 1972; Norton 1973; Väisänen 1977), or 2-3 weeks for the northernmost breeding species (Drury 1961; Parmelee et al. 1968), and is likely due to the relatively long spring and summer on the Queen Charlotte Islands. The hatching period of 34 days was similar to the hatching period on Sable Island (Miller 1983a). The 6-day difference between egg-laying and hatching periods is explained mainly by the fact that some very late clutches at Delkatla were abandoned by one or both sexes and did not hatch.

Brood attendance is discussed in detail in a later section. Briefly, breeding females are present with broods throughout June, but by early July tend to abandon nests and leave the study site before eggs are hatched. Breeding males tend broods longer but all have left the study site by mid or late July. Breeding females leave Delkatla earlier than breeding males, a trend also evident in Least Sandpipers on Sable Island (Miller 1983) and in many other scolopacids (Jehl 1963; Page 1974; Cramp and Simmons 1983). Females are thought to need to depart to winter feeding grounds sooner than males because of their higher accumulated energy deficit (Ashkenazie and Safriel 1979). Miller (1983a) documented delayed departures for adult female Least Sandpipers, compared to males, after the end of parental care on Sable Island, as did Soikkeli (1967) for Dunlin. I found no such relationship at Delkatla. Post-breeding females apparently just disappeared from the study site, although it is possible they moved to foraging or staging areas outside my study area. South-bound migrants begin to appear on the British Columbia coast in early to mid July (Campbell et al. 1990; Paulson 1993). During mid and late July, southward-bound migrant adult Least Sandpipers, presumably from more northern breeding areas, began moving through Delkatla.

Fledglings migrated south later than breeding adults, another widespread trend in scolopacids (Paulson 1983). Fledged chicks from the earliest-hatching nests began to leave Delkatla during the third week of July, when downy chicks from late nests were present. It is unknown whether these fledglings migrated beyond the Queen Charlotte Islands or moved to nearby areas that were unsurveyed. No staging areas for Delkatla birds were found near Masset, however. Although substantiating evidence is lacking I believe that Delkatla birds began to move southward immediately upon leaving their breeding area. However, juvenile Least Sandpipers do not appear on the south coast of British Columbia or in coastal Washington until August (Campbell et al. 1990; Paulson 1983).

Overall, southward movements of resident Delkatla birds were early compared to more northern breeding populations, as is reasonable to assume due to latitudinal effects (Paulson 1983). However, small flocks of migrating juvenile Least Sandpipers began to arrive at Delkatla in early August, while late-hatching Delkatla fledglings were still present. These juvenile migrants were assumed to originate further north because very few Least Sandpipers nested outside Delkatla on the Queen Charlotte Islands.

The relatively long breeding season and mild climate of the Queen Charlotte Islands contrast with conditions in most breeding areas for northern calidridines. As noted by Miller (1983a) for Sable Island, these milder climatic conditions have not resulted in divergence from a one-clutch, monogamous breeding system, in contrast with southern breeding populations of Dunlin (Holmes 1966a; Soikkeli 1966, 1967). Conditions at Delkatla seem even more favourable than on Sable Island for fostering similar divergences. That no changes have occurred at Delkatla in the Least Sandpiper's very conservative breeding system may reflect, in part, the relatively brief period since the habitat was colonized and the deeply-rooted genetic traits governing breeding behaviour in the species.

## Body Measurements

Consistent with the "reversed" sexual dimorphism in many monogamous shorebirds, female Least Sandpipers at Delkatla were larger than males. Measurements of culmen, wing chord and mass were comparable generally to measurements reported elsewhere for this species (Cramp and Simmons 1983; Miller 1986; Paulson 1993). Culmen lengths were shorter than those reported on Sable Island (Miller 1986); on average females were about 0.8 mm shorter and males about 0.6 mm shorter. Mass of breeding birds in northern Alaska were 1-2 g lighter than breeding birds at Delkatla; those of wintering birds in Surinam and the Caribbean were about 4 g lighter (Cramp and Simmons 1983); and migrants along the Pacific Northwest were about 1-2 g lighter (Paulson 1993).

Older females were about 1 g heavier and had longer wings than yearling females, but culmens were similar in length. Older males had longer wings than yearling males but weight and culmen were similar. These are the first such data presented for different age classes of Least Sandpipers on the breeding grounds. Cramp and Simmons (1983) reported no differences in wing lengths between age classes for wintering birds. In Semipalmated Sandpipers in northern Manitoba, there were no differences in body measurements or mass between older and yearling breeders (Gratto et al. 1983). In wintering Purple Sandpipers (*C. maritima*), yearlings were about 2 g lighter than older birds (Summers et al. 1992).

Differences in mass of breeding females could be explained if food resources were greater for older birds that nested earlier, than for yearlings that nested later, thereby allowing more rapid recovery of mass for older females after laying a clutch of eggs. However, no assessment of food resources was made so this hypothesis was not tested. Another explanation is that older birds arrive in better condition than yearlings due to age-related fat storage in wintering areas. Differences in wing length between age classes for both sexes could be explained by differing age-related moult schedules (Cramp and Simmons 1983). Mass was related to culmen or wing chord only in yearling males.

## Eggs and Clutches

The typical clutch size for all clutches was four eggs, as expected in most northern-breeding scolopacids (MacLean 1972) and as reported for Least Sandpipers on Sable Island (Miller 1979), in northern Manitoba (Jehl and Smith 1970), and in northwestern British Columbia (J.M. Cooper unpub. data). I discovered only one clutch of five eggs in nearly 300 clutches found. Five-egg clutches have not been reported previously for Least Sandpipers.

Clutch size was not related to age, body size, experience or laying date. The evolutionarily conservative clutch size of four eggs is a remarkable feature of scolopacid breeding. Explanations that have been offered include: (a) four eggs is the optimal clutch size for minimizing cooling of uncovered pyriform-shaped eggs (Norton 1970); (b) shorebirds cannot brood and care for more than four chicks (Safriel 1975); and (c) shorebirds cannot incubate adequately more than four eggs (Hills 1983). I believe that the first and third hypotheses offer the best explanations for a definitive clutch size of four eggs. Both of these hypotheses are related to thermal stability in incubated eggs, significant fluctuations in which can cause slower embryonic development or mortality (Webb 1987). While Norton (1970) showed that heat loss was minimized for pyriform-shaped eggs in four-egg clutches, Nethersole-Thompson (1973) noted that shorebird species that laid fewer than four eggs laid more ovate-shaped eggs, which maintained higher surface contact and reduced heat loss than would pyriform-shaped eggs, among eggs within a clutch. Hills (1983) then showed, in three species of arctic-nesting scolopacids, that five-egg clutches resulted in fewer young produced than four-egg clutches, because of variability in incubation temperatures of individual eggs within a clutch, which caused increased embryonic mortality. It is not surprising then, that the single five-egg clutch of Least Sandpiper eggs that I found at Delkatla produced only one chick that was able to leave the nest. One other chick hatched, after being abandoned in the nest by its parents, and died the next day after a foster attempt was made in another nest with newly hatched young. Two eggs had not developed at all, while another egg appeared to have begun embryonic development before becoming rotten. The normal scenario for successful nests is that, if one egg hatches then all eggs hatch, and all chicks leave the nest. Body size and the ability to incubate five eggs at temperatures sufficient to maintain embryonic development are likely more critical to embryonic survival than lower ambient temperatures; temperatures are significantly milder at Delkatla than in arctic breeding areas.

If scolopacid clutch size has been selected because of thermal constraints, then there are two ways in which individuals can increase their reproductive output. One is to lay additional clutches, which will produce additional offspring. Several non-monogamous scolopacid species do this, as mentioned in the Introduction. These species tend to lay smaller eggs relative to body weight than monogamous species, which likely is an adaptation to a multiple-clutch breeding system (Ross 1978; Sæther et al. 1986). In monogamous species, however, only one brood is produced and the only way to increase reproductive investment is by increasing egg size, which may enhance the size (quality) of young produced (Bolton 1991). Neonate mass is positively related to egg size for most shorebirds, but was not thought to be significantly related for Least Sandpipers (Ricklefs 1984). Some scolopacids, such as Whimbrel (*Numenius phaeopus*), lay larger eggs during early springs than during later springs, presumably in response to richer food supplies (Grant 1991). My data indicate there are no differences in Least Sandpiper egg size between years or between early and late clutches. This lack of seasonal or annual variation in egg size underscores the extreme conservatism of the Least Sandpiper's breeding system.

Replacement clutches also normally contained four eggs, although they were significantly more likely to contain three eggs than did initial clutches. Each four-egg clutch that a female Least Sandpiper lays represents about 100% of her body weight. Because mean egg volumes did not differ between first and replacement clutches, and replacement clutches were more likely to contain only three eggs, it is possible that energetic costs influence the number of eggs laid in replacement clutches. Energetic constraints related to longterm survival of individual females may also explain the apparent lack of third clutches laid, in the event of the loss of the replacement clutch, in a season. Females may discontinue breeding attempts if further egg production will decrease their overwinter survival.

Another hypothesis explaining the lower numbers of eggs laid in replacement clutches of single-brooded species is that the reproductive value of an egg declines with season, regardless of food supply (Daan et al. 1988). This hypothesis suggests that clutch size is adapted to the probability of eggs surviving to become recruits into the breeding population.

As indicated earlier, damaged eggs were occasionally removed by the parents. A few eggs disappeared for unknown reasons, possibly because of partial predation on a clutch.

Nests were usually abandoned if egg loss or damage occurred during egg laying. However, in one case, a partial clutch of two eggs was depredated by ravens. The female laid the remaining two eggs in the depredated nest and incubation of the reduced clutch commenced normally. These eggs were also eventually depredated. Additional eggs are apparently not laid to replace lost eggs at any stage within one nesting cycle.

Egg volumes (12.2 cc) were significantly smaller than those reported for Sable Island (12.8 cc; Miller 1979) and the Magdalen Islands, Quebec (Philipp 1925), and were mid-range compared to two samples reported for northern Manitoba (Jehl and Smith 1970; Ricklefs 1984). An explanation for the size differences between Delkatla and Atlantic coast populations are unknown. However, because heavier birds generally lay larger eggs (Rahn et al. 1975; this study) then it is possible that Least Sandpipers breeding at Delkatla are lighter than those breeding on the Atlantic coast. Measurements of eggs from other parts of the breeding range are required in order to clarify potential broader geographic variation in egg size.

Egg volumes did not differ between older and yearling Least Sandpiper females, as reported for one yearling female on Sable Island (Miller 1979), but was significantly positively related to weight for both age classes. In addition, there was not a positive relationship between female culmen and egg volume, again as reported for Least Sandpipers on Sable Island (Miller 1979); therefore culmen is a poor measure of body structural size. Although egg size may be smaller for first-time breeders of some bird species [e.g. Redshank (*Tringa totanus*), Thompson and Hale 1991; Tree Swallow (*Tachycineta bicolor*), DeSteven 1978; Herring Gull (*Larus argentatus*), Davis 1975], Väisänen et al. (1972) suggested that, in species with precocial young, egg size should depend less on female age than in species with altricial young. This hypothesis constrasts, as do my results for Least Sandpipers, with the findings for Semipalmated Sandpipers (Gratto et al. 1983) and Redshanks (Thompson and Hale 1991) in which yearling females laid significantly smaller eggs than older females. Because smaller eggs may produce smaller chicks and, possibly, lower chick survival in scolopacids (Soikkeli 1967), as they do in larids (e.g., Bolton 1991), heavier females may have a better chance of fledging young than lighter females. In Least Sandpipers, after having corrected for age-related weight differences between yearling and older females, there were no other age-related differences in egg size. Therefore, heavier females produced larger eggs and so may have had a better chance of fledging chicks than lighter females. Because there is relatively little variation in egg size among individuals in shorebirds compared to other avian taxa (Väisänen 1977), and if larger eggs produce young of higher quality, then there may be a selective advantage for larger females to produce larger eggs.

Mean egg volumes of individual females were highly correlated between years, a result also found for Least Sandpipers on Sable Island (Miller 1979) and Redshanks in England (Thompson and Hale 1991).

## Date of Clutch Initiation

Most females laid their first clutches over a three week period after the laying of the first egg of the year, a longer period than for more northern calidridine populations (Holmes 1966a; Soikkeli 1967; Jehl 1970). Egg laying is often more synchronous in calidridine populations as latitude increases (Holmes 1966a, 1971b). Although clutch initiation may be more synchronous at higher latitudes in general, some species do not compress their laying period with increasing latitude but, rather, decrease the period between arrival and laying times (e.g., Red Phalaropes (*Phalaropus fulicarius*), Schamel and Tracy 1987). The relatively long period of first-clutch initiation during my study likely reflects the long spring season at Delkatla compared with more northern breeding areas.

The lack of a positive correlation for clutch-initiation dates for individual females during consecutive years was unexpected. I expected that experienced females that reunited with their previous year's mate would nest at similar dates among years. However, an experienced female who had reunited with her previous year's mate laid the first egg of the year for the population during two consecutive years; another experienced female (mate history uncertain) laid her first egg on the third day of the egg-laying period during two consecutive years, suggesting that some females may lay eggs at similar dates in consecutive years. It also suggests that experience increases the likelihood of early nesting.

Pairs with experienced birds initiated clutches earlier than pairs with yearlings, a trend found in many shorebirds [e.g., Semipalmated Sandpiper, Gratto et al. 1983; Dunlin, Soikkeli 1967; Greenshank, (*Tringa nebularia*) Thompson et al. 1986); Red-necked Phalarope, (*Phalaropus lobatus*), Hildén and Vuolanto 1972] and other Charadriiformes [e.g. Western Gull, (*Larus occidentalis*) Pyle et al. 1991; Cassin's Auklet (*Ptychoramphus aleuticus*), Emslie et al. 1992]. This trend is to be expected if one assumes that experienced individuals are more efficient at arriving at breeding areas, establishing pair bonds, and choosing nest sites than inexperienced individuals. My data showed that pairs of yearlings nested later than all other pairs. This trend was previously most well documented for scolopacids in Spotted Sandpipers (*Actitis macularia*), in which yearlings generally mate with other yearlings, and do so relatively late in the season (Lank et al. 1985).

Early nesting is thought to be correlated with higher breeding success in a wide range of bird taxa (e.g., Soikkeli 1967; Newton and Marquiss 1984; Wanless and Harris 1988). Therefore, I expected that pairs with early clutches would have greatest breeding success. This prediction was not supported: for first clutches, there were no significant differences between early and late first clutches in hatching success, fledging success, or return of yearlings to breed.

However, pairs that nested earlier had more time to lay replacement clutches, if their first clutch was lost, than pairs that nested later. Because about two-thirds (65%) of replacement clutches hatched and about three-quarters (73%) of those ultimately fledged young, then pairs that produced replacement clutches would have higher reproductive success than pairs which lost their first clutch but did not produce replacement clutches. The most extreme example of the advantage of nesting early was the early-nesting pair that lost a newly-hatched brood and subsequently produced a replacement clutch and fledged their young. Later-nesting pairs would have more difficulty attaining the same success under similar circumstances, because of the tendency for females to abandon clutches begun after mid June before the eggs hatched. Seasonal factors, then, that influenced female behaviour causing them to abandon their nests and begin southward migration were more important in determining the end of the breeding season than the likelihood of fledging chicks. The nesting period of the breeding cycle ended even though late-hatching chicks were able to fledge with less parental care than earlier hatching chicks and there may have been potential for even late-hatching chicks to fledge.

## Size Dimorphism and Disassortative Mating

Adult Least Sandpipers exhibit subtle, but measurable, "reversed" sexual size dimorphism. At Delkatla females are longer-billed (8%), longer-winged (3%) and heavier (6%) than males. In most pairs females are larger than their mates. Reversed sexual size dimorphism also occurs in most monogamous species of Scolopacidae where males provide most parental care (Jönsson and Alerstam 1990). Overt sexual dimorphism, on the other hand, is thought to evolve more often in lekking birds (Oakes 1992), and is most pronounced among scolopacids in the Ruff (*Philomachus pugnax*), in which males are about 30% larger than females (Hayman et al. 1986). Reversed sexual dimorphism in other monogamous scolopacids, including Least Sandpipers, usually is far less dramatic compared to some other bird taxa, e.g., 5-10% vs. 20-50% in Falconiformes (Newton 1979; Palmer 1988a, 1988b) and Strigiformes (Earhart and Johnson 1970; Mueller 1986).

Disassortative mating based on size occurs when pairs with greater size differences nest earlier than pairs with smaller size differences; i.e. one sex relatively small and one sex relatively large. Because disassortative mating, where pairs with larger differences in culmen length nested earlier than pairs with smaller differences in culmen length, had been reported for Least Sandpipers and Stilt Sandpipers (Jehl 1970) and Dunlin (Jönsson 1987), I expected to find the same trend at Delkatla. Certainly, females were almost always longer-billed and heavier than their mates, but this could be explained by random mating and sexual size dimorphism (Coulter 1986). Analysis of my data for all initial clutches and all experienced pairs during 1986-1988 resulted in non-significant relationships between date of beginning of egg laying and intra-pair size differences. Interestingly, the regression was negative in each year, which hinted that there might be a weak trend toward disassortative mating. I expected that disassortative mating would most likely be found with experienced but divorced pairs, because they would have returned earlier than most inexperienced birds, and females would have to choose mainly from a selection of males whose previous mate did not return. However, no significant relationships were discovered for that sub-population.

Pairs with yearling birds provided somewhat different results, however. Shorter-billed yearling males nested significantly earlier than longer-billed yearling males, but there was no relationship between intra-pair differences in culmen length and beginning of nesting. No other significant direct relationships to body measurements were found for either sex. In Dunlins in southern Sweden, smaller males (shorter-billed, shorter-winged), longer-billed females, and pairs with larger differences in culmen length nested earlier, regardless of age (Jönsson 1987).

Jehl and Murray (1986) proposed that acrobatic flight in aerial displays is an important factor in the evolution of sexual size dimorphism in shorebirds. Smaller males should be able to spend more time displaying than larger males because of lower energetic costs (Peters 1983) and smaller males would be more agile in flight (Andersson and

Norberg 1981). (Note that Least Sandpiper display flights, with their monotonous and repeated calls, are similar to other calidridines; Miller 1983b).

A third advantage to smaller male body size may be during the brood-rearing period, as proposed for Dunlin by Jönsson (1987). Male Least Sandpipers, like Dunlin (Soikkeli 1967), tend their broods longer than females (this study; Miller 1985). Whereas adults forage mainly by probing in tidal, soft mud habitats, unfledged chicks forage on terrestrial arthropods in vegetated meadow areas. Since males appear to accompany their broods virtually at all times, they may have little time for feeding in preferred habitat. (Note that during the incubation period they have plenty of time to feed while the female is on the nest.) Shorter-billed males would be better able to forage on terrestrial insects in upland habitats while tending chicks than would longer-billed males, because of the presumed greater efficiency in foraging with shorter bills (Jönsson and Alerstam 1990). Also, since smaller birds need less food than larger birds (Peters 1983), then a smaller male could spend less time feeding and more time defending his brood and, potentially, could increase the chance of brood survival. Although this relationship was only alluded to for Dunlin by Jönsson (1987), my study indicates that increased male attendance is positively related to the number of chicks fledged; therefore the hypothesis that smaller males could spend more time caring for their broods because of lower food requirements is plausible. Many other species of monogamous calidrids also have males tending broods longer than females (e.g. Bengston 1970; Gratto-Trevor 1991; Holmes 1966a, 1973; Jehl 1973; Nethersole-Thompson and Nethersole-Thompson 1979).

Why my results on disassortative mating differ from Jehl (1970) and Jönsson (1987) is not clear. Because my sample size is relatively large compared to these other studies it is apparent that the process of pair formation is more complex than previously thought, in my study area at least. It is possible that effects related to high density or mild climate have affected the process of pair formation. Further study is needed to clarify my results.

## Hatching of Eggs

Only 57% of 298 clutches hatched. This result is similar to that on Sable Island where 59% of complete clutches hatched successfully (Miller 1983a), and Temminck's Stint in southern Finland where 52% of clutches found hatched (Hildén 1978); it is much lower than in Western Sandpipers in Alaska where 84% of nests found hatched

(Holmes 1972).

During 1987-1988, failure of entire clutches was almost always the result of predation. Exceptions were very late nests in which eggs were abandoned before they hatched, and one case where a bird was mishandled during trapping and subsequently abandoned the nest. Eggs that did not hatch in otherwise successful nests included those that were damaged during incubation, were infertile or ceased embryonic development for unknown reasons.

Hatching success was not related to date. However, experienced females were more likely to hatch eggs from a given clutch than yearling females. Similar results have been found in other scolopacids [e.g., Redshanks (Thompson and Hale 1989) and in one of three years for Semipalmated Sandpipers (Gratto et al. 1983)], but comparable data are not available for other scolopacids. Because experienced females nested earlier than yearling females, then a factor associated with experience, other than a tendency to nest earlier, must be related to successful hatching. Plausible factors could be: (a) better nest-site selection, which could reduce risk of predation; (b) more optimal incubation behaviour and clutch-attendance patterns, which could increase the rate of embryo survival; or (c) higher fertility. During my study, lower rates of hatched clutches for yearling females is explained mainly by higher rates of predation on nests with yearling females. Ravens depredated nests of yearling females at twice the rate of nests of older females. An explanation for this result was not determined.

I was surprised that some very late clutches, in which the female abandoned the nest before the eggs hatched, survived to hatch. Eggs hatched in nests that were abandoned by females 4, 3, 2, and 1 (twice) days before the eggs hatched. Twice I thought one nest was abandoned because eggs had been cold to the touch during nest visits. Yet I found the male incubating later on both occasions. Males from nests which the female had departed prematurely apparently left the nest to obtain food, probably once per day. The length of time that the eggs were left uncovered was unknown, but was obviously considerable. Definitive clutches normally are incubated at virtually all times in monogamous scolopacids. Dunlin, Baird's Sandpiper (*C. bairdii*), and Least Sandpipers incubated complete clutches 98%, 97%, and 99% of the time, respectively (Norton 1972; Miller 1983a). That these partially abandoned nests were able to be successfully incubated by the male alone suggests that Least Sandpipers are capable of incubating a clutch alone, as in some other calidridines that have different breeding systems [e.g., Temminck's Stint, Buff-breasted

Sandpiper (*Tryngites subruficollis*)].

Although egg embryos are progressively less tolerant of low temperatures as they develop (Batt and Cornwell 1972), older embryos cool less rapidly because they lose heat less rapidly (Drent 1970). The length of time that abandoned males were off the nest was, thus, less than that required to cool and kill the embryos. However, a few males left alone to incubate their clutch abandoned their nests before their clutch hatched.

## Replacement Clutches

Replacement clutches were likely laid routinely whenever the first clutch was lost through predation, as long as the loss occurred early enough in the season. As Miller (1983a) pointed out for Sable Island Least Sandpipers, replacement clutches likely are possible because of the relatively long breeding season, which contrasts with conditions throughout more northern calidridine breeding areas. In southern Finland, at latitude 61° 30′ N, Dunlin did not lay replacement clutches after the first few days of June (Soikkeli 1967) and some arctic-nesting shorebirds may not breed at all in years with delayed springs (Mayfield 1978). There is, apparently, more "room for error" in clutch initiation in more southern breeding areas. The most extreme example of laying a replacement clutch (reviewed earlier) was from the 1987 pair that lost its recently hatched brood, then laid a replacement clutch about one month after laying their initial clutch. Replacement clutches are also laid routinely when the first clutch is lost in other calidridines (e.g., Dunlin, Soikkeli 1967; Western Sandpiper, Holmes 1971a).

Although there was sufficient time, phenologically, for third clutches to be laid if necessary (when replacement clutches were lost before 15 June), I found no evidence of second replacement clutches. The energetic investment in laying three clutches in one year (equivalent to about 300% of female body weight) may be too stressful for small sandpipers such as Least Sandpipers because of the high ratio of clutch to body weight. Although they are likely capable of laying additional clutches in one season, there may be a trade-off with longterm survivorship. Another small calidridine, the Temminck's Stint, which normally lays two clutches each year because of a polygamous breeding system, lays a replacement (i.e., third) clutch only rarely. Female Spotted Sandpipers in one Minnesota population, which lay up to five clutches each year, are about twice the size of Least Sandpipers (Oring et al. 1983). It is possible that larger body size or more flexible mating systems may be necessary for production of third clutches in scolopacids.

Replacement clutches were significantly more likely to contain three eggs than were first clutches, a result also found in other caldridines (e.g., Soikkeli 1967; Tomkovich 1991). Mean egg volume did not differ between replacement and initial clutches, as reported for a small sample of Least Sandpipers on Sable Island (Miller 1979). Data for other calidridines are lacking mainly, although in Spoonbill Sandpipers (*Eurynorhynchus pygmeus*) replacement clutches contained eggs that were longer and narrower than eggs in first clutches (Tomkovich 1991). Mean egg volumes did not differ, either, for a population of Redshanks in England (Thompson and Hale 1991).

The mean interval of 5 days between loss of first clutches and initiation of replacement clutches is the same as reported for 5 clutches on Sable Island (Miller 1979). In comparison, replacement clutches in *Charadrius* plovers occurs between 5 and 14 days after the first clutch is lost (Graul 1975; Warriner et al. 1986).

### Fledging of Young

The fledging rate of 67% for chicks during 1987-1988 was much higher than the 40% reported on Sable Island (Miller 1983a). Fledging rates at Delkatla were more similar to the 50-60% reported for Temminck's Stint (Hildén 1978) and 73% reported for Spotted Sandpipers (Oring et al. 1983) than for Least Sandpipers on Sable Island. On Sable Island, Herring Gulls hunted continuously throughout the Least Sandpiper breeding cycle and were a major cause of chick mortality. At Delkatla, ravens were considered the primary predator, but depredation of chicks was not known to occur. Cessation of predation by ravens during the middle of the hatching period may have positively influenced fledging success at Delkatla. However, there was no relationship between date and the number of chicks fledged per brood. Because of lack of evidence of depredation, and the noticeable but unquantified declines in broods surviving following periods of heavy rain, most pre-fledging mortality was attributed to cold, wet weather.

I found little evidence that early clutches were more likely to produce fledged young, or more of them, than late clutches. It is widely thought that high-latitude breeding scolopacids have evolved breeding strategies to foster nesting at the earliest possible date, due to the relatively short spring and summer seasons, and that early nesting is related to higher fledging rates in shorebirds (e.g., Soikkeli 1967). My results may reflect the influence of a less extreme environment where successful breeding is constrained mainly by influences that induce nesting birds to abandon the breeding area and migrate.

Although pairs with older females fledged more young than pairs with yearling females because more clutches hatched, during 1987-1988 there were no significant age- or experience- related differences in fledging rates for clutches that hatched. My data support a widespread trend in birds for older parents to fledge more young than younger parents (Lack 1966). There are no comparable data in the literature for any other monogamous scolopacid. In contrast, in the polyandrous Spotted Sandpiper, experienced females produced more fledglings than inexperienced females, but there was no difference in males (Oring et al. 1983). My data support the view that yearling birds are relatively inefficient breeders compared to older birds (Curio 1983). At Delkatla, it is possible that environmental conditions compensate for age-related behavioural and phenological differences so that yearlings breed as successfully as older birds, once they successfully hatch their clutch.

## Duration of Parental Care

Although I did not measure the amount of time each sex spent incubating clutches, incubation was shared in similar ways as reported for this species in northern Manitoba (Jehl 1970) and Sable Island (Miller 1985). Females were regularly found on the nest between dawn and about 0900 hrs. After about 1000 hrs, and continuing to dusk, males were generally found on nests. A few pairs were exceptions to this pattern, with males being found on nests during the early morning as well. Thus, incubation was shared with each sex taking one "shift" each day. Although I did not determine when females replaced males on the nest, my observations suggest that females replace males at night. This pattern of males incubating during the day and females during the night is typical of some other monogamous calidridine species (Soikkeli 1967; Jehl 1973). Other monogamous species, however, have variable patterns [e.g., Semipalmated Sandpiper (Ashkenazie and Safriel 1979)] or patterns that are not well understood (e.g. Drury 1961; Norton 1972).

Sharing of incubation is typical of single-clutched monogamous scolopacids and other shorebirds, with males contributing a greater proportion of incubation as incubation progresses (Cramp and Simmons 1983). In birds in general, in which males provide large amounts of parental care, most species are monogamous (Lack 1968). Miller (1985: p. 1598) suggested that male Least Sandpipers "may assume a greater share of incubation as it proceeds." Although I did not determine precise incubation schedules for each sex, males certainly provided most of the incubation effort during the latter half of the breeding season. This trend culminated with males incubating late clutches (during the first week of July) for as long as 4 days without any assistance from the female.

Both parents attended broods during most of the breeding season, although males attended broods longer than females in almost all cases. One male, that tended his brood for a typical period during 1987, abandoned his brood after only a few days during 1988, leaving the female to care for their chicks. Overall, the duration of attendance decreased for both sexes as the season progressed. Brood attendance was highly negatively correlated with date for females, and moderately negatively correlated for males. This trend culminated late in the season with females departing their nests before eggs hatched and males leaving their broods when their chicks were only about one-half to two-thirds of the way to attaining flying ability. My data strongly confirm a weak trend that Least Sandpiper broods on Sable Island were tended more briefly late in the season (Miller 1985). In addition, I found several cases, all from late clutches, that modify the assertion that Least Sandpipers "attend young until well after they can fly strongly" (Miller 1985: p. 2895). During my study, late-hatching broods were typically abandoned several days before chicks could attain sustained flight.

Brood attendance for males and females averaged 16 and 7 days, respectively. These data are similar to Miller's (1985) estimates for Least Sandpipers of 20 and 6 days, and Soikkeli's (1967) estimates for Dunlins of 19 and 6 days. Among calidridine species, however, there appear to be substantial differences between the sexes in brood attendance (Bengston 1970; Norton 1973; Ashkenazie and Safriel 1979). Least Sandpipers, along with other monogamous calidridines in which males provide the majority of parental care, are relatively rare in birds (Ridley 1978).

During my study there were no differences in duration of brood attendance between yearling and older females. However, older males tended broods longer than yearling males. This difference between the sexes is largely accounted for by yearling males nesting later than yearling females. This reduced the length of brood attendance expected compared with yearling females due to seasonal effects.

Parental care likely is most critical during the first few days after hatching, when brooding of young is required during cold or wet periods (Norton 1973). Brooding of newly hatched chicks was observed most frequently while young were still in the nest or in its vicinity. Brooding of week-old chicks was also observed, immediately following disturbance by an observer. During my study, severe rain and low temperatures occurred often during June, whereas July was relatively dry and warm. Many broods were thought to perish during wet and cold weather, presumably because downy chicks could not withstand the effects of weather even with both parents in attendance. Late in the season during milder weather, however, broods were able to fledge with relatively little attendance by the male and no attendance by the female.

The pair (previously discussed) that hatched two clutches during 1987, but fledged young only from the second clutch, were engaged in parental care of eggs and young longer than any other pair. This period, between laying of the first egg in the initial clutch (13 May), and when the male was last seen tending his brood from the replacement clutch (22 July), was 71 days. This is the longest estimate of parental care ever reported for a northern scolopacid species.

Temperature and weather have apparently not had any major influence on the evolution of parental behaviour in calidridine sandpipers (Miller 1985). The evolutionary impetus that compels northern-latitude scolopacids to abandon their breeding areas and migrate south seems exaggerated for Least Sandpipers at Delkatla, although there may be good reasons to leave quickly after breeding. Although breeding occurs relatively early at Delkatla compared with other areas, and the local climate seems to allow survival of broods later in the season, adults still abandon their broods before it seems warranted. Early-nesting females at Delkatla, in fact, begin to abandon their broods during the same period (fourth week of June) as when some females in extreme northwestern British Columbia are still incubating eggs (J.M. Cooper unpub. data). If females leave Delkatla on their migration south as I suspect, then my data do not agree with Myers' (1981) suggestion that shorebirds that have farther to go will depart earlier in migration.

## Age of First Breeding

In most small scolopacids some individuals in some populations breed as yearlings - Spotted Sandpiper (Oring et al. 1983), Western Sandpiper (Holmes 1971a); Temminck's Stint (Hildén 1978); Dunlin (Holmes 1966a; Soikkeli 1967);

Semipalmated Sandpiper (Gratto et al. 1983); and Red-necked Phalarope (Hildén and Vuolanto 1972). Some Least Sandpipers are also known to breed as yearlings on Sable Island (Miller 1979).

However, the extent to which yearling calidridines breed is generally unknown. This information is important in order to better estimate the reproductive potential of individuals or populations. My results conclusively indicate that, at Delkatla, virtually all Least Sandpipers breed for the first time as yearlings. Yearlings also constitute a significant percentage (about 20% during 1987-1988) of the breeding population at Delkatla. Comparable data are not available for Least Sandpipers anywhere else in its range, although 1 of 13 nesting Least Sandpipers captured in northern Manitoba was identified as a yearling (C. Gratto-Trevor pers. comm.). The mean percentage of yearling breeders in my study population is about three times the mean percentage (6.7% during 1980-1982) of yearling breeders reported for Semipalmated Sandpipers in northern Manitoba (Gratto et al. 1983). It is possible, however, that the relatively high percentage of yearling breeders found during my study is unique to this study area due to latitudinal effects (shorter migration distance; longer breeding season than farther north), or because the species had recently pioneered.

Deferred breeding is common in larger shorebirds [e.g., about 50 % of yearlings in Redshanks do not breed (Thompson and Hale 1989,1991); other birds in general (Western and Ssemakula 1982); and in small calidridines breeding at extreme northern latitudes (Myers 1981; Gratto and Cooke 1987)]. Myers (1981) proposed that the risk of mortality contributes to delayed maturation in sandpipers, whereas Gratto and Cooke (1987) suggest that climatic influences inhibit breeding by yearling Semipalmated Sandpipers in areas of extreme climate. My data for Least Sandpipers seem to support Gratto and Cooke's (1987) suggestion of climatic influences. Virtually 100% of yearling Least Sandpipers breed at Delkatla, while about 7% of yearling Semipalmated Sandpipers breed in northern Manitoba, and none breed as yearlings in arctic Alaska. The lack of deferred breeding in the Least Sandpiper population at Delkatla is one of the least conservative aspects of the species' breeding system.

## Return of Young to Breed

My data on the return of young to natal areas are the first substantial data available for Least Sandpipers, and are the most detailed for any scolopacid except Spotted

Sandpipers (Oring and Lank 1982). Miller (1977) found that significantly more adult males than adult females returned to Sable Island, but noted only one yearling returning to breed. Data comparable to mine are available for four other calidridines: 12 male and 13 female yearling Temminck's Stints returned to natal areas in western Finland (Hildén 1979); 30 male and 27 female yearling Dunlin returned to natal areas in southern Finland (Soikkeli 1970a,b); and 11 male and 9 female yearling Semipalmated Sandpipers returned to natal areas in northern Manitoba (Gratto et al. 1985). Although I captured more breeding yearling males than yearling females (35:25), the difference in the numbers of each sex captured was statistically nonsignificant. Therefore, my data support the general trend in scolopacids of equal return rates between the sexes (Oring and Lank 1982). Because the sex ratio of hatched eggs in birds is unity (Clutton-Brock 1986), and there seems to be little reason for differential survival of chicks or fledglings, an equal sex ratio for returning scolopacid yearlings seems reasonable. In scolopacids, male-biased philopatry has been reported only for Long-billed Curlew (*Numenius americanus*) (Redmond and Jenni 1982) whereas female-biased philopatry has been reported only for Spotted Sandpiper (Oring and Lank 1982).

For the one brood year (1987) for which I could determine the return of fledglings the following year (1988), 29% of fledglings returned to breed. The only comparable data available are for Temminck's Stint in which 50% of fledglings returned as yearlings (Hildén 1978). My results represent a minimum survival rate for chicks fledging at Delkatla because it was impossible for me to determine if yearlings not accounted for had dispersed to other breeding areas.

If my estimate of 90 pairs of breeding birds at Delkatla is correct, then only 19% (17/90) of those pairs produced chicks that returned to breed in their natal area. Those 31 yearlings would account for 18% of the breeding population of 85 pairs, very close to the actual ratio (1:5) of yearlings/adults captured each year.

### Mate Fidelity

Reunited pairs nested in the vicinity of their previous year's nest and began clutches slightly earlier than all other pairs. Unlike some arctic and alpine species [e.g., Western Sandpipers (Holmes 1971a) and Wandering Tattler (*Heteroscelus incanus*, Weeden (1965)], or more northern populations of Least Sandpipers (Jehl 1970), southern-nesting Least Sandpipers apparently do not use their previous year's nest cup (Miller 1977, 1983; this study). Laying eggs in a previous year's nest cup would be virtually impossible at Delkatla, in any event, because of the vigorous annual growth of vegetation and extremely wet climate that obliterates all traces of nest cups among years.

During my study 97% of pairs reunited the following year when both were known to be alive. This rate of mate fidelity is substantially greater than that reported for other calidridines (e.g., Dunlin - 44% to 80%, Soikkeli 1967; Western Sandpiper - 61.5%, Holmes 1971a; Semipalmated Sandpiper - 80%, Gratto et al. 1985), but comparable to some intermediate and larger-sized scolopacids that appear to mate for life typically (e.g., Redshank, Hale and Ashcroft 1982; Willet (*Catoptrophorus semipalmatus*), Howe 1982). One explanation for the high degree of mate fidelity between years during my study may be that breeding habitat on the Queen Charlotte Islands is restricted mainly to one discrete area and, therefore, there is little opportunity for birds to settle elsewhere.

The high degree of mate fidelity in this population suggests that both sexes exhibit high nest-site fidelity among years, as postulated for many monogamous scolopacids with biparental care (Oring and Lank 1984). A reasonable scenario is that males return first and establish territories in the vicinity of the previous year's nest. Later-arriving females return to their previous nest site and, upon finding a familiar male, reform their pair bond quickly, and initiate egg laying earlier than pairs that form later. Females that return to the area of their previous nest site and do not find their mate from the previous year then must prospect for a new mate, and may end up nesting a considerable distance from that site. Males that return to their previous nesting area acquire a new mate if their previous mate does not return, and nest near their previous year's nest site. Similar results were reported for reunited pairs in Semipalmated Sandpipers (Gratto et al. 1985). The duration of pair formation likely is fairly brief (a few days), but is unknown for my study population.

In some other shorebirds and many other bird taxa (e.g., Haig and Oring 1988; Linden 1991), pairs that experience poor breeding success are thought to be more likely to divorce and pair with a new mate the following year, when both members of the pair are present, than pairs with higher breeding success. Although numerous studies show increased probability of divorce in years following reproductive failure (e.g., Coulson 1966; Johnston and Ryder 1987; Ollason and Dunnett 1988), Ens et al. (1993) have proposed a "better option" hypothesis that predicts that divorce will occur when expected benefits outweigh expected costs. In this hypothesis, the expectation of improvement, rather than previous failure, determines the decision to divorce. At Delkatla it is probable that previous reproductive performance had little impact on reuniting of pairs because virtually all pairs reunited if both birds were known to be present.

Pairs remained together for all known replacement clutches. Within-season divorces of pairs occurred only once during 1986-1988, although the circumstances surrounding this case were quite unusual: one male was found incubating two clutches from two different females during one season. Both clutches hatched, with the male tending the later-hatching clutch. This case, in which the male that appeared to stay with his original nest until the eggs hatched and then abandoned the brood to the female as he began incubating at a second nest, is very unusual in the Scolopacidae and violates one of the three inclusive definitions of monogamy (Wittenberger and Tilson 1980). This case most closely resembles the breeding system of Temminck's Stint, i.e, males are involved with two females and two clutches. In this polygynous system males mate with two different females and females mate with two different males, with females laying a clutch for the first male, which he incubates alone and then laying the second clutch which she incubates alone (Hildén 1975; Breiehagen 1988). Within-season divorce is also exceedingly rare in monogamous Semipalmated Sandpipers, occurring only once during eight years of observation in northern Manitoba (Gratto-Trevor 1992). In addition, even in all of the non-monogamous shorebird breeding systems, including Spotted Sandpipers in which males may have multiple mates and multiple nests during a season, males do not normally incubate two different clutches that produce chicks during one breeding season (Parmelee 1970; Hildén 1975; Oring et al. 1991).

### Predation, abandonment, and observer effects

Nest destruction by bird or mammal predators is the overwhelming primary cause of nest failure in shorebirds, followed by weather (e.g., Holmes 1971; Colwell and Oring 1988). Nest predation is the primary source of nest failure for many species of ground-nesting birds [e.g. Ricklefs (1969); shorebirds - Gratto et al. (1983); Oring et al. (1983); ducks - Arnold et al. (1987); grouse - Bergerud (1988); Morton et al. (1993)]. During my study, heavy losses of Least Sandpiper nests were caused by depredation by a single pair of ravens. Depredation of eggs ceased after this pair's young fledged and the entire raven family moved to the local dump. No other potential predator was confirmed as having destroyed nests, although Northwestern Crow depredation may have occurred at one nest.

Predation may have significant effects on local shorebird populations. For example on Sable Island, Herring Gulls preyed heavily on Least Sandpiper eggs and chicks, and were thought to be causing a decline in the population (Miller 1983a). Maxson and Oring (1978) found heavier predation of Spotted Sandpiper eggs earlier than later in the season, with the main predator being mice. Early (experienced) nesting birds suffered greater nest losses than later (inexperienced) nesting birds, but were able to compensate by renesting and ended up fledging as many chicks. Total breeding failure can occur as a result of intensive predation in isolated sites such as islands [e.g., one mink (*Mustela vison*) depredated all clutches of Spotted Sandpipers during one breeding season, Oring et al. (1983)]. The intensity of predation may also influence the onset of breeding in some populations of shorebirds. Ringed Plovers (*Charadrius hiaticula*) were thought to delay nesting until later in the season because of reduced predation risk (Pienkowski 1984). This phenomenon did not occur at Delkatla, even though depredation of nests ceased late in the season, and nesting success surely would have been higher if egg laying had been delayed until later in the season.

Free-ranging cattle, during years when they were present, were also responsible for a significant number of nest losses at Delkatla (18 of 160 nests). In comparison, only one of 62 nests was destroyed by horses on Sable Island (Miller 1983a). This type of "accidental" nest destruction is likely very unusual over most of the Least Sandpiper's breeding range where domestic animals do not normally occur.

Abandonment of nests occurs very seldom. Abandonment most often occured very late in the season when incubating birds abandon clutches before they hatch or after accidental egg breakage.

Although there were no differences in nest mortality following three different types of nest visits by human observers, it seems unlikely that frequent nest visits, trapping attempts and measurement-taking at individual nests would not increase the risk of predation at those nests. Several experimental studies using artificial eggs have suggested that predation risk increases when nests are marked and visited (e.g., Hammond and Forward 1956; Picozzi 1975). Other studies, using natural clutches, have detected no effect (e.g., Willis 1973). The influence of marking and visiting nests has been well documented for shorebirds only in the Lapwing (*Vanellus vanellus*; Galbraith 1987). Galbraith found no differences in nest mortality between marked and unmarked nests, or among three types of observer visits: (a) observed nest through binoculars without flushing the adult; (b) walked to the nest and flushed the adult; or (c) flushed the adult and handled the eggs. Unlike Least Sandpipers, however, Lapwings are able to defend their nests from corvid predators (Dyrcz et al. 1981), and may be able to compensate behaviourally for potentially increased nest exposure due to research activity by humans. Least Sandpipers apparently are not capable of deterring depredation by ravens (pers. obs.). During my study it is possible that marking nests may have influenced the risk of nest detection by ravens, particularly early in the season when vegetation was sparse.

## SUMMARY

Least Sandpipers breeding on the Queen Charlotte Islands initiated nesting earlier than any other population studied, probably because of a relatively mild climate. Experienced breeders nested earlier than yearling breeders and had higher hatching success. Once eggs hatched there were no age-related differences in fledging of chicks or return of yearlings the next year. Replacement clutches were laid after first clutches were lost, but only during the first month of the breeding season. Incubation was shared between the sexes with males assuming a large proportion of incubation later in the nesting season. Patterns of disassortative pairing based on intra-pair size differences were not found; however shorter-billed yearling males nested earlier than longer-billed yearling males. Males tended broods longer than females, and longer male parental care was related to increased survival of chicks within broods. Late in the season females abandoned clutches before eggs hatched, but some males were able to hatch their clutch alone and raise chicks that fledged. Age of first breeding in this population was one year. Male and female yearlings returned to breed in equal numbers. Yearlings comprised about 20% of the breeding population. Predation by ravens had a considerable impact on nesting success.

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Appendix 1. Nesting and brood-rearing habitat of Least Sandpipers in Delkatla Wildlife Sanctuary.

Hummocky and wet nesting habitat (foreground) and brood-rearing habitat (right background) along slow-moving creek in south end of Delkatla. (Photo: John M. Cooper - 1 June 1988).

Appendix 1 continued.

Nesting habitat in drier area near centre of upland in the south end of Delkatla. Least Sandpipers nested in open areas between patches of rush. (Photo: John M. Cooper - 2 June 1988).

Appendix 1 continued.

Brood-rearing habitat in wetland along the southeastern edge of Delkatla. (Photo: John M. Cooper - 2 July 1987).

Appendix 1 continued.

Marginal nesting habitat (foreground) and brood-rearing habitat (background) in the south end of Delkatla; Village of Masset in the distant background. (Photo: John M. Cooper - 3 July 1987).

| | | Langara Island | | Sewall | | Tlell | |
|---|---|---|---|---|---|---|---|
| Month | Year | Mean temp. (Celsius) | Rainfall (mm) | Mean temp. (Celsius) | Rainfall (mm) | Mean temp. (Celsius) | Rainfall (mm) |
| April | 1988 | 5.9 | 164 | 6.3 | 117 | 6 | 105 |
| April | 1987 | 6.4 | 219 | 6.4 | 143 | 6 | 139 |
| May | 1988 | 8.5 | 126 | 8.9 | 80 | 8.7 | 75 |
| May | 1987 | 8 | 227 | 8.9 | 149 | 8.8 | 94 |
| June | 1988 | 10.3 | 110 | 11.3 | 113 | 11.1 | 107 |
| June | 1987 | 10.1 | 120 | 11.9 | 76 | 11.4 | 68 |
| July | 1988 | 12 | 176 | 13.2 | 89 | 13 | 86 |
| July | 1987 | 11.9 | 46 | 14.1 | 52 | 13.5 | 47 |

**Appendix 2. Mean temperature and rainfall from weather stations near Masset, Queen Charlotte Islands, 1987-1988. (Data from Environment Canada).**

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## Publications:

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Title of Thesis: Breeding biology of the Least Sandpiper (*Calidris minutilla*) on the Queen Charlotte Islands, British Columbia.

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