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Experimental assessment of mating opportunities in three shorebird species

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Mating opportunities may differ between closely related species, although the evidence for such variation is scant. Here we compare remating opportunities and courtship behaviour between three shorebird species: the Kentish plover, *Charadrius alexandrinus*, the Kittlitz's plover, *Charadrius pecuarius*, and the white-fronted plover, *Charadrius marginatus*, using data and an experimental approach from a previous study of the Kentish plover. By experimentally creating unmated males and females, we found that remating opportunities differed between these closely related plover species: remating times were shorter for females than males in a Kentish plover population that had a male-biased adult sex ratio, and in which most brood care after hatching was carried out by males. In contrast, remating times were male-biased in the uniparental Kittlitz's plover and unbiased in the biparental white-fronted plover. Male Kentish plovers spent significantly more time on courtship than females, whereas courtship behaviour was not sex biased in the other two plover species. The mate removal experiments also provided insights into pair bond stability. In the Kittlitz's plover, all 16 newly formed pairs remained together after the release of their former mates from captivity, whereas newly established pairs were replaced by their former mates upon release in all 12 white-fronted plover pairs. Taken together, these results are important in highlighting interspecific variation in mating activities, and suggest that both operational sex ratio and pair bond stability may differ between closely related species. These variations, in turn, may influence mating systems and parental care.

The different evolutionary interests of males and females over reproduction (termed sexual conflict; Parker, 1979) are a pervasive evolutionary force influencing the behaviour, ecology and life histories of many organisms (Arnqvist & Rowe, 2005; Chapman, Arnqvist, Bangham, & Rowe, 2003). A common issue when the interests of males and females are antagonistic concerns offspring care (Houston, Székely, & McNamara, 2005; Lessells, 2012; Maynard Smith, 1977; Trivers, 1972). By caring for the offspring, parents often improve the growth and survival of the young (Clutton-Brock, 1991; Klug, Alonzo, & Bonsall, 2012); for example, by gestating, nursing, protecting and feeding them, parents improve the offspring's chances of survival (Baeza & Fernández, 2002; Balshine-Earn & Earn, 1998; Klug et al., 2012; Tyler et al., 1983). However, care is costly in terms of time and energy, and the caring parent can be killed by predators or may lose additional mating opportunities (Klug et al., 2012; Li & Jackson, 2003; Veasey, Houston, & Metcalfe, 2001). Therefore, although both biological parents benefit from providing care for the offspring, each parent is expected to withhold his (or her) parental contribution in order to raise further offspring in future (Houston et al., 2005; Lessells, 2012; McGraw, Székely, & Young, 2010).

Theory suggests that a key component of conflict resolution between male and female parents is mating opportunity (Klug et al., 2012; Kokko & Jennions, 2008; McNamara, Székely, Webb, & Houston, 2000; Székely, Webb, & Cuthill, 2000). If one sex has more favourable mating opportunities than the other, this parent is expected to reduce (or completely terminate) care more often than its mate, and seek out a new partner (Balshine-Earn & Earn, 1998; Owens, 2002; Pilastro, Biddau, Marin, & Mingozzi, 2001). One approach used by researchers to assess mating opportunities is to estimate the ratio of sexually active males to females (operational sex ratio, OSR; Forsgren, Amundsen, & Bjelvenmark, 2004; Kvarnemo & Ahnesjö, 1996). An alternative approach to estimating mating opportunities is to create unmated individuals experimentally, and to quantify their remating behaviour, for

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example time to remate, remating success and reproductive success with the new mate (Lessells, 1983; Székely, Cuthill, & Kis, 1999). This experimental approach is powerful, since it directly assesses the mating potential of unmated individuals at a given time in a population.

In this study, we estimated remating opportunities for two small plover species, the white-fronted plover, *Charadrius marginatus*, and the Kittlitz's plover, *Charadrius pecuarius*, and we compared these data with the results of a previous study on the Kentish plover, *Charadrius alexandrinus* (Székely et al., 1999). Small plovers (*Charadrius* spp.) exhibit substantial variation in their breeding systems, since some of these species are monogamous and both parents rear the young, whereas others exhibit polygyny and/or polyandry whereby a single parent (the male or the female) raises the young to independence (Székely, Thomas, & Cuthill, 2006; Thomas, Székely, & Reynolds, 2007). In addition, plovers typically breed in open areas, and their nests and broods are therefore accessible for experimental manipulations (Székely & Cuthill, 2000).

A previous experiment established that remating opportunities were female-biased in the Kentish plover (Székely et al., 1999), and this result was consistent with demographic analyses that estimated about six times more adult males than females in the population (Kosztolányi, Barta, Küpper, & Székely, 2011). Skewed adult sex ratios (ASRs) are common in wild populations (Donald, 2007), and recent studies suggest that biased ASRs predict sex roles, mating systems and pair bonds (Liker, Freckleton, & Székely, 2013). We used an identical experimental protocol with two close relatives of the Kentish plover, the white-fronted plover and Kittlitz's plover, to compare remating opportunities between these three plover species. All three species are insectivorous ground-nesting birds with similar life histories and ecology (adult body mass: Kentish plover: 41.8 g; white-fronted plover: 37.1 g; Kittlitz's plover: 35.3 g, Hockey, Dean, & Ryan, 2005; Urban, Fry, & Keith, 1986). The latter two species are common breeding birds in Africa, and their parental care systems differ from those of the Kentish plover which exhibits male-biased parental care after hatching (Amat, Fraga, & Arroyo, 1999; Lessells, 1984; Székely & Lessells, 1993). White-fronted plovers exhibit biparental brood care, whereas Kittlitz's plovers are reported to exhibit uniparental brood care, carried out by either the male or the female parent (Hockey et al., 2005; Tree, 1974; Urban et al., 1986).

Based on theoretical models (Klug et al., 2012; Kokko & Jennions, 2008) and available information on patterns of parental care (Hockey et al., 2005; Urban et al., 1986), we derived three predictions. First, we predicted higher remating opportunities in uniparental species (Kittlitz's plover) than in biparental species (white-fronted plover), since in biparental species both parents are engaged with care until the offspring are fully independent (henceforth, between-species comparison). Second, we predicted no difference in remating opportunities between males and females in biparental white-fronted plovers given that both sexes are fully engaged in parental care. Similarly, no difference in remating opportunities between males and females was predicted for the uniparental Kittlitz's plover in which either parent is free to seek a new mate (henceforth, between-sexes comparison). Third, we predicted intense courtship behaviour by males and females in both biparental white-fronted plovers and uniparental Kittlitz's plovers where care is provided by either parent (henceforth, courtship behaviour).

In addition to the experimental assessment of remating opportunities, we also monitored pair bond stability among newly established pairs. We include the Kentish plover in our analyses (using the data from Székely et al., 1999), since the same experimental methodology was used in all three species. Nevertheless, our main conclusions remain consistent when restricting the analyses to the white-fronted and Kittlitz's plovers.

METHODS

Study Species and Study Sites

White-fronted plovers and Kittlitz's plovers were investigated in southwest Madagascar (for Kentish plover, see details in Székely et al., 1999). Kittlitz's plovers were studied between 6 February 2010 and 13 May 2010 in Andavadoaka (22° 02′S, 43° 39′E) where they breed around alkaline lakes. Approximately 300 Kittlitz's plovers breed in Andavadoaka (J.E. Parra, S. Zefania, & T. Székely, unpublished data). Fieldwork with the white-fronted plover was carried out between 1 April 2011 and 23 June 2011 at Lake Tsimanampetsotsa National Park (24° 3′S, 43°44′E), a large alkaline lake (approximately 15 km × 0.5 km), surrounded by sandy shores, short grass and saltpans. Approximately 150 white-fronted plovers breed around the lake (J.E. Parra et al., unpublished data).

In the field, we searched for nests on foot, identified incubating parents and watched the parent(s) returning to nests in potential breeding sites. In total, we captured 18 Kittlitz's plover pairs (36 individuals) and 14 white-fronted plover pairs (28 individuals) with funnel traps placed on their nests. The traps were continuously monitored until a parent entered the trap and sat on the eggs. Parents were immediately removed from the traps to reduce stress and the risk of injury. Morphological traits (body mass, tarsus length, wing length and bill length) were measured using a spring balance, a sliding calliper and wing ruler (see details in Kentish plover field guide, www.bath.ac.uk/bio-sci/biodiversity-lab/pdfs/KP_Field_Guide_v3.pdf). All adults were ringed with an individual combination of colour rings and a numbered SAFRING metal ring from the University of Cape Town, South Africa.

Experimental Manipulation

We used the methodology developed by Székely et al. (1999) to estimate remating times in the Kentish plover. Briefly, both parents were trapped, ringed, measured and a blood sample was taken for sex determination (see below). One parent was then selected at random (the male or the female) and was released at the capture location immediately. The other parent was taken into captivity (see below). In both Kittlitz's and white-fronted plovers, both the male and female incubate the eggs (Hockey et al., 2005; Urban et al., 1986). Only pairs incubating two eggs (modal clutch size in both species) were manipulated. Egg length and breadth were measured with a sliding calliper, and the number of days for which the eggs had been incubated was estimated based on the floatation stage of each egg in a transparent jar with clean water (mean ± SD number of days incubated: Kittlitz's plover: 9.0 ± 4.32 days, $N = 36$; white-fronted plover: 11.5 ± 3.16 days, $N = 20$). Eggs were distributed to other nonexperimental plover clutches at approximately the same stage of incubation in the local populations. Monitoring the augmented clutches was beyond the scope of the experiment, although casual nest checks suggest that at least 33.3% and 19.4% of augmented nests survived until hatching in the Kittlitz's plover ($N = 36$ nests) and the white-fronted plover ($N = 20$ nests), respectively. Survival in these nests appeared to be higher than for unmanipulated nests (13.4% and 8.9%, based on $N = 101$ Kittlitz's plover nests and $N = 56$ white-fronted plover nests, respectively; J.E. Parra et al., unpublished data).

Removed plovers were transported in an air-conditioned vehicle to a purpose-built aviary near the field camp at both study sites. Lightweight bird bags were used to keep the plovers undisturbed and ventilated during the transport. Distance from capture areas to