SHORT COMMUNICATION

Persistence of an extreme male-biased adult sex ratio in a natural population of polyandrous bird

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Introduction

One of the primary notions in social behaviour is that females tend to care for the offspring, whereas males focus more on mating (Bateman, 1948; Trivers, 1972; Clutton-Brock, 1991). The origin of sex roles is usually linked to anisogamy and parental investment: females make large gametes, whereas males usually produce many but small gametes, and this initial difference in parental investment precipitates into female-biased post-hatch (or post-parturition) care (Alcock, 2009). Recent theoretical models predict that biased parental care may be a response to biased adult sex ratios (ASRs). However, estimating ASR is challenging in natural populations, because males and females often have different detectabilities. Here, we use demographic modelling with field data from 2101 individuals, including 579 molecularly sexed offspring, to provide evidence that ASR is strongly male biased in a polyandrous bird with male-biased care. The model predicts 6.1 times more adult males than females (ASR = 0.860, proportion of males) in the Kentish plover Charadrius alexandrinus. The extreme male bias is consistent between years and concordant with experimental results showing strongly biased mating opportunity towards females. Based on these results, we conjecture that parental sex-role reversal may occur in populations that exhibit extreme male-biased ASR.

Abstract

In a number of insects, fishes and birds, the conventional sex roles are reversed: males are the main care provider, whereas females focus on matings. The reversal of typical sex roles is an evolutionary puzzle, because it challenges the foundations of sex roles, sexual selection and parental investment theory. Recent theoretical models predict that biased parental care may be a response to biased adult sex ratios (ASRs). However, estimating ASR is challenging in natural populations, because males and females often have different detectabilities. Here, we use demographic modelling with field data from 2101 individuals, including 579 molecularly sexed offspring, to provide evidence that ASR is strongly male biased in a polyandrous bird with male-biased care. The model predicts 6.1 times more adult males than females (ASR = 0.860, proportion of males) in the Kentish plover Charadrius alexandrinus. The extreme male bias is consistent between years and concordant with experimental results showing strongly biased mating opportunity towards females. Based on these results, we conjecture that parental sex-role reversal may occur in populations that exhibit extreme male-biased ASR.

Keywords:

adult sex ratios; mating system; parental care; sex ratio; sex roles.

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are likely to lead to different detectabilities of sexes, i.e. different sighting rates or trapping success (Domenech & Senar, 1998; Newson et al., 2005). Because of these limitations, reliable estimates of ASR are rare (Donald, 2007; but see Chapron et al., 2009; Veran & Beissinger, 2009).

Testing the proposed effect of ASR on parental roles is especially relevant in taxa where the sex roles are evolutionary reversed: in a number of insects, fishes and birds, males look after the young, whereas the females compete for males. However, the reversal of sex roles is not always complete and may dynamically depend on timing in the season and on ecological variables (Clutton-Brock, 1991; Forsgren et al., 2004; Gwynne, 2008). Explaining why some organisms deviate from the conventional sex roles and exhibit male-biased care is often considered as a major challenge in evolutionary biology (Clutton-Brock, 1991; Alcock, 2009).

Shorebirds (plovers, sandpipers and allies) have variable parental care roles, and they provide some of the best known avian examples of paternal care and female polygamy; they are often used to illustrate sex-role evolution (Darwin, 1871; Emlen & Oring, 1977; Andersson, 2005; Clutton-Brock, 2007). Here, we investigate a small shorebird, the Kentish plover Charadrius alexandrinus. This species, and the closely related snowy plover Charadrius nivosus, have male-biased care: many females desert their brood and remate so that females may have up to four mates in a single breeding season, whereas the males care for the chicks (Warriner et al., 1986; C. Küpper et al., unpublished). Simultaneous polyandry is low, because < 8% of broods contain extra-pair young (Küpper et al., 2004). Here, we use demographic modelling to test the prediction of theoretical models in a well-studied polyandrous species (Szkely et al., 2006; Kosztolányi et al., 2009). In particular, we test whether the ASR is male biased in a population where males provide more brood care than do females.

Materials and methods

Study site and field methods

Fieldwork was carried out at Lake Tuzla (36°43′N, 35°03′E), southern Turkey, from 1996 to 1999, and in 2004 during the peak breeding activities form mid-April to early July. Kentish plovers nest on the ground, and we ringed chicks either in the nest scrape on the day of hatching or at the first encounter when the chicks had already left the nest scrape. Chicks were sexed molecularly (n = 579) or by plumage as recruited adults (n = 16). Adults were trapped on the nest or with chicks. To determine fledging success, broods were visited approximately every other day until the chicks perished or fledged at the age of approximately 25 days (1996–1999, n = 100 broods). For detailed description of field methods and molecular sexing, see Székely et al. (2004) and Kosztolányi et al. (2006).

Demographic modelling

In short, we first set up cohorts of fledglings in the model according to the sex ratio (proportion of males) among fledglings estimated from field data (FSR). Then, we followed the fate of these cohorts using the survival estimates in Sandercok et al. (2005). From the resulting age distributions of adult males and females, the ASR was calculated (Fig. 1).

As data changed seasonally, FSR was derived as the weighted average of brood sex ratios at the age of fledging estimated for four roughly equal periods (BSR, i = 1...4) by a binomial Generalised Linear Model (GLM) fitted to the brood sex ratio over brood age. BSRs were weighted by the fledglings’ numbers of the periods. These were calculated as the products of fledging success (FS, from a binomial GLM), the number of broods hatched (B), and the average brood size at hatching (BS), each estimated for the four periods. To obtain a reliable estimate of FSR, all BSRs, FS, and BS, were randomly sampled 10^5 times from the corresponding distributions determined by the statistical fits. We followed cohorts of fledglings for k = 1...10 years: we calculated the number of surviving males and females in each age category using 10 independent estimates of FSR, and from the distributions of age categories, we also calculated ASR. Thus, using the 10^5 estimates of FSR, we obtained 10^4 estimates of ASR and estimated ASR from this distribution. Sample sizes used in the demographic model are given in Table 1 (for full details of the modelling, see Appendix S1 in Supporting Information).

Sensitivity analyses

To check the influence of between-year variation on ASR, we excluded 1 year from the dataset and repeated the calculations. In addition, to control for the fieldwork effort, i.e. in some periods of the breeding season, more broods were encountered than in another, we permuted the number of broods per period and re-calculated ASR for all possible permutations. Calculations and statistical analyses were carried out using R version 2.12.1 (R Development Core Team, 2010).

Results

Our model predicts a strongly male-biased ASR = 0.860 (proportion of adult males, 95% confidence interval: 0.791–0.904, Fig. 2). The strong male bias was robust because it remained consistent by both (i) excluding 1 year from the dataset (Fig. 2, Table S1) and (ii) permuting the number of broods per breeding period (range of ASRs: 0.853–0.895, Table S2).
Our demographic model predicts a strongly male-biased ASR in the Kentish plover: 6.1 times (95% CI: 3.8–9.4 times) more adult males than females. This result is robust: consistent between years and not sensitive to data resampling, and consistent with experimentally estimated mating opportunity in the same population: after removing the mate and clutch of mated plovers, the remating probability of females was 5–8 times higher than that of males (Szekely et al., 1999). Furthermore, the male-biased ASR is also consistent with the predictions of theoretical models (McNamara et al., 2000; Kokko & Jennions, 2008), because 96.4% of Kentish plover males provide parental care until the chicks fledge or die, whereas only 59.1% of females do so (n = 110 broods, Kosztolanyi et al., 2006). As brood caring males and females are unavailable for new pair bonds and matings, the OSR estimated by the mating opportunity experiment (Szekely et al., 1999) should be somehow more conservative than the actual ASR. Our result is also consistent with a recent study of snowy plovers that showed consistent male-biased ASR over an 11-year period (Stenzel et al., 2011). In addition, Stenzel et al. (2011) used capture-recapture modelling to infer female-biased adult mortalities and argue that biased adult mortalities contribute to the male-biased ASR.

Table 1 Sample sizes (no. of broods or chicks) included in the demographic model of adult sex ratio in a polyandrous Kentish plover population.

<table>
<thead>
<tr>
<th>Year</th>
<th>Brood sex ratio (no. of broods, no. of chicks)</th>
<th>Fledging success (no. of broods)</th>
<th>Broods hatched (no. of broods)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td>10, 10</td>
<td>14</td>
<td>94</td>
</tr>
<tr>
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<td>29, 45</td>
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<td>1998</td>
<td>84, 235</td>
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<td>106, 281</td>
<td>13</td>
<td>112</td>
</tr>
<tr>
<td>2004</td>
<td>12, 24</td>
<td>0</td>
<td>44</td>
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Discussion

Our demographic model predicts a strongly male-biased ASR in the Kentish plover: 6.1 times (95% CI: 3.8–9.4 times) more adult males than females. This result is consistent between years and not sensitive to data resampling, and consistent with experimentally estimated mating opportunity in the same population: after removing the mate and clutch of mated plovers, the remating probability of females was 5–8 times higher than that of males (Szekely et al., 1999). Furthermore, the male-biased ASR is also consistent with the predictions of theoretical models (McNamara et al., 2000; Kokko & Jennions, 2008), because 96.4% of Kentish plover males provide parental care until the chicks fledge or die, whereas only 59.1% of females do so (n = 110 broods, Kosztolanyi et al., 2006). As brood caring males and females are unavailable for new pair bonds and matings, the OSR estimated by the mating opportunity experiment (Szekely et al., 1999) should be somehow more conservative than the actual ASR. Our result is also consistent with a recent study of snowy plovers that showed consistent male-biased ASR over an 11-year period (Stenzel et al., 2011). In addition, Stenzel et al. (2011) used capture-recapture modelling to infer female-biased adult mortalities and argue that biased adult mortalities contribute to the male-biased ASR.
Our results are important for three reasons. First, we show that the ASR is male biased in a species with male-biased care. This result is fully consistent with our previous experimental and nonexperimental studies (Székely et al., 1999, 2004). Because adult males and females appear to provide comparable brood care in the Kentish plover (Székely & Cuthill, 1999), we conclude that the most plausible explanation for the sex-role reversal in this species is the male-biased ASR. Second, Jennions & Kokko (2010) make a convincing case that to understand breeding system evolution and sex roles, researchers should move beyond gametic investments, sperm competition and paternity. Rather, research workers should consider mating and parental behaviour as a dynamic system and investigate their interactions with population sex ratio. Here, we make a key step by testing a prediction of Jennions & Kokko (2010) for the first time in a highly suitable model organism in its natural environment. Our results support the theoretical expectation. Third, we propose a novel method to calculate ASR based on molecular sex-typing and use demographic modelling that avoids the shortcomings of conventional ASR estimates based on counting of individuals (Donald, 2007).

We focused on an open population, although locally observed sex ratios may change owing to sex-different dispersal. However, if one considers sex ratio at a metapopulation level, then immigration and emigration between population demes are expected to balance each other out (Dale, 2001). In line with this argument, genetic differentiation between Eurasian Kentish plover populations including the population in this study was not different for males or females based on both autosomal and sex chromosomal markers (Küpper et al., 2009, unpublished). Therefore, it is unlikely that immigration or emigration differs between sexes and thus confound our results.

How does the male bias emerge in the population? To answer this question in full, one needs follow-up studies, and here we only wish to note that the fledging sex ratio is already male biased (FSR = 0.870, 95% CI = 0.715–0.945). We suggest two mutually nonexclusive explanations that may produce male-biased FSR. First, hatching sex ratio shifts towards female bias over the breeding season, and broods hatched late in the season have lower fledging success (Appendix S1). Second, female chicks grow slower than male chicks, and thus female chicks may be more vulnerable to predators (A. Kosztolányi et al., unpublished).

Our results are in line with Donald (2007) that reported overall male-biased ASRs in wild bird populations. The estimated ASR in the Kentish plover, however, falls in the top 3% of the distribution of ASRs (n = 201 studies). Male-biased care, however, is not widespread among avian taxa, and therefore, ASR may not always predict parental care bias, and other life-historic and ecological traits need to be taken into account. In addition, sperm competition lowers the benefits of male care, and the variance in male reproductive success is usually higher than the variance in female reproductive success (Bateman, 1948; Trivers, 1972; Queller, 1997). The latter implies that mated males are unlikely to care, because these males are in a selected group so that they may benefit more from additional mating than from providing care (Jennions & Kokko, 2010).

In conclusion, using a demographic model, we tested a prediction of recent theoretical models in a polyandrous shorebird, the Kentish plover. By modelling a cohort of male and female chicks using estimated adult survival, our model predicts a persistent male-biased ASR, and this bias emerges before the chicks fledge. We argue that the combination of demographic modelling and experimental assessment of mating opportunities in the wild is an excellent approach to understand the complex dynamics of sex ratios, mating systems and parental care patterns.

Acknowledgments

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References


Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details of demographic modelling.

Table S1 Sensitivity analyses of year effects.

Table S2 Sensitivity analyses of seasonal distribution of hatched broods.

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