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Author(s): Donald Blomqvist, Bart Kempenaers, Richard B. Lanctot, and Brett K. Sandercock
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Genetic Parentage and Mate Guarding in the Arctic-Breeding Western Sandpiper

DONALD BLOMQVIST,[1] BART KEMPENAERS,[1,4] RICHARD B. LANCTOT,[2] AND BRETT K. SANDERCOCK[3,5]
[1]*Konrad Lorenz Institute for Comparative Ethology, Austrian Academy of Sciences, Savoyenstrasse 1a, A-1160 Vienna, Austria;*
[2]*Alaska Biological Science Center, U.S. Geological Survey, 1011 East Tudor Road, Anchorage, Alaska 99503, USA; and*
[3]*Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada*

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 embrago, huellas dactilares genéticas de 98

[4] Address correspondence to this author. Present address: Research Center for Ornithology of the Max Planck Society, P.O. Box 1564, D-82305 Starnberg (See-

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

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 initia-

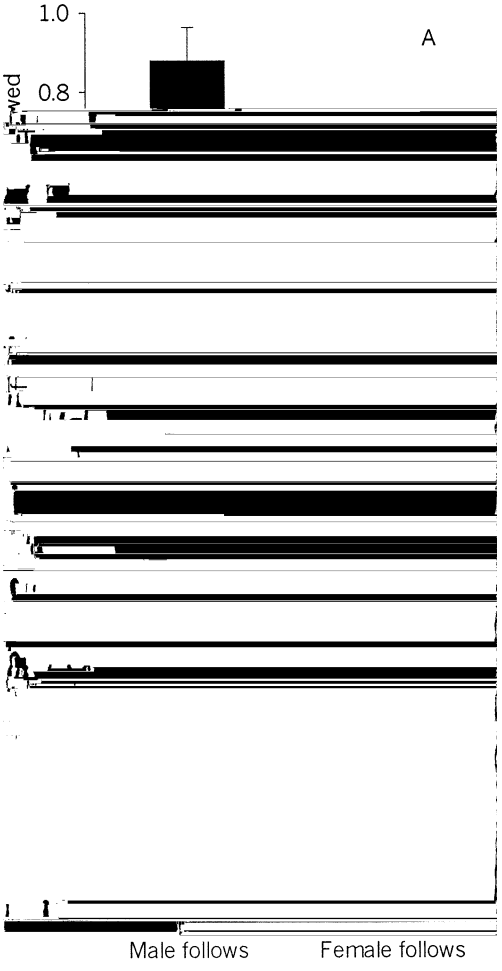

FIG. 2. Mate guarding in Western Sandpipers. (A) proportion of flights (mean + SE) followed by the male or the female (Wilcoxon signed ranks test, $T = 0$, $P = 0.003$, $n = 13$ pairs where both sexes initiated at least one flight), and (B) proportion of time (mean ± SE) males were separated from their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

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 vociferous*; 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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