CHRONOLOGY OF NESTING EVENTS IN WESTERN AND SEMIPALMATED SANDPIPERS NEAR THE ARCTIC CIRCLE

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

CRONOLOGÍA DE LOS EVENTOS DE ANIDAMIENTO DE *CALIDRIS MAURI* Y *C. PUS-ILLA* CERCA DEL CÍRCULO ARTICO

Sinopsis.—Se examinó la cronclogia de los eventos de anidamiento de *Calidris mauri* y *C. pusilla* en Nome, Alaska. La duración de la puesta (5 dias para una camada de 4 huevos) y el eclosionamiento (53.0 ± 26.6 DE horas, para emerger y secarse de un huevo picado) fue similar para ambas especies. La tasa de puesta de *C. pusilla* en Nome fue menor que para otras poblaciones, posiblemente debido a que el intérvalo de puesta fue mayor a 30 horas. El periodo de incubación fue significativamente menor en *C. mauri* (21.5 ± 0.5 dias) que en *C. pusilla* (20.3 ± 1.9 dias). Las camadas producidas temprano tuvieron un exito significativamente mayor que las camadas producidas tardes en *C. pusilla* (60%, *n* = 105 vs. 22.9%, *n* = 70), pero no asi en la segunda especie (68.2%, *n* = 88 vs. 47.3%, *n* = 55).

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

STUDY AREA AND METHODS

Field methods.—The reproductive biology of Western and Semipalmated Sandpipers was studied at a 4 km^2 study site, 21 km east of Nome, Alaska (64°20'N, 164°56'W) during May–July in 1993–1995. The two species breed in the same habitat at this site, and nests are placed on low, dry ridges that are close to shallow tundra ponds.

Nests were located by walking the tundra and observing sandpiper behavior. Incubating birds flushed from the nest at short distances and used distraction displays to lead the observer away. If the clutch was not found immediately after the parent flushed, the bird was observed from 20–30 m until it returned to the nest. Nests were marked with a line of small sticks and a wooden stake 10 m from the nestcup. Date and the time of day were recorded on all nest visits; most effort was in the daylight hours of 0800–0100 h.

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

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

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

Egg-laying rates were calculated for four-egg clutches that were found during laying. Three-egg clutches were excluded because a long laying interval could be caused by eggs lost to partial nest depredation or disturbance during laying. The few nests that were not visited at least daily during laying were also excluded. The laying interval between successive eggs was calculated by using the elapsed time between two different nest visits. To obtain a minimum estimate, I assumed that an egg had been

laid just previous to the first visit, and I only included cases where an additional egg was known to have been laid subsequent to the last nest check. If egg number did not change between two daily visits, the elapsed time was a minimum estimate of one laying interval (e.g., 3 eggs on day 1 at 1000 h to 3 eggs on day 2 at 1800 h gives a laying interval of 32 h). If egg number increased by one during a 2–3 d period, the elapsed time was a minimum estimate of two laying intervals (e.g., 2 eggs on day 1 at 1300 h to 3 eggs on day 4 at 1300 h gives a mean laying interval of 36 h). Both estimates are sensitive to check frequency, thus minimum intervals of less than 15 h were discarded. The estimates may be biased towards longer laying intervals because it was not possible to determine the time of laying when an egg appeared between two daily nest visits.

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

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

Determining nest success.—Nest fate was defined as one of three outcomes: (1) *abandoned:* eggs were consistently cold for a week or more; (2) *depredated:* eggs disappeared before the expected hatching date, or there were signs of predator activity (broken egg shells, fox urine in the nestbowl); or (3) *hatched:* at least one chick was banded and left the nest. Predators often remove all eggs from shorebird nests (pers. obs.), but the fate of an empty nestbowl can be ambiguous because parents remove eggshells from the nest at hatching (Sandercock 1996). To clarify uncertainty in nest fate, I used flotation of eggs to determine stage of incubation (Alberico 1995, Rahn and Ar 1974, Van Passen et al. 1984). If a nest was found after laying was completed and subsequently disappeared, I compared the date it was last seen with the estimated stage of incubation and predicted hatching date. Egg buoyancy was a good predictor of stage of incubation, the number of days of incubation could be estimated with an error of ±2–3 d if the nest was found within the first week after laying (Fig. 1). This accuracy is comparable to float curves for other shorebirds (Van Paassen et al. 1984).

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

RESULTS

Sandpiper nests were usually found after laying was completed (Western: 79.3%, $n = 164$; Semipalmated: 85.8%, $n = 183$). Most of the clutches found during laying that eventually contained four eggs were discovered when the clutch was almost complete (Western, 1-egg: 7.4%, 2-egg:
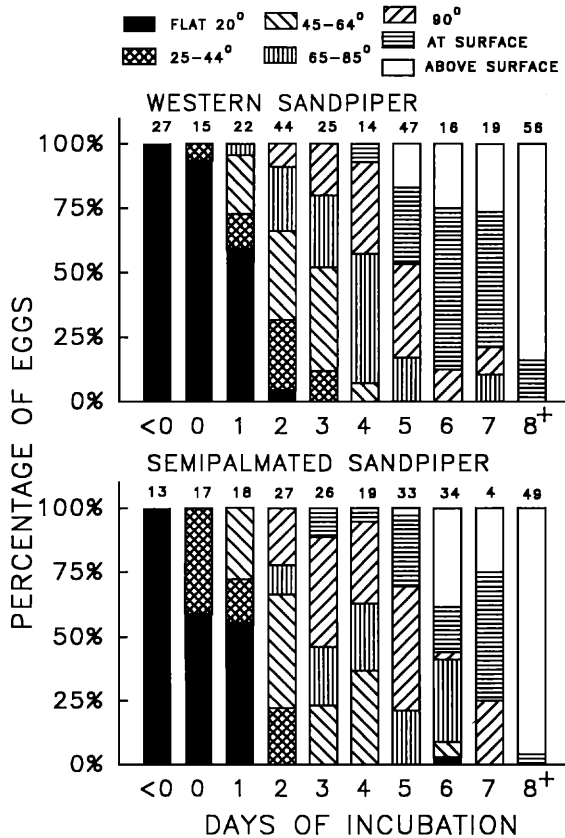
FIGURE 1. Changes in the buoyancy of sandpiper eggs during incubation. Day 0 is the
    estimated date of laying for the last egg; it was determined from either observations
    during egg-laying or by back-dating from the date of hatch. Observers recorded the
    angle between the centre axis of the egg and the bottom of the float cup. Numbers
    above each bar indicate the sample size of eggs, the totals are based on 90 visits to 71
    Western Sandpiper nests and 80 visits to 64 Semipalmated Sandpiper nests. The egg
    that was flat on day 6 was probably infertile.

25.9%, 3-egg: 66.6%, $n = 27$; Semipalmated, 1-egg: 5.5%, 2-egg: 33.3%,
3-egg: 61.1%, $n = 18$). Nests found early in laying were more likely to
have a laying schedule that included visits where there was no new egg
(100% of nests found at 1-egg, $n = 3$; 63.6% of 2-egg nests, $n = 11$; 25.0%
of 3-egg nests, $n = 24$; Fisher's exact test, $P < 0.01$ [pooling 1- and 2-egg
clutches]). In the following laying schedules, numbers indicate days
where new eggs were found during nest visits. A dash indicates a day
where egg number was unchanged in Western (1–2–34, $n = 1$; 12–3–4,
$n = 1$; 2–3–4, $n = 1$; 2–34, $n = 2$; 23–4, $n = 1$; 234, $n = 2$; 3–4, $n = 4$;
34, $n = 10$) and Semipalmated Sandpipers (1–2–34, $n = 1$; 2–34, $n = 1$;

23–4, $n = 2$; 234, $n = 2$; 3–4, $n = 2$; 34, $n = 8$). The days that eggs were not found did not appear more frequently towards either the start or end of laying.

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

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

I examined the success rate (hatched vs. depredated) of nests laid before and after the mean annual laying dates. Abandoned clutches were not included in the totals because few nests were deserted each year (Western, $n = 0$–7; Semipalmated, $n = 0$–2). In Semipalmated Sandpipers, the success rate of early nests (60.0%, $n = 105$) was significantly higher than that of late nests (22.9%, $n = 70$, Fisher's exact test, $P < 0.001$). The success rate of early Western Sandpiper nests (68.2%, $n = 88$) was also higher than late nests (47.3%, $n = 55$) but the difference was not significant (Fisher's exact test, $P = 0.15$). The pattern was the same in all years, and similar conclusions were reached if survival rates were calculated with the Mayfield method.

<div align="center">DISCUSSION</div>

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

Gaps in laying schedules may be due to the time of day a nest visit

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

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

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

Length of incubation.—Incubation averaged 21 d in Western Sandpipers
and 20 d in Semipalmated Sandpipers, which is consistent with previous
reports (Ashkenazie and Safriel 1979, Gratto-Trevor 1992, Holmes 1972).
Length of incubation in other calidrine sandpipers varies from 20 d (n
= 5, Least Sandpiper, Miller 1983), 21 d (n = 6, Temminck's Stint, Breie-
hagen 1989), 21–22 d (n = 23, Dunlin, Soikkeli 1967) to 22 d (n = 1,
White-rumped Sandpiper *C. fuscicollis*, Parmelee et al. 1968). Interspe-
cific variation in shorebird laying intervals and length of incubation is

probably related to variation in egg size, all of these factors are also positively correlated with body size (Rahn and Ar 1974, Sæther et al. 1986).

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

Hatching chronology.—I found that sandpiper young usually finished hatching about 3 d after they had begun tapping on the eggshell. Past estimates of hatching duration in Western Sandpipers (24 h, Holmes 1972) and Semipalmated Sandpipers (24 h, Ashkenazie and Safriel 1979) appear to have been calculated from the hatching of the first egg to the last egg. If so, they are comparable to my estimates of 28 h for the hatching of nests with hole-pipped eggs. In a comparative study of other calidrine sandpipers, Norton (1972) also found that hole-pips preceded hatching by 12–48 h. The total time required by sandpiper young to emerge from eggs is longer than previously recognized. Future studies should be explicit in defining how estimates of different hatching stages are measured.

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

Shorebird numbers are affected by variation in productivity (Ryan et al. 1993), but variable nesting success should not have a major effect on population size because adult survival rates are high in shorebirds (Evans 1991, Sandercock and Gratto-Trevor 1997). Recent population models

support this notion, and show that sandpiper numbers are most sensitive to changes in the rates of adult mortality (Hitchcock and Gratto-Trevor 1997).

ACKNOWLEDGMENTS

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