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## COPULATION BEHAVIOR, MATE GUARDING, AND PATERNITY IN THE SEMIPALMATED PLOVER<sup>1</sup>

YURI ZHARIKOV<sup>2</sup>

*Watershed Ecosystems Graduate Program, Trent University, Peterborough, Ontario, Canada, K9J 7B8*

ERICA NOL<sup>3</sup>

*Biology Department, Trent University, Peterborough, Ontario, Canada, K9J 7B8, e-mail: enol@trentu.ca*

**Abstract.** We present behavioral observations and multilocus DNA fingerprinting data on Semipalmated Plovers (*Charadrius semipalmatus*) breeding in the sub-Arctic. We predicted that, where a large time/energy investment by males during incubation and chick-rearing is crucial for successful reproduction, both ex-

tra-pair copulation and fertilization rates would be low. Extra-pair copulations were infrequent (7% of total copulations), as were within pair copulations (0.44 hr<sup>-1</sup>). Copulations occurred, on average 6.2 days prior to clutch initiation. Males spent 64% of their time in visual contact with their mates. Mate guarding during the laying period was significantly more pronounced in coastal neighborhoods of breeding birds than among solitary-nesting pairs. Extra-pair fertilizations occurred in 4% of families resulting in an extra-pair paternity rate of 4.7%.

**Key words:** *breeding densities, Charadrius semipalmatus, extra-pair paternity, multilocus DNA fingerprinting, open habitat, Semipalmated Plover.*

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<sup>2</sup> Current address: Department of Zoology, University of Queensland, Brisbane, Queensland, QLD 4072 Australia, e-mail: yzharikov@zoology.uq.edu.au

<sup>3</sup> Corresponding author.

Semipalmated Plovers (*Charadrius semipalmatus*) are small shorebirds nesting in coastal and inland tundra in the North American sub-Arctic. Although they are precocial, the survival of eggs and young depends on biparental care. Both incubation and brooding are divided almost equally between both members of a pair, although males often resume complete care of the brood after chicks reach about 15 days of age (Sullivan Blanken and Nol 1998). The species is socially monogamous, although about 45% of pairs divorce between seasons (Flynn et al. 1999).

Semipalmated Plovers nest in areas of open gravel or tundra habitat where visual contact between individuals is possible over distances up to 100 m. Two breeding densities exist in the Churchill, Manitoba region, with pairs nesting solitarily (no neighbors within 100 m), mostly at distances of at least 1 km from the coast of Hudson Bay, and in loose nesting aggregations (neighborhoods), primarily at coastal locations (Rippin Armstrong and Nol 1993). With substantial investment by the male in reproduction, and observations of frequent territorial disputes between males (Sullivan Blanken and Nol 1998), we predicted low rates of extra-pair paternity (Schwagmeyer et al. 1999). Because of the cost to the male of extra-pair fertilization, we also predicted that in those pairs nesting with close neighbors, we would observe either more intense mate guarding or more frequent copulations for paternity assurance than we would observe at the solitary nests. We tested these predictions by observing copulation and mate guarding behavior in the field and examining paternity using multilocus DNA fingerprinting.

## METHODS

The study was conducted in June–July of 1996–1997 with additional behavioral observations obtained in June 1998, along a 30-km stretch of the Hudson Bay coast east of Churchill, Manitoba (58°45'N, 95°04'W). As pair formation in the species starts immediately upon arrival to the breeding grounds, systematic observations of mate-guarding/within-pair distances were restricted to a few days during the egg-laying stage (in 1998). Scan sampling of 12 pairs at 1-min intervals for 30 min was conducted to determine distances between males and females in a pair and the proportion of time males and females spent within apparent visual contact with each other. If one member of the pair was out of view and clearly not within visual contact (easy to determine as nesting areas were very open), 100 m was assigned to the distance, although the mate could have been even farther away. Solitary nesting pairs nested usually greater than 1 km from the coast and at least 100 m (but usually much farther) from other pairs, whereas neighborhood nesting pairs were always on the coast nesting within 30–70 m of each other. Adult birds were captured on nests with walk-in-traps and banded with an individual specific combination of three plastic color bands and one aluminum Canadian Wildlife Service band. Extra-pair as well as within-pair interactions between individuals were recorded only when at least one of the interacting birds could be identified by its band combination.

Normally 100 to 150  $\mu$ l of blood was collected from

adult birds and chicks, although in some cases less blood (ca. 20–50  $\mu$ l) was obtained from chicks. DNA extraction and digestion were carried out following standard procedures as in Lifjeld et al. (1993). Gel running, Southern blotting, baking, and hybridization procedures were conducted following the protocol described by Gurlich et al. (1991) with minor modifications. When analyzing DNA profiles, all bands in the 2.0 kb to 20.0 kb region were identified. Two bands were considered to match if they displayed no more than a two-fold difference in intensity and their centers differed in electrophoretic mobility by less than 0.5 mm (Westneat 1990). Within pairs, males and females were presumed to be unrelated and were used to calculate the background band sharing coefficient.

Scoring was performed as per Westneat (1993). Parentage and relatedness were analyzed through band sharing coefficients (D) and when both putative parents were available, through the number of novel bands (offspring bands unmatched by those detected in social parents, Westneat 1990). Band sharing was determined as per Wetton et al. (1987). An offspring was classified as extra-pair when three or more bands were novel and band sharing between the offspring and a parent was less than 0.35, roughly the mid-point between maximum and minimum values of the background and parent-offspring band sharing coefficients, respectively. All data are presented as mean  $\pm$  SE.

## RESULTS

Pair formation in Semipalmated Plovers at the study area in Churchill began immediately upon arrival of both potential partners to a breeding territory/site. The overall sex ratio in the study area appeared to be close to 1:1 as in both years when fingerprinting data were collected we observed only a small number of males (3 [7.5%] in 1996; 4 [6.0%] in 1997) that did not secure territories and/or mates.

Associations between males and females were formed within a day of a female's first appearance at a foraging site defended by a male. Breeding synchrony in the study area (after Stutchbury and Morton 1995) was 38.3% in 1996 ( $n = 29$  females) and 46.7% in 1997 ( $n = 36$  females), reaching maximum day values of 70 and 94% during the second week of June in 1996 and 1997, respectively.

Copulations usually took place in the vicinity of demonstration scrapes (scrapes at which courtship but not nesting took place) following a courtship flight. Thirteen within-pair and one extra-pair copulations were observed in 30 hr of observation in 1996 and 1997. Within-pair copulations occurred at a frequency of 0.43 copulations  $\text{hr}^{-1}$ . In 1998, three additional copulations were observed during 6.3 hr of scan sampling (0.48 copulation  $\text{hr}^{-1}$ , for a rate of 0.44 copulations  $\text{hr}^{-1}$  for the 3 years) and an additional four copulations were observed outside of these times, all between mated pairs. Time elapsed between observed copulation and clutch initiation in the pairs was extremely variable (range: -1 to 18 days before egg laying) and averaged  $6.2 \pm 2.0$  days ( $n = 11$  nests for which we were able to determine clutch initiation dates). Too few copulations occurred during scan sampling periods (3)

TABLE 1. Band sharing coefficients (D) between pairs of Semipalmated Plovers whose relationship has been determined by band exclusion.

Relationship	D $\pm$ SD	95% CI	n
Unrelated adults	0.18 $\pm$ 0.05	0.16–0.20	20
Parent–offspring	0.60 $\pm$ 0.08	0.58–0.61	147
Male–offspring	0.60 $\pm$ 0.08	0.58–0.61	81
Female–offspring	0.61 $\pm$ 0.08	0.58–0.62	66
Father–extra-pair young	0.24 $\pm$ 0.03	0.18–0.29	4
Mother–extra-pair young	0.64 $\pm$ 0.09	0.52–0.77	4
Extra-pair young–extra-pair young	0.65 $\pm$ 0.08	0.44–0.85	3

The expected D value for first-order relatives was 0.59 (Lynch 1991).

to statistically compare the rates of copulations of neighborhood versus solitarily nesting pairs.

The only observed extra-pair copulation (7.1%) occurred on 9 June 1997, early in the laying period of the population, at a coastal neighborhood. A paired female feeding on the coastal mudflats was briefly courted by an extra-pair male who subsequently mounted her and achieved cloacal contact. No apparent solicitation by the female was observed and the extra-pair male appeared to be unpaired at the time. Immediately after the two birds separated, the social mate of the female arrived and drove the intruder away. He then courted the female and copulated with her. The copulation took place in a courtship/feeding area. We also observed a single case of an unpaired female soliciting a copulation from a paired (color-banded) male. The female assumed the pre-copulatory position but was attacked by the paired male after his own mate appeared at the site. On 10 other occasions when unsuccessful copulation attempts were made between mated individuals, the males attacked or pecked their mates after the attempt. We also observed two cases of unsuccessful copulation attempts by extra-pair males to paired females, and in one of these cases the extra-pair male also attacked the female after the attempt.

Mate-guarding occurred during the pre-laying period with males following and staying less than 100 m from their mates on average  $64 \pm 14\%$  of the 30-min observation periods (pairs spent either 100% or 0% of the period together). The average distance between members of a pair was significantly closer in neighborhood nesting pairs than in solitary nesting pairs where frequently the second bird could not be seen by the observer (solitary pairs:  $63.6 \pm 14.7$  m,  $n = 5$ ; neighborhood pairs:  $12.7 \pm 12.4$  m,  $n = 7$ ,  $t_{10} = 2.64$ ,  $P < 0.03$ ). After clutch completion, males and females in both sites spent little time in close proximity of each other because one member of the pair was incubating while the other was usually feeding.

DNA fingerprints from 24 Semipalmated Plover families (7 from 1996 and 17 from 1997) comprising a total of 130 individuals (45 adults and 85 chicks; solitary pairs: 6 families, 12 adults, and 21 chicks; neighborhoods: 16 families, 33 adults, and 64 chicks) were obtained. The average number of scorable bands observed in an individual was  $27.3 \pm 0.4$  (range 15–39). Band sharing values (Table 1) did not differ sig-

nificantly between male-offspring and female-offspring pairs ( $t_{136} = 0.78$ ,  $P > 0.05$ ).

Single novel bands were observed in 2 chicks (from different families) out of 62 matched by both parents, resulting in the probability of observing 1 chick with a novel band of 0.032. The probabilities of observing offspring with two and three novel bands were 0.001 and 0.00003, respectively. Presuming that the unique bands found in two hatchlings with determined parentage resulted from mutations (Burke and Bruford 1987), the mutation rate in the species is 0.0012 per meiotic event (for the loci concerned). Band sharing coefficients of unrelated adults (0.05–0.28) and parents and their offspring (0.42–0.77) were clearly separated (Table 1).

Egg-dumping was never detected as no clutches exceeded the modal size of four eggs. This observation was supported by DNA fingerprinting results as all chicks could be matched to their putative mothers. Out of 85 hatchlings, 66 were from full families, whereas for the remaining 19, DNA was only available from the social father. Because no instances of intraspecific brood parasitism were suspected in the population and subsequently discovered in 66 young (Table 1), only the father-offspring band sharing coefficient was used for the 19 chicks to determine their paternity.

Four chicks (4.7%, 4/85), all from one 1996 brood (4%, 1/24) satisfied the conditions for assigning extra-pair paternity as they possessed between 4 and 8 novel bands and their father-offspring band sharing coefficient ranged from 0.19 to 0.27, whereas the mother-offspring coefficient was well above 0.5 (Table 1). The band-sharing coefficient among the four chicks was 0.65 (Table 1), suggesting that all four young were fathered by the same extra-pair male. This brood was from a coastal neighborhood with at least eight other breeding pairs in the immediate vicinity. The male was a 5 year old and not significantly older than the average male in the population ( $3.34 \pm 0.23$  years,  $n = 38$ ). The female also was not significantly older than average (4 versus  $3.14 \pm 0.26$  years,  $n = 29$ ). In 1997, the same female was not seen in the study area but the male returned to the same nesting site and paired with a different female that also was present in 1996. The 1997 brood was fingerprinted and contained no extra-pair offspring.

## DISCUSSION

The low rate of extra-pair paternity (EPP) in Semipalmated Plover families is similar to the rates reported for two other socially monogamous shorebird species: European Oystercatcher *Haematopus ostralegus* (1.5% EPP, Heg et al. 1993) and Purple Sandpiper *Colidris maritima* (1.2% EPP, Pierce and Lifjeld 1998). Like the Semipalmated Plover, the European Oystercatcher and Purple Sandpiper possess patterns of parental care requiring substantial investment by the male in incubation and chick-rearing. Both species also have pronounced male-biased territorial defense, and breed in open habitats where extra-pair copulations can readily be observed, but neither of these species exhibit mate-guarding behavior during the prelaying period.

Mate-guarding is an alternative to frequent copulations as a method of assuring paternity (Freeland et al. 1995), and because of its cost in terms of time and energy, it is probably used only when there is a high likelihood of contact with potential extra-pair partners, as supported by our observations of increased mate guarding in neighborhoods as compared to solitary nesting pairs. In Purple Sandpipers and European Oystercatchers where breeding synchrony is relatively low (Purple Sandpiper, 26%, Pierce and Lifjeld 1998; European Oystercatcher, egg-laying spread over 2 months [no direct measure of synchrony], Ens et al. 1996), there may not always be a receptive partner within close distance, and thus preventing EPCs through mate guarding may be too costly. In Semipalmated Plovers, where up to 90% of females in a neighborhood can be fertile on a given day, the probability of encountering an unguarded fertile female by a potential cuckold is very high (Stutchbury and Morton 1995).

We observed frequent physical contact between both mated pairs and extra-pair birds, and all of these observations were from neighborhoods. Within-pair male physical punishment may be a way of discouraging a female's contact with other males, facilitating in-pair copulations or may perhaps initiate courtship (Moy-nihan 1955). Extra-pair males may also employ physical punishment to make it more costly for females to reject a copulation, as well as to expel an uncooperative female from a defended territory, thus vacating space for other females.

Frequent within-pair copulations found in some socially monogamous species do not occur in the Semipalmated Plover or other shorebirds (Birkhead et al. 1987, Pierce and Lifjeld 1998), and in fact, copulations were surprisingly infrequent (< 30 observed over 3 years of observation on 25–30 pairs per season). This observation meshes well with the observation of extremely short sperm in Semipalmated Plovers, as sperm length is positively correlated with the strength of sperm competition in shorebirds (Johnson and Briskie 1999).

All four chicks in the brood containing extra-pair young were fathered by the same male. Given the infrequency with which all copulations were observed, we suggest that one copulation was sufficient to fertilize offspring over the 5–6 day laying period, a period that matches closely the average that we obtained between the date of copulations and the date at which laying began (despite substantial variation in this val-

ue). Given that sperm can potentially survive for this period, and that extra-pair copulations can be disproportionately successful (Birkhead et al. 1995), this is a reasonable conclusion.

Whenever females are unable to assess all potential partners, either through limited time or in a widely dispersed nesting site, there is a potential advantage to a female in seeking EPFs, by choosing a superior male, as long as her social partner does not withdraw paternal care (Gowaty 1996). We cannot, however, reject the hypothesis that this one case of EPF in Semipalmated Plovers may also have occurred simply because the cost to the female for resisting the extra-pair male was greater than the cost to being inseminated (Reyer et al. 1997), especially given the frequent cases of attacks by males on females that we observed.

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## RUFIOUS HUMMINGBIRD SUCROSE PREFERENCE: PRECISION OF SELECTION VARIES WITH CONCENTRATION<sup>1</sup>

CHARLES R. BLEM AND LEANN B. BLEM

*Virginia Commonwealth University, Department of Biology, Academic Division, Richmond, VA 23284-2012, e-mail: cblem@saturn.vcu.edu*

JOEL FELIX AND JENNIFER VAN GELDER

*Flathead Lake Biological Station, University of Montana, Polson, MT 59860*

**Abstract.** We tested concentration preferences of Rufous Hummingbirds (*Selasphorus rufus*) offered sucrose solutions in small feeders in the field. When sucrose solutions differing in increments of 10%, from 10% to 70%, were presented simultaneously, hummingbirds preferred 50% to higher and lower concentrations. They did not show a significant preference in the range from 50% to 70%. When options were offered in pairs of choices differing from 1–25%, hummingbirds demonstrated statistically significant preferences that varied with mean concentration in a curvilinear manner. At concentrations approximating those of hummingbird-pollinated flowers (20%), hummingbirds showed greatest specificity and could distinguish solutions differing by only 1%. At concentrations above and below 20%, greater differences between choices were required to elicit significant preferences.

**Key words:** *Rufous Hummingbird*, *Selasphorus rufus*, *sugar preference*.

The ability of hummingbirds to choose optimal sugar sources is of obvious adaptive significance to their survival, migration, and reproduction. Previous studies suggested that Rufous Hummingbirds (*Selasphorus rufus*) prefer relatively high sucrose concentrations, up to 60%, when presented concentration options differing by 10% or more (Roberts 1996, Blem et al. 1997). However, lick volumes and licking rates decrease with increased nectar concentration (Kingsolver and Daniel 1983, Roberts 1995), resulting in higher energy-intake rates at 25–35% than at higher concentrations. Hummingbird feeding preferences may be influenced by flower color (Stiles 1976, Miller et al. 1985), flower position (Miller et al. 1985), sugar composition (Martinez del Rio 1990), viscosity of nectar (Stromberg and Johnsen 1990), nectar secretion rate (Pyke and Waser 1981, Gill 1988, Stiles and Freeman 1993), and the fit of the bird's bill within the flower's corolla (Stiles

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