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BREEDING GROUND FIDELITY AND MATE RETENTION IN THE PACIFIC GOLDEN-PLOVER

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ABSTRACT.—We found male-biased site fidelity in Pacific Golden-Plovers (*Pluvialis fulva*) on breeding grounds in western Alaska. Males (8 of 8) returned to the same territories annually, while few females (1 of 4) were seen in subsequent seasons. Nest sites in successive years were usually within 100 m, and the same nest cup may be used in more than one year. First-year birds of both sexes mated with older birds and also with each other, but first-year females may breed less commonly than first-year males. The numbers of nesting birds on our study sites varied sharply both within and between seasons. *Received 13 Jan. 1992, accepted 21 May 1992.*

The Pacific Golden-Plover (*Pluvialis fulva*) is a monogamous shorebird in which both parents defend the breeding territory and care for the young. Recent studies indicate that this bird is a separate species from the American Golden-Plover (*P. dominica*). The two forms mate assortatively in areas of sympatry, and show clear differences in breeding vocalizations, nesting habitats, and plumages (Connors 1983, Connors et al. 1993). Despite resolution of taxonomic questions, many aspects of the breeding biology of *P. fulva* are poorly understood. Much of what is known about this plover's breeding habits comes from Sauer's work (1962) on St. Lawrence Island, but that study covered only a single breeding season and did not involve uniquely marked birds. Although Pacific Golden-Plovers of both sexes are known to be very site faithful on wintering grounds (Johnson et al. 1989), information regarding breeding site fidelity and mate retention was lacking. In fact, the only previous study of breeding ground fidelity in the genus *Pluvialis* was Parr's (1980) investigation of the Eurasian Golden-Plover (*P. apricaria*).

During parts of four summers, we observed marked Pacific Golden-Plovers on breeding grounds in western Alaska. We now report findings on site fidelity, mate retention, annual variation in local abundance, and other features of reproductive behavior.

METHODS

Work was conducted each June from 1988–1991 at two sites along roads emanating from Nome, Alaska. Our two study areas were located near the Feather River, at mile 37 on the

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Nome-Teller Road (Lat. 64°51′N, Long. 166°05′W), and near Nugget Creek at mile 31 on the Nome-Kougerok Road (Lat. 64°54′N, Long. 165°14′W). The Feather River study area covers about 550 ha, the Nugget Creek site about 350 ha. The Feather River site was readily accessible by road in each year; Nugget Creek could not be reached in 1989 because of heavy snowfall. Straight line distance between the two sites is approximately 45 km. Connors et al. (1993) give further descriptions of both areas.

We captured plovers with nest traps and each bird was marked with a unique combination of color bands plus a USFWS aluminum band. We banded eight males (four adults, four first-year birds) and five females (four adults, one first-year bird), including both members of the pair in six instances. Trapping had to be timed relative to incubation schedules. Typically, males incubated during the daytime (about 08:00–20:00 h) and females at night (about 20:00–08:00 h). A small survey flag was set at 12 paces from each nest to facilitate finding nests within and between seasons. We conducted systematic searches of the study areas in each season to locate and monitor banded birds. If we were unable to find a bird banded in a previous season, we expanded our search 1–2 km beyond the boundaries of the study sites.

We collected ten plovers for related taxonomic studies. These were taken by shotgun at various sites along the road system well away from the study areas. Age and sex criteria for all birds (banded and collected) followed Johnson and Johnson (1983): first-year individuals show worn juvenile primaries, and the sexes are dimorphic in breeding plumage. Also, the reproductive organs of collected birds were examined by dissection.

RESULTS AND DISCUSSION

Sex-biased philopatry.—Among shorebirds, high rates of breeding area fidelity typically occur in species exhibiting monogamy, biparental care of young, and joint defense of a breeding territory. This relationship suggests that site familiarity is of major significance during competition for resources (Oring and Lank 1984, Colwell and Oring 1989). Greenwood (1980) hypothesized that "partitioning of resources by males prior to selection of mates by females should result in female dispersal." This would lead to sex-biased philopatry in which males would be more site-faithful than females. Statistical evidence favoring Greenwood's predictions has been rare in studies of shorebirds. In various species, including the Eurasian Golden-Plover (Parr 1980), the return rates of males and females are nearly equal or favor males only slightly (Oring and Lank 1984; Gratto et al. 1985; Haig and Oring 1988a, b; Colwell and Oring 1989; Thompson and Hale 1989; Schamel and Tracy 1991). Contrary to these widespread observations, our results appear to support Greenwood's hypothesis. We found that males were very site-faithful to specific territories. All eight banded males were found near previous nests in years subsequent to banding. Of the four females banded prior to 1991, only one (No. 6, Fig. 1) was seen in a subsequent season. Thus, new pairings were the norm and re-mating the exception (Figs. 1 and 2). Similar male-biased fidelity was reported in Killdeers (*Charadrius vociferus*; Lenington and Mace 1975) and in Wilson's Phalaropes (*Phalaropus tricolor*; Colwell

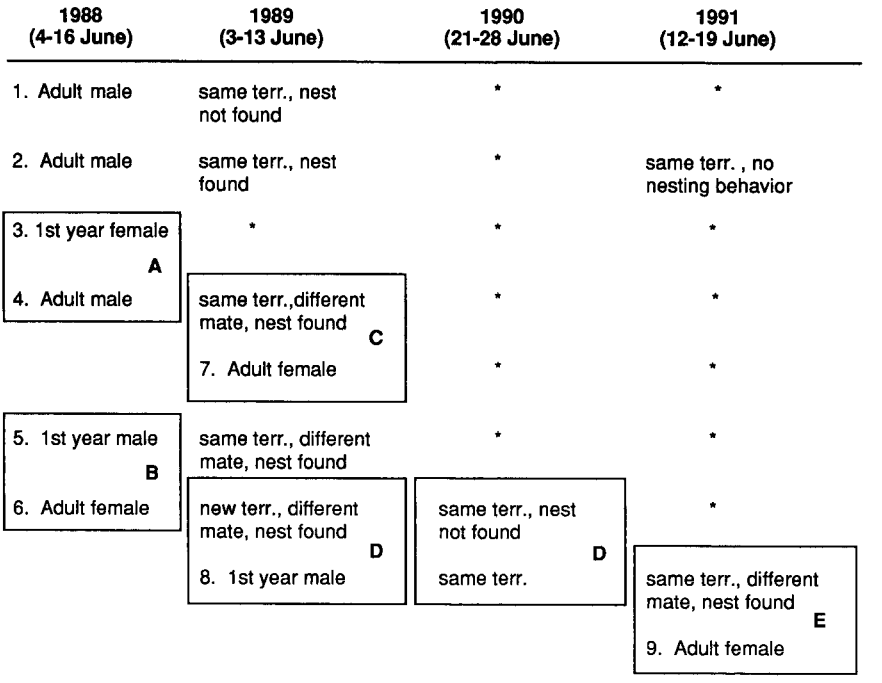

FIG. 1. Observation of *P. fulva* banded at Feather River (mile 37, Nome-Teller Road). Each individual is numbered in accordance with the sequence of banding, and its subsequent history is traced from left to right. An asterisk indicates that the bird was not found in that year. Each banded pair is designated by a letter and enclosed in a rectangle. Dates indicate the period of field work in each year.

et al. 1988). Colwell and Oring (1989) found no sex-bias among Killdeers but their sample was small.

Additional studies involving larger numbers of female *P. fulva* will be necessary to substantiate present findings. The possibility that chance mortality in our small sample of females has been misinterpreted as dispersal cannot be ruled out, although 0% mortality of males vs 75% mortality of females is statistically unlikely ($P = 0.018$, by Fisher's Exact Test). That the natural rigors of reproduction might cause females to suffer higher mortality than males is another possibility, but this is not supported by observations from the wintering grounds. There has been no significant difference between sexes ($P = 0.706$) in the survival of color-banded plovers monitored over 12 seasons (N = 73 males, 50 females) on Oahu, Hawaiian Islands (Johnson and Bruner, unpubl. data). Assuming that survival in breeding males and females is equal and that female *P. fulva* do indeed disperse, the sex-bias might reflect differences in arrival times

1988 (4-16 June)	1989 (3-13 June)	1990 (21-28 June)	1991 (12-19 June)
1. 1st year male	site inaccessible	same terr., same nest cup as in 1988	*
2. Adult male	"	same terr., nest about 120m from 1988 nest, hatching 28 June	same terr. on 15 June, no nesting behavior, not seen during final visit on 18 June
3. 1st year male **A**	"	same terr., different mate, nest about 370m from 1988 nest, hatching 28 June	*
4. Adult female	"	*	*

FIG. 2. Observations of *P. fulva* banded at Nugget Creek (mile 31, Nome-Kougerok Road). See legend, Fig. 1.

(see Oring and Lank 1984). Returning females may find their previous mates already taken and thus be forced to move elsewhere. The only female we observed in more than one season (No. 6, Fig. 1) was mated in 1988 to male No. 5, forming Pair B. The following year she joined a new male (No. 8), producing Pair D, and male No. 5 mated with an unbanded female. The two territories in which these rearrangements took place were adjacent, with the nest sites about 400 m apart. Had similar shifts over relatively short distances occurred with other banded females it is likely that we would have found them. This suggests that females usually disperse longer distances than female No. 6. Lengthy female dispersal movements occur in other plovers. Wilcox (1959) reported that female Piping Plovers (*C. melodus*) taking new mates moved an average distance of about 1250 m, with some individuals dispersing much farther (also see Haig and Oring 1988b).

In 1990, female No. 6 and male No. 8 re-mated (pair D), but in 1991, male No. 8 was mated to a different female (forming Pair E), and female No. 6 was not found (Fig. 1). Infrequent re-mating similar to this has been reported in Killdeers (Lenington and Mace 1975), Piping Plovers (Wilcox 1959, Haig and Oring 1988a), and Ringed Plovers (*Charadrius hiaticula*; Laven 1940). In various other shorebirds, including the Eurasian Golden-Plover, re-mating is common (Parr 1980, Wiens and Cuthbert 1988).

In other species, age and breeding experience influence return rates, and successful breeders are more likely to return (for references see Colwell and Oring 1989). We have no data on fledging success and scant data on hatching success among our banded plovers. However, with respect to

TABLE 1
AGE-RELATED PAIRING IN THE PACIFIC GOLDEN-PLOVER

Male : female	Banded	Collected	Total
Adult : adult	3	2	5
First-year : adult	3	0	3
Adult : first-year	1	0	1
First-year : first-year	0	1	1

age and breeding experience, it is notable that four of the eight site-faithful males were banded as inexperienced first-year birds, while only one of four site-unfaithful females was a first-year individual.

Nest locations.—Most nests were located close to the last known nest (used one or two seasons previously). All (N = 4) of the nests at Feather River were within 100 m of the last known nest. At Nugget Creek we can only compare the locations of nests used in 1988 and 1990 (the area was inaccessible in 1989, and no plovers were found nesting in 1991). One bird used the same nest cup in both years; two others moved to new sites over distances of about 120 m and 370 m, respectively (Fig. 2). Reuse of the same nest has been reported in Eurasian Golden-Plovers (Parr 1980), Semipalmated Sandpipers (*Calidris pusilla*; Gratto et al. 1985), Western Sandpipers (*C. mauri*; Holmes 1971), and Common Greenshanks (*Tringa nebularia*; Thompson et al. 1988). While searching for plover No. 2 at Nugget Creek in 1991, we found two nest cups located near the bird's 1988 and 1990 cups. They were very similar to the latter, perfectly formed and trimmed with lichens, and probably were nest cups used by No. 2 in other years. The four nests fell along a roughly L-shaped pattern of dimensions 120 m × 48 m.

Age-related pairing and first-year breeding.—Banded pairs were composed of either two adults (Pairs C, D in 1990, and E, Fig. 1) or an adult with a first-year bird (Pairs A, B, D in 1989, Fig. 1; and Pair A, Fig. 2). In first-year/adult pairings, we found one first-year female with an older male (Pair A, Fig. 1) and three first-year males with older females (Pairs B, D in 1989, Fig. 1; and Pair A, Fig. 2).

Of the plovers collected (see Methods) there were, by design, equal numbers of males and females. Among the five males (three adults, two first-year birds) and five females (four adults, one first-year bird) were three pairs, judged on the basis of behavior (vocalizations, displays, copulations). In two pairs all members were adults; in the remaining pair, both individuals were first-year birds. All four possible combinations of adult and first-year pairings occurred among the ten pairs described above (Table 1).

Some first-year Pacific Golden-Plovers remain on the winter range and over-summer, while others acquire breeding plumage and return to the nesting grounds (Johnson and Johnson 1983). Whether these returning first-year birds were breeders had been unknown. It is now evident that first-year individuals of both sexes participate in the breeding process, as in the Eurasian Golden-Plover (Parr 1980). Although it is a small sample (Table 1), the higher frequency of first-year male/adult female pairs (3) compared with adult male/first-year female pairs (1) hints at a possible difference in breeding participation by first-year birds based on sex. Reviewing all banded and collected birds in this study (N = 23), six of 13 males (46%) were first-year birds, but only two of ten females (20%) were first-year birds. If this pattern is real, and widespread, there are three possible explanations: (1) first-year females are less likely to migrate and thus should predominate among over-summering birds on wintering grounds; (2) adult males have higher mortality rates than adult females, leading to higher proportions of surviving adults among females; (3) some first-year females returning to the tundra do not breed (such birds would likely be difficult to detect). Higher mortality of females during the first wintering season, or unequal sex ratios at hatching, would not affect the ratios of first-year birds to adults in either sex. Explanations 1 and 2 above are not favored by available evidence: over-summering males greatly outnumbered females at Enewetak Atoll in the tropical Pacific (Johnson 1979), survival of males on Alaska study areas was high (this paper), and survival rates of adult males and females on a wintering ground in Hawaii appear to be equal (this paper). Pending further study, explanation 3 best accounts for the pattern described.

Breeding density variation.—In 1988, we located seven territories of *P. fulva* at the Feather River site. The following year was a season of late snow-melt throughout the Seward Peninsula, but this site cleared relatively early and nesting density appeared similar to 1988. However, in 1990 (a year of normal snow-melt), the only birds found were the members of Pair D (Fig. 1), and these showed no nest-related behavior. Conditions were similar in 1991, with relatively few plovers present. We found No. 8 male from the previous Pair D mated to a different female (No. 9, Pair E, Fig. 1) and the birds were incubating. We also located one other marked individual (No. 2 male, Fig. 1), on the same territory where originally banded and in the company of an unbanded female, but observed no nest-associated behavior. During six visits at Feather River in 1991, we saw an additional three to five unbanded plovers. These appeared to be only passers-by in that there were no repeat sightings.

In 1988, there were six *P. fulva* territories at the Nugget Creek site. Conditions were very different in 1989. On 10 June, Maron viewed the site from an aircraft and reported 95% snow cover. Nugget Creek is at

TABLE 2
PACIFIC GOLDEN-PLOVER DENSITIES[a] AT TWO STUDY SITES, 1988–1991

Site	1988	1989	1990	1991
Feather River	High (7)	High	Low (1)	Low (2)
Nugget Creek	High (6)	Low (?)	High	Low (0)

[a] Numbers in parentheses indicate known territories (pairs) present. "Highs" in 1988 are exact counts. Comparable data for the "highs" in 1989 and 1990 are lacking, but populations were judged similar to 1988. "Lows" are precise figures, except for 1989 (an unusual season at Nugget Creek, see text).

higher elevation than Feather River, which can produce significant differences in snow-melt on the two areas. On 9 and 12 July, Robert E. Gill, Jr. (pers. comm.) visited Nugget Creek for a total of about six hours and found patches of snow still present. He located four *P. fulva* males, including one marked bird (No. 2, Fig. 2), but found no broods or nests. In 1990, snow-melt at Nugget Creek was earlier, and all three of the males marked in 1988 were present and nesting. Two of the clutches were hatching during our final visit on 28 June (Fig. 2). In mid-June 1991, there were few birds and no evidence of nesting *P. fulva* at Nugget Creek. The only plovers found were male No. 2 on 15 June (Fig. 2), and a pair of unbanded birds on 18 June. Plant phenology suggested that snow-melt had been relatively late.

The marked year-to-year changes in plover nesting densities described above are summarized in Table 2. The striking result is that all possible combinations of two sites and two densities occurred in just four years. Some of the low densities (Nugget Creek 1989 and possibly 1991) perhaps reflect late snow-melt and failure to nest. In other cases, snow-melt did not appear to be a factor and if nests were established they must have been lost early in incubation, whereupon birds deserted the area. Admittedly, these data are quite limited and important aspects of nesting ecology remain poorly understood. Nevertheless, our observations suggest great variation in nesting densities and/or nesting success over time and space in this region of the Pacific Golden-Plover's breeding range.

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LITERATURE CITED

COLWELL, M. A. AND L. W. ORING. 1989. Return rates of prairie shorebirds: sex and species differences. Wader Study Group Bull. 55:21–24.

———, J. D. REYNOLDS, C. L. GRATTO, D. SCHAMEL, AND D. M. TRACY. 1988. Phalarope philopatry. Proc. XIX Int. Ornithol. Congr. :585–593.

CONNORS, P. G. 1983. Taxonomy, distribution, and evolution of golden plovers (*Pluvialis dominica* and *Pluvialis fulva*). Auk 100:607–620.

———, B. J. MCCAFFERY, AND J. L. MARON. 1993. Speciation in golden-plovers, *Pluvialis dominica* and *Pluvialis fulva*: evidence from the breeding grounds. Auk (in press).

GRATTO, C. L., R. I. G. MORRISON, AND F. COOKE. 1985. Philopatry, site tenacity, and mate fidelity in the Semipalmated Sandpiper. Auk 102:16–24.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28:1140–1162.

HAIG, S. M. AND L. W. ORING. 1988a. Mate, site, and territory fidelity in Piping Plovers. Auk 105:268–277.

——— AND ———. 1988b. Distribution and dispersal in the Piping Plover. Auk 105:630–638.

HOLMES, R. T. 1971. Density, habitat, and the mating system of the Western Sandpiper (*Calidris mauri*). Oecologia 7:191–208.

JOHNSON, O. W. 1979. Biology of shorebirds summering on Enewetak Atoll. Stud. Avian Biol. No. 2:193–205.

——— AND P. M. JOHNSON. 1983. Plumage-molt-age relationships in "over-summering" and migratory Lesser Golden-Plovers. Condor 85:406–419.

———, M. L. MORTON, P. L. BRUNER, AND P. M. JOHNSON. 1989. Fat cyclicity, predicted migratory flight ranges, and features of wintering behavior in Pacific Golden-Plovers. Condor 91:156–177.

LAVEN, H. 1940. Beiträge zur Biologie des Sandregenpfeifers (*Charadrius hiaticula* L.). J. Ornithol. 88:183–287.

LENINGTON, S. AND T. MACE. 1975. Mate fidelity and nesting site tenacity in the Killdeer. Auk 92:149–151.

ORING, L. W. AND D. B. LANK. 1984. Breeding area fidelity, natal philopatry, and the social systems of sandpipers. Pp. 125–147 *in* Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations (J. Burger and B. L. Olla, eds.). Plenum Press, New York, New York.

PARR, R. 1980. Population study of golden plover *Pluvialis apricaria*, using marked birds. Ornis Scand. 11:179–189.

SAUER, E. G. F. 1962. Ethology and ecology of Golden Plovers on St. Lawrence Island, Bering Sea. Psychol. Forsch. 26:399–470.

SCHAMEL, D. AND D. M. TRACY. 1991. Breeding site fidelity and natal philopatry in the sex role-reversed Red and Red-necked phalaropes. J. Field Ornithol. 62:390–398.

THOMPSON, D. B. A., P. S. THOMPSON, AND D. N. THOMPSON. 1988. Fidelity and philopatry in breeding Redshanks (*Tringa totanus*) and Greenshanks (*T. nebularia*). Proc. XIX Int. Ornithol. Congr. :563–574.

THOMPSON, P. S. AND W. G. HALE. 1989. Breeding site fidelity and natal philopatry in the Redshank *Tringa totanus*. Ibis 131:214–224.

WIENS, T. P. AND F. J. CUTHBERT. 1988. Nest-site tenacity and mate retention of the Piping Plover. Wilson Bull. 100:545–553.

WILCOX, L. 1959. A twenty year banding study of the Piping Plover. Auk 76:129–152.