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Genetic Parentage and Mate Guarding in the Arctic-Breeding Western Sandpiper

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ABSTRACT.—Extrapair copulations and fertilizations are common among birds, especially in passerines. So far, however, few studies have examined genetic mating systems in socially monogamous shorebirds. Here, we examine parentage in the Western Sandpiper (*Calidris mauri*). Given that Western Sandpipers nest at high densities on the Arctic tundra, have separate nesting and feeding areas, and show high divorce rates between years, we expected extrapair paternity to be more common in this species compared to other monogamous shorebirds. However, DNA fingerprinting of 98 chicks from 40 families revealed that only 8% of broods contained young sired by extrapair males, and that 5% of all chicks were extrapair. All chicks were the genetic offspring of their social mothers. We found that males followed females more often than the reverse. Also, cuckolded males were separated from their mates for longer than those that did not lose paternity. Although these results suggest a role for male mate guarding, we propose that high potential costs in terms of reduced paternal care likely constrain female Western Sandpipers from seeking extrapair copulations.

RESUMEN.—Las copulaciones y fertilizaciones extra-pareja son comunes entre las aves, especialmente las paserinas. Hasta ahora, sin embargo, pocos estudios han examinado la genética de los sistemas de apareamiento en aves playeras sociales monógamas. Aquí examinamos relaciones de parentesco en *Calidris mauri*. Dado que *C. mauri* nidifica en altas densidades en la Tundra Ártica, que presenta áreas de nidificación y forrajeo separadas, y que muestra altas tasas de divorcio entre años, esperábamos que la paternidad extra-pareja fuera más común en esta especie comparada con otras aves playeras monógamas. Sin embargo, huellas dactilares genéticas de 98

pichones provenientes de 40 familias revelaron que sólo el 8% de las nidadas contenían jóvenes engendrados por machos extra-pareja, y que sólo el 5% de los pichones provenían de relaciones extra-pareja. Todos los pichones fueron los descendientes genéticos de sus madres sociales. Encontramos que los machos siguieron a las hembras con mayor frecuencia que lo opuesto. También encontramos que los machos de hembras adúlteras estuvieron separados de sus compañeras por más tiempo que aquellos machos que no perdieron la paternidad. Aunque estos resultados sugieren un rol de custodia para los machos de la pareja, proponemos que altos costos potenciales en términos de cuidado parental reducido probablemente limitan a las hembras de *C. mauri* para buscar copulaciones extra-pareja.

Behavioral and genetic studies during recent years have shown that extrapair copulations and fertilizations are common among birds (e.g. reviewed by Birkhead and Møller 1992, Petrie and Kempenaers 1998). The frequency of extrapair paternity (EPP) varies, however, both within and between species, and reasons for that are poorly understood (Petrie and Kempenaers 1998). For example, EPP is generally much less frequent in nonpasserine birds than in passerines (Piper et al. 1997, Westneat and Sherman 1997, Birkhead et al. 2001).

Shorebirds show remarkable variation in parental care and social mating systems (e.g. reviewed by Erckmann 1983). However, relatively few studies have examined their genetic mating systems. Genetic parentage is poorly known especially in monogamous shorebirds (75% of ~200 species; Erckmann 1983), with so far only four published studies (Heg et al. 1993, Pierce and Lifjeld 1998, Zharikov and Nol 2000, Wallander et al. 2001). Comparative studies have shown, however, that sperm length (total length as well as the length of three component parts) and relative testis size are greater in nonmonogamous than in socially monogamous shorebirds, suggesting higher intensity of sperm competition in the former species (Cartar 1985, Johnson and Briskie 1999).

Here, we examine genetic parentage in the Western Sandpiper [*Calidris mauri*], a socially monogamous, Arctic breeding shorebird. In this species, the modal clutch size is four eggs, sexes share incubation, and

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males provide most parental care after hatching (Sandercock 1998). Although shorebirds typically show relatively low levels of EPP (see Wallander et al. 2001), we expected that extrapair young might be more common in the Western Sandpiper for the following reasons. First, breeding densities are relatively high (in our study population more than 16 nests km⁻²; Lanctot et al. 2000) which should reduce time and energy costs for seeking and assessing extrapair partners. In a comparative study, Westneat and Sherman (1997) showed that EPP and breeding density are positively correlated within but not across bird species. Second, nesting territories are usually separated from feeding areas (Lanctot et al. 2000), so males cannot simultaneously defend nest sites and guard their mates. Also, both sexes encounter potential extrapair partners when foraging. Finally, Western Sandpipers show relatively high divorce rates compared to other monogamous shorebirds (e.g. the closely related and sympatric Semipalmated Sandpiper [*Calidris pusilla*]; Sandercock et al. 2000). In a comparative study, Cézilly and Nager (1995) found a positive relationship between EPP and divorce in birds.

We used multilocus DNA fingerprinting to examine genetic parentage in the Western Sandpiper. To investigate the role of male mate guarding, we analyzed intrapair distances, number of flights initiated by each sex, and proportion of flights followed by the mate (see Birkhead and Møller 1992).

Methods.—We studied Western Sandpipers 21 km east of Nome, Alaska (64°20'N, 164°56'W) during May–June 1996. The study site, located along the Bering Sea coast, consists of 4 km² of shallow tundra ponds interspersed with low, dry ridges. For further details, including capture, aging, and sexing of adults, see Sandercock (1998) and Lanctot et al. (2000).

We collected 25–100 µL of blood from the brachial (adults) or jugular (chicks) vein, immediately suspended it in SET buffer (e.g. Hasselquist et al. 1995) and froze samples until analysis. For 13 nests where we had recorded adult behaviors, eggs were replaced with dummy eggs and brought to an incubator. We collected blood samples from those chicks immediately after hatching and returned them to their nests the same day. All adults except two accepted the dummy eggs, and all of them accepted the chicks. We extracted DNA from blood ($n = 184$ samples) or from tissue samples collected from dead chicks or embryos ($n = 21$).

We followed the lab procedures previously described in detail by Krokene et al. (1996). Briefly, we loaded 3–7 µg of HaeIII-digested DNA onto 20 × 40 cm 0.8% agarose gels in 1 × TBE buffer. The gels were electrophoresed at 1.2 V cm⁻¹ for ~40 h. DNA was transferred onto nylon membranes using Southern Blotting and hybridized with the minisatellite probe *per* (Shin et al. 1985). The probe was radioactively labeled with P³²dCTP by random priming us-

ing the Prime-a-Gene labeling system (Promega, Madison, Wisconsin).

We examined parentage in 53 families (73 adults and 132 chicks). The number of analyzed chicks represents 64% of the total number of eggs or chicks produced by these pairs ($n = 207$, assuming a clutch size of four eggs for broods from unknown nests). Losses were due to predation on eggs or chicks or to insufficient amounts of extracted DNA. Twenty-five families consisted of both tending parents and their chicks ($n = 61$), 15 families contained only the male parent ($n = 37$ chicks), and 8 families contained only the female parent ($n = 20$ chicks). In five families, only chicks were analyzed ($n = 14$). Proportion of families containing all chicks and the putative father was 17% (9/53).

All fingerprints were scored by D.B., following Westneat (1993). On average, 33 bands were scored in adults (SE = 0.85, range 20–50, $n = 75$, including one pair without chicks) and 32 bands in chicks (SE = 0.84, range 11–56, $n = 132$). Following other workers (e.g. Westneat 1993, Hasselquist et al. 1995, Krokene et al. 1996), we used novel fragments, that is chick bands not present in either of the putative parents, and band-sharing to determine parentage. Following Hasselquist et al. (1995), we calculated that the probability of finding three novel bands due to mutation or other random causes was 0.0095. We would then expect less than one young (0.58) with three novel fragments in our sample of 61 chicks. The distribution of novel bands was clearly bimodal, with chicks having either two or fewer, or seven or more novel bands (Fig. 1). Therefore, we concluded that chicks with more than two novel bands represented cases of extrapair parentage. The band-sharing coefficient (D), that is, the proportion of bands shared by two individuals, was calculated as described by Wetton et al. (1987). As the expected lower limit of band-sharing between chicks and their genetic parents, we used the observed D -values in young without any novel fragments (e.g. Krokene et al. 1996). To avoid bias due to few scorable bands when setting that level, we excluded one chick with only 11 bands (and low band-sharing with both putative parents, see below), resulting in 0.32 as the lower limit of band-sharing with a genetic parent. We used the same level of band-sharing, that is, $D < 0.32$, for excluding parentage when only one of the putative parents was available for analysis. When only chicks were available, we examined whether broods showed mixed paternity by comparing band-sharing between those chicks (using only adjacent fingerprints) with that found between parents and genetic offspring (i.e. first-order relatives).

We observed color-banded adults from their arrival on the breeding grounds until shortly after clutch completion. Here, we present behavioral data for 27 pairs recorded between days -11 and +2, where day 0 denotes when the first egg was laid (see Lanctot et al. 2000 for determination of clutch initiation date).

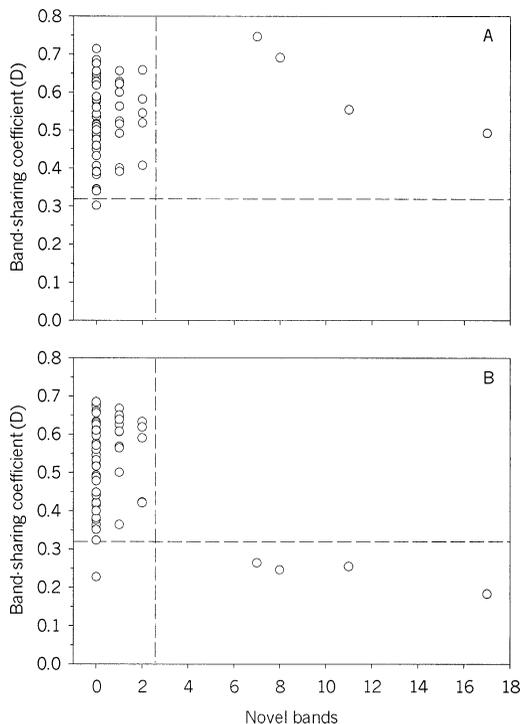


FIG. 1. Relationship between band-sharing with (A) the putative mother and (B) the putative father and number of novel bands in offspring fingerprints ($n = 61$ chicks). Dashed lines indicate criteria for excluding parentage (see text for explanation).

On average, pairs were observed 2.3 ± 0.65 (SE) days before start of egg-laying. We started focal observations whenever a marked individual was detected (between 08.45 and 22.35, usually 10.00–14.00), and each pair was followed for 30 min if possible. Mean observation duration per pair was 55 min (SE = 5.8, range 18–111 min). We continuously recorded the distance between pair members in four categories: <1, 1–5, 5–10, and >10 m. We also noted the number of flights initiated by the focal bird and whether the mate followed within 10 s.

We addressed the following predictions (see Birkhead and Møller 1992). If males guard their mates by close following, they should (1) initiate flights less often than females and (2) follow females more often than the other way around. Finally, assuming that a male is less able to control his mate when the distance between them increases, the risk of losing paternity should be higher for males separated (by >10 m) longer from their mates. Due to limited sample sizes and the relatively short time period between first observation and clutch initiation (see Lanctot et al. 2000), we were unable to examine mate guarding by comparing behaviors before and during the fertile

period (as suggested by Birkhead and Møller 1992). We therefore pooled all behavioral data.

All analyses were performed with STATISTICA V5.1 (StatSoft Inc., Tulsa, Oklahoma). We use two-tailed, nonparametric tests throughout this article, and present means \pm standard errors unless otherwise stated.

Results.—Most chicks (67%, 41/61) had fingerprint profiles completely matching those of their putative parents, that is, they showed no novel bands (Fig. 1). Mean band-sharing with the putative mother was 0.53 ± 0.017 (range 0.30–0.71) and with the father 0.52 ± 0.018 (range 0.23–0.68), considerably higher than that found between pair members, that is, presumably unrelated individuals (0.11 ± 0.011 , range 0–0.23, $n = 26$ pairs). The fingerprints of the remaining 20 chicks contained 1–17 novel fragments (Fig. 1).

With one exception, all chicks shared a high proportion of bands with their social mother (Fig. 1A). The remaining chick was the case mentioned earlier ($D = 0.30$, no novel bands) with only 11 scorable bands, and we conservatively assumed that it was not an extra-pair young. Moreover, none of the putative mothers was excluded in the families where only the female parent was analyzed (band-sharing: 0.57 ± 0.024 , range 0.32–0.73, $n = 20$ chicks). We conclude that all chicks were related to their social mothers.

Except for one young ($D = 0.23$), all chicks with 0–2 novel bands shared a high proportion of bands with their putative fathers (Fig. 1B). The exception was again the chick with few scorable bands, and we concluded that all those chicks were genetic offspring of their social fathers. The remaining four chicks, of which three were from the same brood, fulfilled both criteria for paternity exclusion (Fig. 1B): low band-sharing (0.18–0.26) as well as many novel fragments (7–17). We conclude that those chicks were sired by extrapair males. In the families where only the male parent was analyzed, we found one additional case of EPP. The low band-sharing in this case ($D = 0.29$) was not due to few scorable bands (male: 29, chick: 41). All other chicks in these families showed band-sharing values above the critical level (0.54 ± 0.019 , range 0.36–0.78, $n = 36$).

When only chicks were available for analysis, band-sharing values suggested that broods consisted of full siblings (i.e. no mixed paternity). Mean band-sharing between those chicks (0.53 ± 0.044 , range 0.40–0.77, $n = 8$) was not significantly different from that found between chicks with 0–2 novel bands and their parents (mother-offspring: 0.53 ± 0.017 , range 0.32–0.65; father-offspring: 0.54 ± 0.019 , range 0.39–0.68, $n = 24$ broods; Mann-Whitney U -tests, $U = 90.5$, $P = 0.81$ and $U = 89.5$, $P = 0.78$, respectively).

Overall, we found that 5% (5/98) of chicks were sired by extrapair males in 8% (3/40) of the broods. Assuming no complete loss of paternity in those broods where the tending male was not analyzed, rates were 4 (5/132) and 6% (3/53), respectively. None

of the nine completely sampled broods (all chicks and their putative fathers) contained extrapair young.

All adults tending broods with extrapair young were at least two years old. One of the males that lost paternity was of unknown origin. In the other two cases, males were experienced breeders, that is, they were recorded breeding in the previous year (although with different females). Furthermore, clutch initiation dates did not differ significantly between nests with (20 ± 6.4 , where 1 = 1 May, $n = 3$) and without extrapair young (24 ± 6.3 , $n = 30$, Mann Whitney U -test, $U = 26.5$, $P = 0.25$). Finally, three females produced replacement clutches with new males after losing their first broods. In two of those cases, where data on paternity were available, the tending males sired all chicks.

Males initiated fewer flights than females, though not significantly so (number of flights per 20 min, males: 0.40 ± 0.086 ; females: 0.76 ± 0.20 ; $n = 27$ pairs, Wilcoxon signed ranks test, $T = 44$, $P = 0.12$). As predicted, males followed female flights more often than the other way around (Fig. 2A). Sample sizes were too small to test differences in flight initiations and following behavior between cuckolded and noncuckolded males.

On average, males were separated from their mates by >10 m for $15 \pm 2.6\%$ of the time ($n = 27$ pairs). Examining the 13 pairs with data on paternity and intrapair distance, we found that cuckolded males were separated from their females for longer than those that did not lose paternity (Fig. 2B).

Discussion.—We found that 8% of broods contained young sired by extrapair males, in total 5% of all chicks analyzed. Those cases of extrapair paternity could be the result of extrapair copulations or rapid mate switching. The latter is plausible because the two cuckolded males for which behavioral data were available were first seen with their mates only a few days before the start of egg-laying (on days -2 and -1 , respectively, with one male recorded as unpaired on day -5). Moreover, mate switching has been recorded in a related species, the Dunlin (*Calidris alpina*; D. Blomqvist unpubl. data). Given the short time period between arrival and start of breeding in Western Sandpipers, extrapair paternity could also result from copulations during migration (see Moore and McDonald 1993).

Nonetheless, our results are consistent with most previous studies of paternity in shorebirds; reporting low levels of EPP ($<5\%$ of young) compared with those found in many passerines (although higher levels of EPP have been recorded in some polyandrous and lek-breeding shorebirds; Wallander et al. 2001, and references therein). The generally low EPP rate in shorebirds suggests that either males are efficient in assuring their paternity, or that females are not seeking extrapair copulations (EPCs).

Whereas some studies have found support for paternity-assurance behaviors in shorebirds (Heg et al.

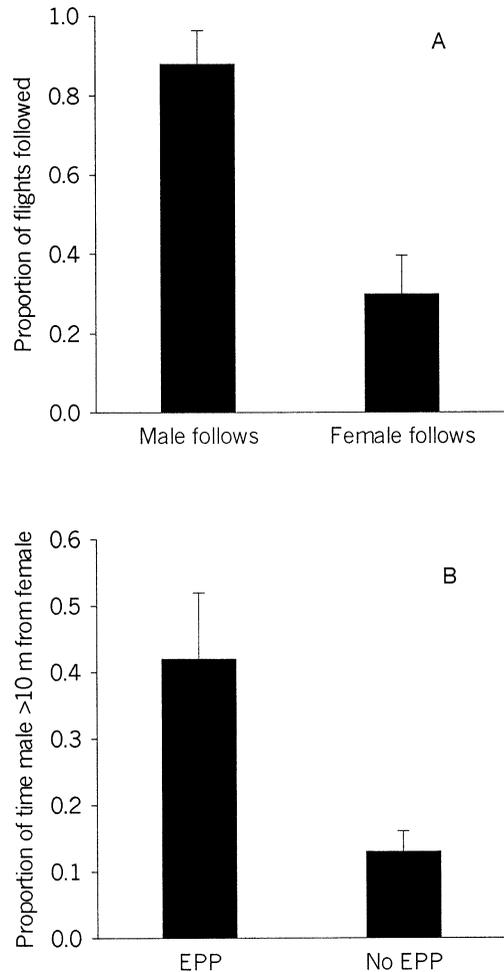


FIG. 2. Mate guarding in Western Sandpipers. (A) proportion of flights (mean \pm SE) followed by the male or the female (Wilcoxon signed ranks test, $T = 0$, $P = 0.003$, $n = 13$ pairs where both sexes initiated at least one flight), and (B) proportion of time (mean \pm SE) males were separated from their mates by more than 10 m in broods with ($n = 2$) or without extrapair young ($n = 11$, Mann Whitney U -test, $U = 0$, $P = 0.03$).

1993, Oring et al. 1994, Owens et al. 1995, Zharikov and Nol 2000), others have not (Pierce and Lifjeld 1998, Currie and Valkama 2000, Wallander et al. 2001). Our results suggest that mate guarding by close following occurs in Western Sandpipers. Males followed female flights more often than vice versa, and males that lost paternity were separated for longer from their mates than those that did not. Nevertheless, we suggest that it is unlikely that male mate guarding constrains females from seeking EPCs. Mate guarding is much more intense in many passerines than in shorebirds, yet passerine birds often show high levels of EPP (e.g. Kempenaers et al.

1995, Johnsen et al. 1998). It also seems unlikely that males use frequent copulations as an alternative paternity guard because within-pair copulation rates are low in Western Sandpipers (Lanctot et al. 2000) as well as in other *Calidris* species (Soikkeli 1967, Pierce and Lifjeld 1998).

Therefore, the relatively low EPP rate suggests that either females do not benefit from seeking EPCs, or that costs are too high. Female Western Sandpipers do not lack opportunities for EPCs. Separate nesting and foraging areas and a relatively high breeding density provide possibilities for both sexes to encounter potential extrapair partners. As in other monogamous shorebirds, however, male Western Sandpipers contribute significantly to parental care (e.g. Erckmann 1983). Mate removal experiments with Western Sandpipers (Erckmann 1983) and Killdeers (*Charadrius vociferus*; Brunton 1988) suggest that biparental care is especially important during incubation. Because male help thus seems crucial in those species, females may refrain from EPCs in order to avoid the risk that males retaliate by providing less parental care (e.g. Whittingham et al. 1992, Westneat and Sargent 1996, Sheldon and Ellegren 1998). Consistently, Lanctot et al. (2000) found that female Western Sandpipers resisted EPCs and even chased males away. We conclude that the need for male help in rearing offspring probably constrains females from seeking EPCs in Western Sandpipers as well as in many other shorebirds (see Gowaty 1996).

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