Animal Behaviour 110 (2015) 61–67

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Cuckolded male ground tits increase parental care for the brood

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ARTICLE INFO

Article history:
Received 13 April 2015
Initial acceptance 7 July 2015
Final acceptance 9 September 2015
Available online
MS. number: 15-00299R

Keywords:
brood provisioning
extrapair copulations
lightened workload
parental care
paternity allocation

Extrapair copulations (EPCs) occur widely in socially monogamous birds. How cuckolded males respond to the infidelity of their social mates is still problematic. We addressed this question in the ground tit, *Pseudopodoces humilis*, in which EPCs occur frequently and successful reproduction relies on biparental care. In solitarily breeding pairs, we calculated the feeding rate of social pairs at polyandrous and monogamous females' nests. Compared with that at monogamous nests, cuckolded males increased their feeding rate whereas polyandrous females reduced theirs. Polyandrous females had larger extrapair partners, although their extrapair young were neither heavier nor had higher heterozygosity than their within-pair young. Extrapair males never provided paternal care for the mixed brood and polyandrous females had no opportunity to forage on the territory of extrapair males. Therefore, the energetic benefit polyandrous females obtained was due to the increased parental care of their social mates. Even losing some share, cuckolded males still gained most of the paternity within the mixed brood. By increasing parental care for the current brood, they could ensure the survival of their own offspring. Thus, we suggest that females place their social male in a cruel bind by creating a larger brood containing some unrelated young: if the social male does not step up provisioning to meet the demands of the larger brood, overcrowding may reduce the survival of his offspring. Polyandrous females maintain the fitness incentive for their social males to provide parental care by limiting the paternity of extrapair males to a minority of the brood.

Ever since extrapair copulations (EPC) were detected in socially monogamous birds (Westneat, 1990), behavioural ecologists have focused on two key questions: first, what benefits do females obtain from engaging in EPCs and second, how do cuckolded males respond to the infidelity of their social mates (Møller & Birkhead, 1993; Reynolds, 1996). It is now generally accepted that females can obtain a variety of benefits from engaging in EPCs, such as ‘good genes’, increased offspring heterozygosity, hatching success or fertility assurance, or additional resources for raising the brood (Akçay & Roughgarden, 2007; Foerster, Delhey, Johnsen, Lifjeld, & Kempenaers, 2003; Gray, 1997; Jennions & Petrie, 2000; Kempenaers, 1993; Petrie & Kempenaers, 1998; Reding, 2015). However, the responses of cuckolded males are less clear and more controversial. In theory males should either abandon a mixed brood or reduce their level of parental care due to the cost to individual fitness of raising unrelated young (Hamilton, 1964). Empirical tests for this prediction are mixed. Some studies found that cuckolded males indeed reduced parental care for the current brood (Briskie, Montgomerie, Põldmaa, & Boag, 1998; Griffin, Alonzo, & Cornwallis, 2013; Lifjeld, Slagsvold, & Ellegren, 1998; Perlut, Kelly, Zalik, & Strong, 2012; Wagner, Schug, & Morton, 1996), whereas others found they did not change (Bouwman, Lessells, & Komdeur, 2005; Kempenaers & Sheldon, 1996; Peterson, Thusius, Whittingham, & Dunn, 2001; Westneat, Clark, Rambo, & Westneat, 1995) or even increased their parental care for mixed broods (Dixon, Ross, O'Malley, & Burke, 1994; García-Vigón, Veiga, & Cordero, 2009; Whittingham & Lifjeld, 1995). Why cuckolded males in some species reduce their level of parenting whereas others remain unchanged or even increase their level of care remains unclear.

The frequency of extrapair paternity (EPP) varies considerably within and between species (Griffith, Owens, & Thuman, 2002; Petrie & Kempenaers, 1998). In most species, extrapair males sire only a minority of the brood, usually less than 25% (Griffith et al. 2002). Given that females are making active choices about mates (Reynolds, 1996) and that the extrapair partners of polyandrous females often have higher quality than their social mates (Canal, Potti, & Dávila, 2011; Kempenaers, et al., 1992), an obvious question arises: why do females not allocate greater paternity to extrapair partners (Hasson & Stone, 2011)?

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http://dx.doi.org/10.1016/j.anbehav.2015.09.023

One possibility is that the mate guarding by social males may constrain the opportunity of females to engage in EPCs (Møller, 1990). A second possibility is that reduced paternity may reduce the fitness incentive for a social male to provide parental care, which is especially important in systems of biparental care (Suter, Bielańska, Röthlin-Spillmann, Strambini, & Meyer, 2009). Females engaging in EPCs may need to balance the potential benefits of matings with higher quality extrapair partners against the risk of reduced parental care or even desertion by their social partners.

We tested this prediction in the ground tit, *Pseudopodoces humilis*, a cooperatively breeding bird that dwells on the alpine meadow of the Tibetan Plateau. There are two major clades of this species on the Tibetan Plateau (Yang, Yin, Ma, & Lei, 2006), which differ both in morphology and in social behaviours; for example the social composition of the Gansu population changes between years (Du & Lu, 2009) whereas that in the Tibet population is stable (Ke & Lu, 2009). The study reported here was on the Gansu population.

Cooperative breeding occurs in both the Gansu and Tibetan populations, but is more common in the latter (Du & Lu, 2009; Ke & Lu, 2009). Moreover, EPP levels are higher in the Gansu population (14.4% in solitarily breeding pairs and 31.3% in cooperatively breeding groups; Du & Lu, 2009) than in the Tibetan population (0.3% in solitarily breeding pairs and none in cooperatively breeding groups, Johannessen, Ke, Lu, & Lifjeld, 2011). In the Gansu population, low-quality males are at greater risk of loss of paternity as females pairing with them are prone to engaging in EPCs with males of higher quality. To avoid paternity loss to unrelated males, low-quality males cooperate with relatives and concede some paternity to the latter (Du & Lu, 2009). It seems that in cooperative groups males have found alternative reproductive options to maximize their reproductive fitness. But in solitarily breeding pairs it is still unclear how they can do this when their social females tend to engage in EPCs. As male ground tits exhibit no obvious mate-guarding behaviours when females are fertile, and their reproductive success relies largely on biparental care (Du, 2009; Du & Lu, 2009), this altricial bird provides a useful system to explore the relationship between the trade-off of polyandrous females and the response of cuckolded males.

In solitarily breeding pairs, we examined the paternity allocation of polyandrous females and the feeding rates of the social pair. We first compared the feeding rates of monogamous and polygamous males and females. We then examined what benefits polyandrous females might obtain from engaging in EPCs. Finally, we examined the factors that influence how polyandrous females allocate paternity between their social and extrapair partners.

METHODS

Study Area and Population

This study was carried out between 2010 and 2012 in Luqu County (102°E, 34°N, 3000 m height), in the Gansu Province located on the northeastern Tibetan Plateau. The climate is cold (with an annual average temperature of 1.2 °C) and wet (with an average annual precipitation of 780 mm). The landscape of Luqu County changes with elevation from *Picea crassifolia* forests to the alpine meadow, with scrublands composed of *Hippophae rhamnoides* and *Berberis hemsleyana* in between. The Tao-River, a tributary of the Yellow River, flows through the county. Ground tits were found mainly along riverbanks and built burrow nests in the walls of riverbanks or on the grassland.

The breeding density in an area of 300 ha was 0.1 nest/ha. Over the 3 years, we located 101 nests in which at least one young fledged successfully: 86.14% (87 nests) were solitarily breeding pairs and 13.86% (14 nests) were cooperatively breeding groups. As in the Gahai population (Du & Lu, 2009), the Luqu population also varied greatly in the social composition across years. Few marked birds were recaptured in subsequent years (two of 294 adults, 0.7%).

Data Collection in the Field

Nests were located by systematic search, primarily by monitoring the burrow-excavating behaviours of adults. After burrow excavation, social pairs construct a nest at the end of the burrow. During this time, adults were captured by placing a mist net at the burrow entrance. No nest desertion occurred after mist netting, indicating that trapping had no negative effect on the nesting success. Each captured bird was sexed by examining the brood patch and then ringed with one numbered metal ring plus two or three plastic colour rings for individual identification. Body weight (to the nearest 0.1 g) and tarsus length (to the nearest 0.1 mm) were measured. From 10 to 20 μl of blood was sampled from the brachial vein, then anticoagulated by 5% EDTA in physiological saline and stored in pure ethanol.

On the day of hatching (inferred from the behaviour of the female as she would then forage outside the burrow instead of being fed by the male), we dug a vertical shaft directly above the nest cup. A removable bag with soil was used to seal the vertical shaft, allowing us to monitor nestling growth with minimal disturbance to the nestlings (Du & Lu, 2009). Hatchlings were distinguished by their hatching sequence (if known) or rank based on their relative body weight within the brood (if hatching sequence was unknown). A number was marked on the abdomen and head of each nestling using colour markers to facilitate individual identification. Thereafter, the body weight and tarsus length of each nestling were measured every 2 days until they fledged. When they weighed more than 20 g, nestlings were bled using the same procedure as with adults.

We observed courtship feeding and copulations of adults in an unfixed time frame, with the aid of 10 × 45 binoculars (The Steiner Company, Germany). We observed provisioning behaviours of the brood at 2-day intervals. During the observation of provisioning, we located ourselves 20 m from the burrow. At that distance, the adult would enter directly into the burrow but, if we were closer, the adults usually stopped momentarily near the entrance of the burrow, indicating our presence disturbed them. Observations commenced on the day of hatching, but in the analysis presented here we used only data obtained for nestlings at least 3 days old. With younger nestlings, the food items delivered were so small that they could not be easily seen in the adult's bill. Since both sexes had the highest feeding rates between 1200 and 1400 hours, we conducted our behavioural observation at this time. We obtained 383.5 h of provisioning data for solitarily breeding pairs (mean ± SE = 6.5 ± 0.5 h, $N = 59$).

Microsatellite-based Parentage Analysis

Genotyping was based on nine polymorphic microsatellite loci (APCo69, Titgata73, Titgata79, Titgata87 and Titgata89, PmaD105, PmaGAn27, PmaTGAn33 and PmaTGAn42, with 7.7 ± 0.6 alleles per locus on average; Du & Lu, 2009). The 10 μl PCR system was composed of 1× buffer, 1.5 mM of $MgCl_2$, 100 nM of each primer, 200 nM of dNTP, 0.5 U of Taq DNA polymerase and 100 pg of genomic DNA. The PCR programme started with a predenaturation step at 94 °C for 5 min, then 35 cycles of 95 °C for 30 s, 47.5–59 °C for 30 s and 72 °C for 30 s, ending with a final extension at 72 °C for 10 min. The PCR product of 2 μl was run on 6% polyacrylamide gel and then silver-stained. Genotypes were scored according to allele sizes.

Parentage analysis was carried out using the software CERVUS (version 3.0, Kalinowski, Taper, & Marshall, 2007). Parameter setup followed the procedure of Rowe and Weatherhead (2007). We