

Parental behaviour in Kentish plovers: who cares?

Are two parents always better than one? If one parent is sufficient, then should the other desert its family? In a recent pair of papers, Tamás Székely, Innes Cuthill and János Kis^{1,2} provide some of the first empirical tests of adaptive desertion in birds. Using field experiments, they estimate the fitness payoffs of care and desertion for both sexes. Their results support long-standing hypotheses about how changes in costs and benefits of parental care for each sex select for biparental or uniparental care.

Adult animals in many species increase the fitness of their offspring by providing food and protection. Such parental care behaviour is a major component of the life histories of the animals concerned³. The general theory of parental care is founded on two ideas: parental care influences sexual selection^{4,5} and the diversity of parental care patterns is determined by fitness tradeoffs⁶.

Some of the best candidates for testing hypotheses about avian parental care are shorebirds. The shorebird suborder Charadrii displays remarkable variation in the sex that provides parental care. Both sexes tend the eggs and chicks in some species, whereas male or female uniparental care occurs in others. Moreover, within some species, there is considerable natural variation in which sex deserts^{7,8}. Biparental care is ancestral in shorebirds and predominates in plovers and closely related species, whereas predominantly male care has evolved in sandpipers and allies⁹.

In the Kentish plover, *Charadrius alexandrinus*, either sex can desert the other. In this species, Székely *et al.*^{1,2} found that: (1) the expected remating time for males was significantly longer than for females, (2) the success of biparental care versus uniparental care was site-specific, and (3) as the breeding season progressed, brood survival decreased and remating times increased. Székely *et al.*¹ use their experimental results as a basis for two interesting theoretical suggestions. First, they argue that remating time is a more useful predictor of mating opportunities than the operational sex ratio (OSR: the ratio of reproductively capable males and females). Second, they argue that male-biased sex ratios might select for polyandry.

Remating times and sexual selection

Why are males usually more competitive than females? Williams⁴ argued that

in addition to males' lower gametic investment, it is crucial that they tend to provide little or no parental care. Trivers⁵ extended and formalized this idea, describing male versus female contributions to offspring survival and growth as 'relative parental investment' and asserting that it controls the direction and the intensity of sexual selection. Quantification of sexual differences in parental investment is straightforward when females provide both the costly, nutrient-rich gametes and parental care (as in many mammals). It is more difficult (if not impossible) when the contribution of each parent differs (e.g. males provide the care for young while females provide substantial gametic investment, as in many fish species), or when both sexes provide different kinds of parental care. Consequently, Emlen and Oring¹⁰ suggested an index of sexual selection based on the OSR. They argued that the relative abundance of available mates directly influences the direction and intensity of mating competition and choice. The more abundant sex will compete; the rarer sex will tend to be more choosy. Sexual differences in variance of mate quality can also play an important role in determining which of the two sexes will be most choosy^{11,12}.

Székely *et al.*¹ are not the first to question the tractability of measuring the OSR

(Refs 13,14). The OSR is difficult to assess because it is not always clear whether an animal is in breeding condition. Additionally, the sex ratio of mature adults on a breeding ground might not necessarily reflect the OSR; floaters of either sex who are capable of mating must be included in any estimate. The authors suggest that remating time is a more accurate and simple measure of the direction of sexual selection in natural populations. For example, in the Kentish plover, males remate more slowly than females and compete, whereas females choose.

However, males might be remating more slowly either because they need more time to recover or because there are fewer available mates, so observed remating times might not provide an accurate estimate of the direction of sexual selection. Instead, remating times can be viewed as a consequence, rather than a cause, of sexual selection patterns. In addition, mate choice can affect remating times. Hence, we caution against using the actual remating times as an indicator of the direction of sexual selection. Alternatively, as suggested by several previous authors^{13,14}, sexual differences in reproductive rates or processing time can be used. The sex that has a faster potential reproductive rate will compete; the sex with a typically slower reproductive rate will tend to be more choosy.

OSR and polyandry

In one of the recently published papers, Székely *et al.*¹ coerced Kentish plovers to remate by removing their mates and clutches. The experiment showed that the remating time differed

Table 1. Polyandry and operational sex ratio in shorebirds^a

Family/Species	Type of polyandry	Operational sex ratio	Refs
Scolopacidae			
Wilson's phalarope (<i>Phalaropus tricolor</i>)	SEQ	Female bias early in the season	20,21
Grey phalarope (<i>Phalaropus fulicarius</i>)	SEQ	Female bias early in the season	22
		Male bias	23
Red-necked phalarope (<i>Phalaropus lobatus</i>)	SEQ	Female bias early in the season	21
Spotted sandpiper (<i>Actitis macularia</i>)	SEQ	Female bias early in the season	24
		Male bias on average	18,25
Charadriidae			
Kentish plover (<i>Charadrius alexandrinus</i>)	SEQ	Male bias	1,2
Eurasian dotterel (<i>Eudromias morinellus</i>)	SEQ	No bias	26
Rostratulidae			
Painted snipe (<i>Rostratula benghalensis</i>)	SIM	Male bias	27
Jacaniidae			
Northern jacana (<i>Jacana spinosa</i>)	SIM	Male bias	28
African Greater jacana (<i>Actophilornis africana</i>)	SIM	Male bias	19
Bronze-winged jacana (<i>Meropidius indicus</i>)	SIM	Male bias	29

^aKey: SEQ = sequential polyandry, SIM = simultaneous polyandry (mainly based on Refs 3, 18). Note that methods for assessing the sex ratio vary between studies.

markedly between the sexes; on average it took males about five times longer than females to find a new mate (corroborating earlier studies of the same species⁸). The reason for this difference was probably that the OSR is skewed towards males (as seems to be the case for all populations of this species). Based on these results, Székely *et al.*¹ suggest that male-biased adult sex ratios, and hence high remating opportunities for females, might facilitate female desertion and polyandry in shorebirds.

Among birds, male uniparental care and classic polyandry (i.e. females producing separate clutches with different males in the same breeding season) occur mainly in shorebirds. Several hypotheses for the evolution of this breeding system have been proposed, but none has gained general acceptance^{3,15,16}. The OSR might be important for the evolution of polyandry, as earlier studies have suggested^{15,17}; the recent results of Székely *et al.*^{1,2} should revitalize interest in this hypothesis.

If male-biased sex ratios have favoured polyandry in shorebirds, should we then expect contemporary polyandrous populations to show such bias? According to Székely *et al.*¹, the answer is 'not necessarily'. The authors argue that the initially male-biased OSR might have changed over evolutionary time (perhaps caused by an increased proportion of deserting females in the population). We might, however, turn the question around and ask how different forms of polyandry could influence present day OSRs.

Polyandry can be categorized by the duration of the pair bond^{3,17}. In phalaropes, for example, pair-bonds are relatively brief and females mate with two males in succession (sequential polyandry), whereas in jacanas, females have prolonged pair bonds with several males at the same time (simultaneous polyandry). For both types of polyandry, and perhaps especially in simultaneously polyandrous species, a limited number of females might monopolize most or all of the males. If so, the OSR should be skewed towards females. Surprisingly, we found little empirical support for this in the literature; species with simultaneous polyandry are generally found to show a male-biased OSR (Table 1). However, several studies of sequentially polyandrous populations have documented female-biased sex ratios (Table 1). Even if some of the variation described in Table 1 can be explained by dominance interactions^{18,19}, the available data suggest a complex relationship between mating systems and present day OSRs.

Conclusions and prospects for future work

The recent work on the Kentish plover by Székely and collaborators contributes

to a central theme in parental care theory: sexual differences in costs and benefits determine whether males, females or both will provide parental care. The papers also suggest that a male-biased OSR, and therefore high remating opportunities for deserting females, might have favoured the evolution of polyandry and male uniparental care in shorebirds. This hypothesis needs to be tested with experimental and/or comparative methods. More data are needed on OSRs and reproductive rates in contemporary populations, as well as accurate methods for assessing the OSR. Theoretical models are also needed to examine the variation in OSR in relation to present day mating systems. We hope these papers will motivate future work on the fascinating topic of adaptive desertion.

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