Ecological correlates of extra-group paternity in mammals

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Extra-group paternity (EGP) can form an important part of the mating system in birds and mammals. However, our present understanding of its extent and ecology comes primarily from birds. Here, we use data from 26 species and phylogenetic comparative methods to explore interspecific variation in EGP in mammals and test prominent ecological hypotheses for this variation. We found extensive EGP (46% of species showed more than 20% EGP), indicating that EGP is likely to play an important role in the mating system and the dynamics of sexual selection in mammals. Variation in EGP was most closely correlated with the length of the mating season. As the length of the mating season increased, EGP declined, suggesting that it is increasingly difficult for males to monopolize their social mates when mating seasons are short and overlap among females in oestrus is likely to be high. EGP was secondarily correlated with the number of females in a breeding group, consistent with the idea that as female clustering increases, males are less able to monopolize individual females. Finally, EGP was not related to social mating system, suggesting that the opportunities for the extra-group fertilizations and the payoffs involved do not consistently vary with social mating system.

Keywords: extra-group paternity; mating systems; oestrous synchrony; mammals

1. INTRODUCTION

One of the most important recent advances in the study of mating systems has been the discovery that social bonds frequently do not reflect genetic mating systems because of extra-pair paternity (EPP; Birkhead & Møller 1992; Petrie & Kempenaers 1998; Griffith et al. 2002). Growing evidence that such EPP can be extensive and can form an important part of the sexual selection process within a population (e.g. Møller & Birkhead 1994; Møller & Ninni 1998; Sheldon & Ellegren 1999; Griffith et al. 2002) has led to an increasing interest in understanding variation in EPP among species. However, although recent evidence suggests that EPP is likely to be important in mammalian mating systems (e.g. Goossens et al. 1998; Fietz et al. 2000; Griffin et al. 2003; Ortega et al. 2003), our knowledge of the extent and ecology of EPP stems primarily from research on birds (reviewed in Griffith et al. 2002; Westneat & Stewart 2003). Patterns in mammals are likely to differ from those in birds, owing to the large differences between these taxa in parental care and social mating systems. Specifically, mammals show little paternal care and polygamy predominates, while birds typically show greater paternal care and are mostly monogamous (Clutton-Brock 1989; Davies 1991).

The growing number of genetic studies of paternity in mammals now allows us to examine interspecific variation in EPP in mammals. In this paper, we describe the extent of variation in EPP among mammals and test three prominent ecological hypotheses for this variation. We refer to extra-pair paternity as extra-group paternity (EGP); that is, the proportion of offspring fathered by males outside the social breeding group. We use the term EGP rather than EPP because mammals commonly live in groups that contain multiple breeding adult males and females. EGP is the same as EPP for species in which breeding groups consist of a single male in association with one or more females (monogamous and unimale polygynous systems).

The spatial and temporal clustering of oestrous females are two key factors thought to influence the ability of males to prevent their mates from engaging in extra-pair copulations (Emlen & Oring 1977; Birkhead & Møller 1992; Shuster & Wade 2003; van Noordwijk & van Schaik 2004). We used female group size (the number of adult females in a breeding group) to represent the spatial clustering of females and the length of the mating season as a measure of the temporal clustering of oestrous females. EGP is expected to be greater when females are in larger groups than in smaller groups, and when mating seasons are relatively short and overlap in oestrus among females is relatively high. Under these conditions, males are less likely to be able to monopolize individual females and prevent them from engaging in extra-group copulations. A third factor, the number of males in a social breeding group, may also influence EGP, because the level of EGP might be expected to decrease as the number of defending males increases (van Noordwijk & van Schaik 2004). Using phylogenetic comparative methods, we investigated the relative strengths of the relationships between EGP and these three ecological factors: female group size; mating season length; and the number of males in a breeding group. Finally, we also examined whether EGP varied among different types of social mating system and tested the suggestion that EGP is higher in polygynous systems than in monogamous ones, because males may be less effective at defending multiple mates (Arak 1984).

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2. MATERIAL AND METHODS

We searched the literature for estimates of EGP, the proportion of offspring fathered by males outside the social breeding group. To limit variation arising from large differences in resolution among genetic methods, we used only estimates that were based on DNA-based methods, such as microsatellite genotyping and multilocus minisatellite fingerprints, and did not use estimates based on other methods, such as allozyme variation (Griffith et al. 2002). Populations for which paternity data are available, but where males and females do not form social breeding groups and instead show other types of social mating system, are not included here because EGP is not defined in these cases (e.g. scramble competition in some ground squirrels and sheep and roving in some ungulates, both of which involve either one or both sexes searching for mates, associating very briefly while mating, and then moving on to search for more mates). We also compiled data on the average number of adult females and males in a breeding group, the length of the mating season and social mating system, wherever possible from the same population from which data on EGP were extracted. We used two measures for social mating system: one categorical and the other continuous. First, based on overt associations between adult males and females, we classified species as: monogamous (one male, one female); polygynous (one male, multiple females); and multimale (multiple males, one or multiple females). Populations with both monogamous and polygynous males were classified as polygynous if more than 15% of males were polygynous (following Dunn et al. 2001). Second, we used a continuous measure of social mating system, namely breeding group sex ratio, which is the ratio of the mean number of females to that of males in a breeding group. This describes the mean number of females that a male associates with in monogamous and polygynous systems and the mean number of females per male for males in multi-male groups. Breeding group sex ratio, unlike categorical mating system, can thus integrate multiple types of mating associations into a single measure.

To take into account potential non-independence among species owing to common ancestry, we used phylogenetic generalized least-squares methods (Martins & Hansen 1997; Pagel 1999; Garland & Ives 2000; Freckleton et al. 2002). This technique addresses the concern that closely related species may be more similar to each other than to distantly related species by incorporating the degree of non-independence among species into the error structure of the statistical model. Unlike ordinary least-squares regression where data points are assumed to be independent, generalized least-squares (GLS) methods can be used to explicitly model how the covariance between species declines as their phylogenetic separation increases (Martins & Hansen 1997; Pagel 1999; Freckleton et al. 2002). We constructed a composite phylogenetic tree for the species in our study (electronic supplementary material 1). Phylogenetic relationships at the level of the family were based on Liu et al. (2001). Smaller-scale phylogenies were used for the relationships among genera and species within families (Purvis 1995; Bininda-Emonds et al. 1999; Michaux et al. 2001). As comparable branch lengths across the whole tree were not available, branch lengths were set to 1 in our analyses (Garland & Ives 2000; Freckleton et al. 2002). Several transformations of branch lengths were explored (Garland & Ives 2000), but these did not improve model fit, and had no qualitative effect on the results.

To test the relative abilities of ecological variables to explain variation in EGP, we ran a GLS regression with EGP as the response variable and the average number of females in a group, length of the mating season and the average number of males in a group as predictor variables. To explore the relationship between EGP and social mating system, we built separate GLS models, with categorical mating system and breeding group sex ratio as predictor variables. We also evaluated whether variation in data quality among studies might influence our findings by using weighted GLS models. These included the same explanatory and response variables as the unweighted ones, but, in addition, weighted the response variable by sample size (the number of offspring assigned paternity); that is, the sampling error variance in EGP was assumed to be inversely related to sample size (Griffith et al. 2002).

In all analyses, EGP was arcsine transformed and predictor variables were ln-transformed to meet assumptions of normality and linearity. We checked residuals for violations of model assumptions. For all analyses, the significance of fixed effects was assessed using conditional t- and F-tests (Pinheiro & Bates 2000). To assess the effect of phylogeny (incorporated into the error structure), models with phylogenetic structure (GLS models) were compared with models with the same fixed effects, but without phylogenetic information (ordinary least squares) using likelihood-ratio tests to see if including phylogeny improved model fit (Pagel 1997; Pinheiro & Bates 2000). Likelihood-ratio (LR) tests were also used to compare weighted and unweighted GLS models. All analyses were carried out in the statistical language R, v. 2.3.0 (R Development Core Team 2004). Models were fit using restricted maximum likelihood, GLS analyses were carried out using the function gls in the nlme package (Pinheiro et al. 2004), the distance matrix was derived by setting branch lengths to 1 and the expected correlation between species was assumed to decline exponentially with phylogenetic distance (Hansen & Martins 1996). All summary statistics for EGP shown in §3 are back-transformed from estimates obtained after arcsine transformation and standard errors are therefore asymmetrical. These are presented as mean (mean−1 s.e., mean+1 s.e.).

3. RESULTS

We obtained estimates of EGP from 26 species in 16 families and 6 orders. EGP ranged from zero in six species, including the California mouse Peromyscus

Figure 1. Frequency distribution of extra-group paternity (EGP) in mammals. N=26 species.
Table 1. The effect of mating season length, female numbers in breeding group and male numbers in breeding group on EGP. (Results from both phylogenetic generalized least-squares and ordinary least-squares analyses are shown. EGP was arcsine transformed and all predictor variables were ln-transformed. N=26 species. Two-way interactions between predictor variables were tested, but none were significant (p>0.1 in all cases.).)

<table>
<thead>
<tr>
<th></th>
<th>generalized least-squares model</th>
<th>ordinary least-squares model</th>
<th>change in $R^2$ when removed from model (%)</th>
</tr>
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<tr>
<td></td>
<td>coefficient (s.e.) $F \ p$</td>
<td>coefficient (s.e.) $F \ p$</td>
<td></td>
</tr>
<tr>
<td>intercept</td>
<td>0.581 (0.096)</td>
<td>0.581 (0.096)</td>
<td></td>
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<td>mating season length</td>
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<td>$-0.243$ (0.065)</td>
<td>13.897 0.0011 33.8</td>
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<tr>
<td>female numbers</td>
<td>$0.113$ (0.045)</td>
<td>$0.113$ (0.045)</td>
<td>6.331 0.0197 15.3</td>
</tr>
<tr>
<td>male numbers</td>
<td>$-0.045$ (0.074)</td>
<td>$-0.045$ (0.074)</td>
<td>0.370 0.5494 0.9</td>
</tr>
</tbody>
</table>

4. DISCUSSION

(a) Variation in EGP

EGP varied widely among mammal species, from little or no EGP to over 60% EGP in several species, including the southern elephant seal Mirounga leonina, the white-lined bat S. bilineata and the red fox V. vulpes. EGP was not restricted to particular mammalian clades, instead it was extensively distributed across phylogenetic groups. In addition to being widely distributed, EGP levels were strikingly high; 46% of species in our dataset showed 20% or higher EGP.

The extensive distribution of EGP among mammals mirrors previous findings for birds (Griffith et al. 2002; Møller 2003). However, levels of EGP appear to be higher in mammals than in birds. For example, 18% of bird species (Griffith et al. 2002) as opposed to 46% of mammals (this study) show EGP levels greater than 20%. This difference may be related to the greater prevalence of paternal care in birds than in mammals. Several authors have suggested that when paternal care is important, females should be less likely to seek extra-pair copulations and thereby risk a reduction in paternal care from their social mate (Mulder et al. 1994; Birkhead & Møller 1996; Gowaty 1996; Bennett & Owens 2002).

(b) Ecological correlates of variation in EGP

Interspecific differences in EGP were most closely related to the length of the mating season, a measure of the degree of oestrous synchrony. EGP levels were the highest in species with short mating seasons (e.g. elephant seals Mirounga spp., fat-tailed dwarf lemur Cheirogaleus medius, Gunnison’s prairie dog Cynomys gunnisoni) and declined as mating season length increased. This finding supports the idea that resident males may find it harder to prevent individual females from engaging in extra-group copulations, when mating seasons are short and, consequently, there is greater overlap among females in oestrus.

Comparative studies of birds report some correlational evidence for a similar relationship between breeding synchrony and EGP (Stutchbury & Morton 1995; Møller & Nøtta 1998; but see Weatherhead & Yeyerinac 1998; Spottiswoode & Møller 2004).

EGP was secondarily related to the number of females in a breeding group, indicating that when females are in larger groups, they may be better able
that polygyny may not impose a consistent cost on males in the form of a reduced paternity certainty (Arak 1984). Apart from the composition of breeding groups, the stability and cohesiveness of groups may also be important. For example, males may be less effective at guarding individual females and, consequently, EGP may be higher when groups are relatively unstable and there is movement into and out of groups (e.g. *Cervus elaphus*; Clutton-Brock *et al.* 1982) or when individuals within a group are dispersed while foraging, so that breeding females are frequently out of sight of resident males (e.g. *Urocyon littoralis*; Roemer *et al.* 2001; Clutton-Brock & Ivaran 2006).

Finally, in contrast to patterns in birds, we did not find a general phylogenetic signal in EGP, suggesting that the observed EGP levels reflect individuals responding to immediate ecological conditions. This result cannot be attributed to restricted sampling across clades, because, although our dataset is relatively small, the species we analysed are widely distributed across the mammalian phylogeny with representatives from 6 orders and 15 families. Furthermore, a simple comparison of EGP among three different orders also did not yield significant differences. In contrast, comparative studies of EGP in birds report a strong phylogenetic signal (Arnold & Owens 2002; Griffith *et al.* 2002). These studies propose that systematic differences among ancient lineages (families and orders) form an important source of variation among birds in EGP. This difference between mammals and birds is possibly related to differences in paternal care. The main hypotheses for the phylogenetic differences in EGP in birds involve variation among lineages in paternal care and the resultant variation in costs and benefits of EGP to females; when male care is essential, females should be less likely to engage in extra-pair copulations and risk a reduction in paternal care (e.g. Møller & Cuervo 2000; Arnold & Owens 2002). As paternal care is rare in mammals, it is unlikely to be an important selective factor leading to the kind of EGP variation among lineages that is seen in birds.

We have examined some of the ecological conditions thought to most strongly influence EGP. Other factors that are likely to be important and for which data are still lacking are variation among species in the costs and benefits to females and males from engaging in extra-pair copulations (Møller 2003; Westneat & Stewart 2003) and in counter tactics, such as mate-guarding (Clutton-Brock & Ivaran in press). An understanding of the nature and magnitude of these costs and benefits will allow an examination of how ecological conditions such as mating season length influence payoffs and thereby lead to variation among species in EGP.

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