Features of breeding biology in Pacific and American Golden-Plovers nesting on the Seward Peninsula, Alaska

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We studied site-fidelity, nesting, and the chronology of hatching in Pacific and American Golden-Plovers (*Pluvialis fulva* and *P. dominica*) from 1988 to 2000 on breeding grounds near Nome, Alaska. Banded males of both species were strongly site-faithful in subsequent seasons with 12 of 16 *fulva* and 11 of 15 *dominica* (at return rates of 77% and 80%, respectively) nesting near, and occasionally in, previous nests. The fidelity of males did not appear to be reduced by lack of breeding success, suggesting that familiarity with a territory is of primary importance. Among females, only 2 of 12 *fulva* and 1 of 11 *dominica* (at return rates of 25% and 15%, respectively) were seen in subsequent seasons. Each of the *fulva* females was present for three consecutive seasons including the season when captured; one mated with the same partner for two seasons, the other with the same male in all seasons. The single *dominica* female paired for one season with a different mate than she had when captured. We estimated that *dominica* females produced replacement clutches in 12–14 days after loss of the first clutch. Hatching began in late June and intra-clutch chronologies were similar in each species. The first indications of hatching were hairline cracks that appeared 5–50 hours before more obvious breakage (star-pip or tiny pip-hole). Most eggs progressed from the latter conditions to emergence of a chick in 10–20 hours. Intervals from the first hairline-cracked shells and the first obvious breakage of shells to four dry chicks in and around the nest were approximately 2–4 days and 1–3 days, respectively. Brood members emerged sequentially over the course of about one day, and often at least two chicks were already foraging near the nest before the last sibling had appeared.

INTRODUCTION

The Pacific Golden-Plover *Pluvialis fulva* and American Golden-Plover *P. dominica* are seasonally monogamous shorebirds with male-biased breeding ground fidelity (Greenwood 1980, Johnson *et al.* 1993, 1997a, Sviridova 2000). Males (sexes are dimorphic in breeding plumage) establish the territories, build nests, and perform most defensive behaviours (Connors *et al.* 1993, Johnson & Connors 1996, Byrkjedal & Thompson 1998). Returning to a familiar place presumably lessens intra-sexual competition among males and facilitates rapid re-occupancy in the spring (Greenwood & Harvey 1982, Flynn *et al.* 1999, Sviridova 2000). However, variation in the quality of a male's territory (related to timing of snowmelt) may reduce his attractiveness to females in certain seasons. Although some pairs probably form before arrival on breeding territories (Sauer 1962, Connors *et al.* 1993, Johnson & Connors 1996, Sviridova 2000), the response of most females to variable spring conditions appears to be site-unfaithful opportunistic pairing with males possessing suitable territories (Tomkovich & Soloviev 1994, Johnson *et al.* 1997a). A useful overview of nesting-site fidelity in male shorebirds together with additional references is provided by Flynn *et al.* (1999).

Our studies on the Seward Peninsula began in 1988, and some of the plovers we banded in earlier years survived after initial accounts of site fidelity were published (Johnson *et al.* 1993, 1997a). We continued to record their breeding activities in subsequent seasons, and also marked additional birds. General knowledge of reproductive biology in Pacific and American Golden-Plovers is reasonably good, but many details are lacking (Johnson & Connors 1996, Piersma *et al.* 1997, Byrkjedal & Thompson 1998). In this paper, we quantify fidelity more thoroughly by combining data on returning birds in all seasons up to and including 2000, and report findings on interannual spacing of nests, re-nesting, and time intervals associated with hatching.

STUDY AREAS AND METHODS

We conducted fieldwork from 1988 to 2000 at two sites on golden-plover breeding grounds north of Nome, Alaska. Most data are from the Feather River site, an area of about 550 ha near mile 37 on the Nome-Teller Road (64°51'N,

Table 1. Selected records of banded Pacific Golden-Plovers (PGP) and American Golden Plovers (AGP) at the Feather River and Nugget Creek study areas, 1989–2000.

No., species, sex & breeding season when banded	Last season recorded on territory (bold) & other notes
(1) PGP, male[a] 1988	**1998**. Nesting uncertain in 1989[b]; nested 1990, 1995 & 1997, probably nested[c] in 1992; alone on territory 1991, 1993, 1994, 1996 & 1998.
(2) PGP, male 1993	**2000**. Nested 1994 to 1996, alone on territory 1997, nested 1998, alone on territory 1999 & 2000, one reuse of a nest cup.
(3) PGP, male 1993	**1999**. Nested in 1994, not found from 1995 to 1997, nested 1998 & 1999
(4) PGP, female 1988	**1990**. Changed mates in 1989, mated again with same male in 1990 (i.e., the same pair for two consecutive seasons).
(5) PGP, female 1993	**1995**. Mated 1994 & 1995 with the same male as when captured (i.e., the same pair for at least three consecutive seasons).
(6) AGP, male 1989	**1996**. Not found 1990, 1992 & 1993, probably nested in 1991, nested 1994, alone on territory 1995 & 1996.
(7) AGP, male 1993	**2000**. Nested in 1994, not found 1995 to 1997, nested 1998 to 2000, re-nested in 2000 with the same female after loss of first clutch.
(8) AGP, male 1993	**2000**. Alone on territory 1994, nested 1995 & 1996, not found 1997, nested 1998, probably nested 1999 & 2000, one reuse of a nest cup.
(9) AGP, male 1994	**2000**. Alone on territory 1995, nested 1996 to 2000, re-nested in 1998 & 2000 after loss of first clutches.
(10) AGP, female 1993	**1998**. Not found 1994 to 1996; nested in 1997 with No. 9 (a different mate than she had when captured); chased and evicted by No. 9 in 1998, not seen again that season.

[a] This individual had his territory at Nugget Creek; all other birds in the table were at Feather River.

[b] The Nugget Creek study site was inaccessible in 1989 because of late snowmelt.

[c] The term "probably nested" indicates that a female was present with the male, but no nest was found. Pairs did not show nest-related agitation, and from the timing of our observations may have been between loss of one clutch and laying of another.

166°05'W); the other site covers about 350 ha at Nugget Creek near mile 31 on the Nome-Kougarok Road (64°54'N, 165°14'W). We captured plovers in nest traps, and marked each individual with a unique combination of colour-bands plus a USGS metal band all placed on the tibiotarsi. The typical clutch in these plovers consists of four eggs, and to avoid breakage during trapping we temporarily removed actual eggs from the nest and replaced them with either plaster of Paris-filled eggs (prepared from an abandoned clutch) or with more durable painted wooden replicas (Robinson & Oring 1997). We marked birds of both species at the Feather River site, but only *fulva* at Nugget Creek. Altogether, 28 *fulva* (16 males, 12 females) and 26 *dominica* (15 males, 11 females) were banded. Except for one *fulva* and one *dominica* trapped in 1998, all plovers were captured from 1988 to 1994.

The timing and duration of fieldwork in post-banding seasons varied from year-to-year: 1989, 3–13 June; 1990, 21–28 June; 1991, 12–19 June; 1992, 20–25 June; 1993, 10–30 June; 1994, 27 May–27 June; 1995, 18–29 June; 1996, 17–28 June; 1997, 21 June–6 July; 1998, 6 June–6 July; 1999, 20 June–6 July; 2000, 4 June–5 July. We surveyed study sites intensively each season, and were confident that all plovers present were found and checked for bands. Site-faithful males usually were easy to locate. Their distraction displays and defensive behaviours around the nest were within a relatively small core area of the overall territory, and typically near the previous season's nest (for additional information about breeding territories, see Johnson & Connors 1996, Byrkjedal & Thompson 1998). Several times per season, we expanded the hunt for missing birds by searching a 1–2 km wide band of tundra bordering the perimeter of each study site.

Return rates are based on the 1989–2000 records of all plovers marked during the study, and represent the cumulative totals of birds re-sighted as a proportion of birds potentially available for re-sighting. The latter value for each season was the number of marked birds found (plus others banded, if any) in the previous season. Males that went undetected in certain seasons and later reappeared were counted as returnees in seasons when missing (see Discussion).

We used small survey flags or rock cairns to locate nests within and between seasons, and measured distances between interseason nests (and intraseason re-nests) by pacing along a straight line with each pace considered to be one metre. We report here all distances measured since 1989 (including several mentioned in earlier publications; Johnson *et al.* 1993, 1997a). We gathered information concerning hatching and re-nesting mostly during the 1998–2000 seasons. We visited each nest about every other day until flotation testing (Van Paassen *et al.* 1984, Tulp *et al.* 1997, Sandercock 1998) indicated that incubation was nearing completion. At that point, we began checking the nest 2–3 times/day to measure time intervals associated with hatching.

RESULTS

Site fidelity

In Table 1 we show interannual records of various returnees. The birds listed (selected males and all females) are representative of overall findings. Those birds not shown in the table are included within the totals and otherwise considered in the text. From 1989 to 2000, 12 of 16 *fulva* males, 2 of 12 *fulva* females, 11 of 15 *dominica* males, and 1 of 11 *dominica* females returned to the study sites. All returning males re-

occupied the territories on which they were banded; females were more variable (see below). Male *fulva* returned for up to 10 seasons after banding (no. 1, Table 1), and male *dominica* for up to 7 seasons (nos. 6–8, Table 1). Based on all birds marked, the average number of post-banding seasons that birds returned was 3.0 for *fulva* males, 2.8 for *dominica* males, 0.33 for *fulva* females, and 0.18 for *dominica* females. The return rates of males compared to females were: *fulva*, 77% (46/60) vs. 25% (4/16); *dominica*, 80% (43/54) vs. 15% (2/13). Rate differences between the sexes were statistically significant ($P < 0.001$ by χ^2 tests).

Several unmated males were observed on their territories in various seasons, sometimes for two consecutive years (e.g., nos. 1, 2, 6, 8, 9, Table 1). In each case, the individual occupied his territory alone for the duration of that season's fieldwork. Altogether, we recorded 9 instances of this in *fulva* (involving 3 males), and 7 in *dominica* (involving 5 males). Despite apparent reproductive failure, lone males, and also males that disappeared from territories following loss of eggs to predators, typically returned the next season. Because the 11-season *fulva* male (no. 1, Table 1) was an adult of unknown age when captured (age-characteristic primary feathers of *fulva* separate adult from first-year birds; Johnson & Johnson 1983, Johnson & Connors 1996), the full duration of his tenure on a specific breeding territory was uncertain. Our observations suggested that this plover nested in only 5 or 6 of his known seasons at Nugget Creek. Four males in each species were not found in certain seasons, then reappeared on their usual territories in subsequent years (e.g., nos. 3, 6, 7, 8, Table 1).

Both of the female *fulva* returnees (nos. 4 and 5, Table 1) were present for three consecutive years, including the season when captured. Also, both reunited with previous mates. The first bird returned and paired with a different male on a territory near to where she had been banded, then mated with this same male again the next season. The other female returned to the territory where she had been captured and reunited with the same male in both the first and second post-banding seasons (i.e., the same pairing three consecutive times). The single *dominica* female that returned (no. 10, Table 1) was banded in 1993, and then not seen from 1994 to 1996. In 1997, she paired with a marked male (no. 9, Table 1) on a territory near to where she was originally captured. By then, her 1993 partner had disappeared being last recorded in 1996. In spring 1998, we saw the female again (our last sighting), but only briefly during a skirmish with male no. 9 (already paired with another female) who chased her away.

Interseason nest placement, reuse of nest cups, and re-nesting

We collected information on 24 nests of 11 marked *fulva* males, and 20 nests of 8 marked *dominica* males. Of these, 11 nests of each species were in consecutive years such that interseason distances could be measured. Mean distances were essentially identical for both species: *fulva* 114 m (20–280 m), *dominica* 115 m (0 [reuse of cup] –334 m). The greatest distance between the nest where captured and any subsequent nest was 370 m in *fulva* (two seasons after marking, no nest was found in the first post-banding season), and 334 m in *dominica* (in the first post-banding season). We found three instances of nest cup reuse in *fulva* and one in *dominica*. Relative to first known use, reuse was in the next

year (one bird), two years later (two birds), and three years later (one bird). None of the marked female *fulva* and *dominica* nested in cups they had used previously. The overall frequency at which males reused their earlier cups was 12.5% in *fulva* (3 of 24 nests) and 5.0% in *dominica* (1 of 20 nests).

We observed three instances of re-nesting in *dominica* (nos. 7 and 9, Table 1) which are the first records for this species involving banded males. The 4-egg clutches of both individuals (probably first clutches) were depredated in early to mid-June at unknown stages of incubation. The new clutches (two of 3 eggs, one of 4 eggs) were laid in nest cups at 32, 155 and 163 m, respectively, from the first nest. With the 4-egg re-nesting, there was little question that the same female had produced both clutches. Though unbanded, this particular individual was recognizable from distinctive white cheeks. The first clutch was destroyed after 14 June (we lack the exact date), the second clutch was completed on 27 June. Thus, the estimated time required for replacement laying was at most 13 days. The second clutch suffered the same fate as the first, whereupon both birds disappeared from the territory. In the other two re-nesting situations, the females were unbanded and had no distinguishing colouration. In each instance, the time of first clutch destruction was unknown. However, the intervals between our last records of intact clutches and the finding of replacements, together with allowance for egg-laying (1.5 days/egg, Johnson & Connors 1996), indicated that the maximum time from loss of the first clutch to completion of the second was 12 days in one case and 14 days in the other. It was not unusual for predators to destroy 25% or more of clutches being monitored on our study sites. Unfortunately, various factors (unavoidable interyear variations in the timing of our fieldwork, cessation of monitoring each season while some clutches were still being incubated, lack of information concerning the frequency of replacement laying) preclude meaningful estimates of the full impact of predation on nesting success.

Hatching and associated behaviours

Hatching in both species began during the last week of June and continued into early July (confirming the schedule projected by Kessel, 1989), with a tendency for *fulva* to hatch later than *dominica*. During seasons when our fieldwork extended into the hatching period, we monitored a total of 29 *fulva* and 25 *dominica* nests (both marked and unmarked birds) in which clutches had either hatched by or were still being incubated at the date of our departure. In this sample, the earliest hatching date, total hatched (of the total, number hatching in June), and number still being incubated were as follows for each species:

> *fulva* 26 June, 12 (7), 17;
> *dominica* 23 June, 20 (15), 5.

The following details concerning hatching are based on records from eight nests of each species (all 4-egg clutches) in which hatching was completed. Unless otherwise indicated, the information pertains to both species. Four of the *fulva* and six of the *dominica* nests were those of banded males. In an effort to avoid potentially harmful chilling of eggs and nestlings and/or attraction of predators, we tried to keep displacement of parents from nests to a minimum. With that restriction, we were able to measure hatching-times for 15 eggs of *fulva* and 19 eggs of *dominica*. The earliest indi-

cation of pipping (Smith 1983) in a clutch was the appearance of minute hairline cracks, often requiring close scrutiny to detect, in the shell of one or two eggs. Progression from initial fine cracks to obvious, easily seen breakage in the form of a star-pip with distinctly raised surface of shell or a tiny pip-hole, varied from 5 to 50 hours. From the latter conditions, emergence of individual chicks (which happened at all hours of the day and night) occurred in 9.5–25.0 hours (*fulva*) and 9.5–27.5 hours (*dominica*); with most chicks (21 of 34) emerging in 10–20 hours. The interval from first hairline cracks to four dry chicks in and around the nest was approximately 2–4 days (47–67 hours in *fulva*, and 42–96 hours in *dominica*); and from first obvious breakage in one or two eggshells to four dry chicks required about 1–3 days (26–50 hours in *fulva*, and 21–67 hours in *dominica*). The emergence of brood members was sequential and asynchronous, with time-intervals between newly hatched (still wet) first and fourth chicks ranging from 18 to 22 hours. Presumably, there was a direct relationship between laying-order and hatching-order, but we were unable to determine this because none of the 16 nests were found at the beginning of egg-laying. Finding nests required "assistance" from the birds (i.e., a desire to return to the nest when flushed) and this behaviour seldom occurred until at least the third egg had been laid. Generally, the earliest hatched chicks (often one and two, sometimes three) gained sufficient mobility to explore up to about 3 m from the nest well before the last chick had emerged from its egg. We estimated that the time between emergence of the first chick and abandonment of the nest by the brood ranged from 26 to 30 hours. Hatching-times for three *fulva* chicks (we did not measure the fourth) from a clutch not included in any of the time-intervals above far exceeded all other measurements. For these individuals to progress from small pip-holes to emergence ranged from 42 to 50 hours. We interpreted this as a probable aberrancy associated with chilling, as the parents were wary (see Discussion) and the weather cold during hatching.

Parents removed eggshells promptly from the nest while hatchlings were still wet, and dropped them many metres away. We estimated drying-time of newly hatched chicks at 3–5 hours, during which they were brooded in the nest. Once dry, chicks began short feeding forays in the vicinity of the nest returning to the latter at frequent intervals for brooding. At this stage, the nest was a hub of activity since a parent remained thereon as a source of warmth both for returning chicks and for eggs in the process of hatching. The other parent often brooded one or more chicks near the nest. During hatching, males were invariably present either on the nest or close by if the female was on the nest. Females were frequently in attendance, but sometimes were absent, especially during the early stages of hatching. Presumably, missing females were at extraterritorial feeding grounds (Johnson & Connors 1996, Byrkjedal & Thompson 1998), or in some cases, particularly with *fulva*, were so elusive that their presence went undetected. Generally, within a day of the fourth egg hatching, families (broods accompanied by both parents) had deserted their nests and travelled 100 m or more from them. We have no information on the fate of chicks once they departed from nest sites. At one *dominica* nest, parents continued to incubate three unpipped eggs for at least 48 hours post-emergence of a single chick. After these two additional days, and with the chick very mobile, they deserted the remaining eggs. Upon examination, the latter proved to be infertile.

DISCUSSION

Site-faithful male Pacific and American Golden-Plovers returned to their breeding territories on the Seward Peninsula at high rates (near the upper end of the measured range for male shorebirds; see Oring & Lank 1984, Haig & Oring 1988, Sandercock & Gratto-Trevor 1997, Tomkovich & Soloviev 1994, Tomkovich 1996, Flynn *et al.* 1999, Handel & Gill 2000). These findings, together with the site-unfaithful behaviour of females, further substantiate previous reports of male-biased fidelity and female dispersal in *fulva* and *dominica* (Johnson *et al.* 1993, 1997a). The same adaptations have been described in these species (and also in the Grey Plover *P. squatarola*) on breeding grounds elsewhere (Tomkovich & Soloviev 1994, Moitoret *et al.* 1996, Sviridova 2000). That sample females might be dying rather than dispersing was highly improbable in *fulva* because long-term studies on wintering grounds in Hawaii showed equal return rates for the two sexes (Johnson *et al.* 2001a). Although there has been no comparable work in South America, the Hawaii findings suggest a similar pattern for *dominica*. In both species, the male and female return rates we found on the Seward Peninsula (*fulva*, 77% and 25%; *dominica*, 80% and 15%) were higher than those reported elsewhere. Comparable values [though other studies were relatively short-term, and at higher latitudes where birds may be less site-faithful (Svirodova 2000)] were 50% and 9% for *fulva* on the Taimyr Peninsula of Siberia (Sviridova 2000), and 57% and 0% for *dominica* on the North Slope of Alaska (Moitoret *et al.* 1996). Given the strong site-fidelity of males on the Seward Peninsula, their return rates probably reflect overall survival within populations. Substantial evidence supports a major migratory link between Alaska and the Hawaiian Islands (Johnson & Connors 1996; Johnson *et al.* 1997b, 2001b; O.W. Johnson, unpubl. data). Notably, the return rate of male *fulva* reported here (77%) falls at about the midpoint of estimated annual survival (67%–90%) for plovers monitored over a 20-year period at a wintering ground on Oahu (Johnson *et al.* 2001a). In the latter study, plovers that defended winter territories appeared to survive at higher rates than non-territorial birds, but emigration of non-territorial individuals from the research site was an uncertain variable.

We have only partial knowledge of breeding success, as the fates of some clutches and all chicks were unknown. Nonetheless, continued fidelity of males after obvious reproductive failure clearly indicated that their site-faithfulness was not lessened by unsuccessful breeding seasons. For example, males that disappeared from their territories after losing clutches to predators or males that failed to attract a mate typically returned in the subsequent season. The same was generally true for males not found on the study sites in one or more seasons. For the most part, lone unpaired males appeared to represent situations where localized accumulations of snow covering territories during the pre-breeding period in some years made it impossible to attract or retain mates. In a few instances, lone males may have resulted from loss of clutches and desertion by females (see Sviridova 2000) before we arrived on the study areas. Seasonal absence of males usually occurred only in years when we began work relatively late in the spring. Thus, we discounted erratic fidelity and assumed instead that breeding failure had caused these individuals to abandon their territories by the time of our arrival. Returns of unsuccessful males support the concept that familiarity with a territory, which probably reduces

intra-sexual competition, is the major determinant of male site-faithfulness. Sviridova (2000) came to a similar conclusion (return rate of males independent of "egg incubation success") in her studies of *fulva* on the Taimyr Peninsula. None of the long-surviving males (11 seasons *fulva*, 8 seasons *dominica*; Table 1) constituted a longevity record. Pacific Golden-Plovers ranging to at least 18 years 10 months of age have been documented in Hawaii (Johnson *et al.* 2001a); and the three longest-returning American Golden-Plovers (nos. 6–8, Table 1) had reached 8 years of age in summer 2000 (assuming they were in their second calendar year when captured) which equals a previous longevity record for this species (Johnson *et al.* 1997a).

From early spring observations in northwestern Alaska, Connors *et al.* (1993) concluded that pair formation in *fulva* and *dominica* occurs mostly after arrival on breeding territories, but some pairing may begin earlier as birds linger on snow-free patches while en route "especially if the breeding-territory habitat remains snow-covered until late spring". Pre-arrival pairing of *fulva* was also observed in Siberia by Sviridova (2000). It is uncertain how our records of *fulva* females relate to the foregoing. Reunion of the same pairs in consecutive seasons has never been reported in this species, and we do not know whether these findings indicate previously unknown variation in the breeding system or were simply chance happenings. If the members of these pairs spent non-breeding seasons in geographically separate areas, their re-associations would require relatively close synchronization of spring arrival (so as to preclude the opportunistic formation of a new pair) or ability of the returning female to drive off a usurping female (Flynn *et al.* 1999, Handel & Gill 2000). Our observation of an already-paired male rejecting a previous mate (no. 10, Table 1) argues against the latter ability. All of this raises an obvious question: Do paired *fulva* sometimes remain associated during non-breeding seasons and return together in the spring? If this does occur, it might explain the behavioural interactions seen occasionally among spring pre-migrants in Hawaii that suggest pairing before departure (Johnson & Connors 1996).

Measured distances between successive nests of Pacific and American Golden-Plovers on other breeding grounds all imply greater interseason spacing than we found on the Seward Peninsula. On the Taimyr Peninsula, the average for 19 *fulva* nests exceeded 250 m (15–530 m) over 1–2 post-banding seasons (Sviridova 2000), and two nests of one male were separated by 200 m (Underhill *et al.* 1993); on the North Slope of Alaska, the nests (number not given) of three *dominica* averaged 175 m (46–289 m) over 1–2 post-banding seasons (Moitoret *et al.* 1996), and at Lake Clark National Park and Preserve in southwestern Alaska, four nests of two *dominica* averaged 231 m (95–500 m) over two post-banding seasons (P.S. Tomkovich *in litt.*). Aside from our observations of nest cup reuse, the only other record known to us in Pacific and American Golden-Plovers is a report of interspecific reuse in which a male *dominica* nested in the previous cup of a Stilt Sandpiper *Calidris himantopus* (Moitoret *et al.* 1996).

Interyear nest spacing has been described in numerous species of arctic- and subarctic-nesting shorebirds. Measurements in Grey Plovers (Tomkovich & Soloviev 1994, Moitoret *et al.* 1996), Semipalmated Plovers *Charadrius semipalmatus* (Flynn *et al.* 1999), Whimbrels *Numenius phaeopus* (Skeel & Mallory 1996), Black Turnstones *Arenaria melanocephala* (Handel & Gill 2000), Red Knots *Calidris canutus*

and Sanderlings *C. alba* (Tomkovich & Soloviev 1994), Semipalmated Sandpipers *C. pusilla* (Gratto-Trevor 1992, Moitoret *et al.* 1996), Western Sandpipers *C. mauri* (Holmes 1971a), Pectoral Sandpipers *C. melanotos* (Moitoret *et al.* 1996), Dunlins *C. alpina* (Moitoret *et al.* 1996), Stilt Sandpipers (Moitoret *et al.* 1996, Klima & Jehl 1998), Red-necked Phalaropes *Phalaropus lobatus* (Rubega *et al.* 2000), and Grey (=Red) Phalaropes *P. fulicaria* (Moitoret *et al.* 1996), varied widely both within and among species ranging from 0 (reuse of the same cup) to about 1,000 m. Compared to our measurements for golden-plovers, the data available for Grey Plovers indicate wider interseason spacing of nests, averaging >250 m (Moitoret *et al.* 1996, Tomkovich & Soloviev 1994). Reuse of nest cups has been observed in Eurasian Golden-Plovers *P. apricaria* (Parr 1980); also in Semipalmated Plovers (Flynn *et al.* 1999), Semipalmated Sandpipers (Gratto-Trevor 1992, Moitoret *et al.* 1996), Western Sandpipers (Holmes 1971a), Dunlins (Moitoret *et al.* 1996), and Stilt Sandpipers (Moitoret *et al.* 1996, Klima & Jehl 1998).

Our measurements of hatching-associated time intervals, together with other reports (Sauer 1962, Hussell & Page 1976, Johnson & Connors 1996, Byrkjedal & Thompson 1998), indicate similar chronologies throughout the four-member *Pluvialis* group (Pacific, American, Eurasian Golden-Plovers, and Grey Plover). The sequential emergence of brood members over a period of about one day showed that full incubation begins before the clutch is complete, probably with laying of the third egg (Johnson & Connors 1996). Prior to full incubation by both parents, males tend to cover the eggs (Byrkjedal & Thompson 1998). Although we have observed this behaviour, we lack data on its frequency and duration. Whether males provide sufficient warmth to trigger early embryonic development in the first two eggs is uncertain.

Mated pairs remaining together for production of replacement clutches (both birds marked) has been documented in three of the *Pluvialis* plovers (*fulva*, Sviridova 2000; *apricaria*, Parr 1980; *squatarola*, Tomkovich & Soloviev 1994); and also in the Semipalmated Plover (Flynn *et al.* 1999), Black Turnstone (Handel & Gill 2000), Semipalmated Sandpiper (Gratto-Trevor 1992), Western Sandpiper (Holmes 1971a), Least Sandpiper *C. minutilla* (Miller 1983, Cooper 1994) and Dunlin (Soikkeli 1967, Holmes 1971b). From this collective evidence, it seems reasonable to assume, despite lack of banded females, that re-nestings of *fulva* and *dominica* (those described in this paper, and by Sauer 1962, Schekkerman & van Roomen 1995, Johnson & Connors 1996) were replacement clutches of specific pairs of birds. Thus, *fulva* and *dominica* females weighing about 140–150 g and laying eggs of 25–29 g (body and egg mass data from the Seward Peninsula, Johnson & Connors 1996) apparently can produce at least two clutches with combined mass of 175 g or more (depending on egg weight and whether the replacement clutch contains 3 or 4 eggs) during the period from mid-May to late June. Further evidence of impressive egg-laying ability in tundra shorebirds was demonstrated in 1999 by a Western Sandpiper that laid three consecutive replacement clutches totalling 11 eggs in 41 days (B. J. McCaffery, pers. comm.).

Golden-plovers occur sympatrically on the Seward Peninsula, but the two species nest in distinctly different habitats. Typically, nests of *dominica* are on higher well-drained, sparsely vegetated rocky slopes; and those of *fulva* are on

lower moist sites with denser vegetation (Connors *et al.* 1993, Johnson & Connors 1996). Therefore, the tendency of *fulva* to hatch later than *dominica* at our study sites suggests an interspecific difference in spring arrival schedules or in the start of nesting as related to snowmelt in their respective nesting habitats. During the course of our investigation, we were unable to arrive on the study areas early enough in the season to evaluate these possibilities. However, Connors *et al.* (1993) concluded from early spring observations that there was no interspecific difference in arrival time and that nesting habitats opened "on a similar schedule". As an alternative explanation for later hatching in *fulva*, we raise the possibility that an interspecific difference in behaviour during nest checks might be a significant variable. When disturbed at the nest, *dominica* usually responded with vigorous distraction displays (Johnson & Connors 1996) performed close at hand, and then resumed incubation promptly when the observer departed or sometimes while the observer was still present. In contrast, the reactions of *fulva* were much less predictable. Many individuals were extremely wary, and sneaked stealthily away from nests when an approaching human was 200 m or more distant ("early surreptitious departure", Gochfeld 1984; Johnson & Connors 1996, Tulp *et al.* 1997). These birds often ran or flew a considerable distance to a vantage point where alarm calls were interspersed with feeding, preening, and head-scratching (the latter is indirect in both *fulva* and *dominica, contra* Johnson & Connors 1996). Other individuals left their nests, flew off without a sound and simply disappeared. Compared to *dominica*, such behaviour resulted in longer periods with eggs exposed to cool ambient temperatures. We suspect the disproportionate repeated chilling of embryos may have been sufficient to lengthen the incubation period of *fulva* clutches, a possibility also mentioned by Sauer (1962). For additional insight about events in and around nests during incubation, hatching, and early life of broods, see especially the detailed field observations of Sauer (1962); also, Drury (1961), Parmelee *et al.* (1967), Gunther 1993, Johnson & Connors (1996) and Byrkjedal & Thompson (1998).

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