

Territory quality drives intraspecific patterns of extrapair paternity

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Despite the potential reproductive benefits of extrapair matings, extrapair paternity rates in many avian species often vary greatly among populations. Although ecological factors have been shown to influence intraspecific patterns of extrapair paternity in some species, for cooperatively breeding species living in family groups, social/demographic factors may also play a role. This study examined how ecological factors related to territory quality (vegetation cover, insect abundance) and social/demographic factors (group size, number of breeding pairs, genetic relatedness) influenced intraspecific patterns of extrapair paternity in cooperatively breeding superb starlings, *Lamprotornis superbus*. Superb starlings inhabit spatiotemporally variable African savannas where high temporal variability drives reproductive decisions (adoption of breeding roles, offspring sex allocation) and where territories suitable for breeding are limited. Although extrapair paternity rates were only 14% of offspring and 25% of nests, they varied greatly among groups, ranging from 4% to 32% of offspring and from 7% to 60% of nests. These among-group differences in extrapair paternity were not related to social/demographic factors but instead to territory quality; extrapair paternity was higher on lower quality territories (lower vegetation cover and grasshopper abundance) than on higher quality territories (higher vegetation cover and grasshopper abundance). These results suggest that even in a heterogeneous landscape where suitable breeding territories are limited, subtle differences in habitat quality can have profound effects on reproductive decisions and patterns of extrapair paternity. Understanding the interaction between spatial (habitat heterogeneity) and temporal (temporal variability) environmental variation will be important for determining how environmental and social factors drive avian reproductive and mating decisions. *Key words*: cooperative breeding, extrapair fertilization, habitat heterogeneity, spatiotemporal environmental variation, temporal variability, territory quality. [*Behav Ecol* 18:1058–1064 (2007)]

In many species of birds, females who copulate with extrapair males outside of the pair-bond may gain indirect, genetic benefits such as increased heterozygosity for their offspring or direct, nongenetic benefits such as additional resources or increased parental care (reviewed in Birkhead and Moller 1992; Griffith et al. 2002; Cockburn 2004). Increased heterozygosity has been shown to increase offspring survival and fitness (Foerster et al. 2003, but see Arnqvist and Kirkpatrick 2005; Hadfield et al. 2006; Qvarnstrom et al. 2006), whereas having additional helpers at the nest can also increase offspring survival (Rabenold 1990; Emlen and Wrege 1991; Komdeur 1994; Woxvold and Magrath 2005; Rubenstein 2007c). Despite the potential benefits of extrapair paternity, females are often constrained by the potential costs of reduced paternal care from their social mate if they seek extrapair fertilizations (Cockburn 2004). For example, males may respond to an increased extrapair paternity risk by actively guarding their mates to prevent them from seeking extrapair fertilizations altogether or by reducing their nestling provisioning rates when they believe that females have had extrapair fertilizations (Birkhead and Moller 1992; Albrecht et al. 2006). This tension between pair-bonded males and females over extrapair matings leads to sexual conflict (Westneat and Stewart 2003), which may be particularly high in cooperatively breeding species where the presence of alloparental helpers

may compensate for a loss of paternal care and liberate females to mate more promiscuously outside of their pair-bond (Mulder et al. 1994).

Extrapair paternity has been observed in nearly 90% of all avian species studied (Griffith et al. 2002), including many cooperative breeders (Cockburn 2004). However, extrapair paternity rates often vary greatly among populations, and this intraspecific variation may be related to ecological factors such as food availability or to social/demographic factors such as group structure (Westneat and Stewart 2003). In cooperatively breeding species like Australian magpies, *Gymnorhina tibicen*, where extrapair paternity rates ranged from 44% to 87% of offspring (Hughes et al. 2003; Durrant and Hughes 2005), differences in the genetic relatedness among group members may influence patterns in extrapair paternity because females seek extragroup extrapair fertilizations to avoid mating with close kin (Durrant and Hughes 2005). However, in most noncooperatively breeding birds, intra- and interspecific variation in extrapair paternity rates are not typically related to social or demographic factors like breeding density, breeding synchrony, or genetic variation within a population (Westneat and Sherman 1997; Griffith et al. 2002; Westneat and Stewart 2003), but often to ecological factors such as habitat quality and food availability (Westneat 1994; Gray 1997; Hoi-Leitner et al. 1999; Charmantier and Blondel 2003; Vaclav et al. 2003). The goal of this study is to examine how ecological and social/demographic factors influence intraspecific patterns of extrapair paternity in a cooperatively breeding bird.

Environmental factors and food availability are known to influence a variety of reproductive decisions in social species (e.g., Komdeur 1992; Covas et al. 2004; Dickinson and McGowan 2005; Rubenstein 2007b). There are 2 alternative hypotheses to explain how food resource availability might directly influence

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intraspecific patterns of extrapair paternity in birds. According to the constrained female hypothesis, females on high-quality territories (with high food availability) will be able to resist a male's control efforts better and thus seek more extrapair fertilizations than females on low-quality territories (with low food availability) (Gowaty 1996). That is, the increased resource availability may allow females on high-quality territories to compensate for the potential reduced paternal care if they seek extrapair fertilizations. In contrast, females on low-quality territories might be expected to seek more extrapair fertilizations than females on high-quality territories in order to gain extra food resources (Gray 1997). Evidence for these alternative explanations is mixed. Although experimentally increased food availability led to an increase in extrapair paternity in serins, *Serinus serinus* (Hoi-Leitner et al. 1999), it led to a decrease in extrapair paternity in red-winged blackbirds, *Agelaius phoeniceus* (Westneat 1994), and house sparrows, *Passer domesticus* (Vaclav et al. 2003). Moreover, comparisons of extrapair paternity rates in 2 populations of blue tits suggested that extrapair paternity rates were lower in birds living on lower quality territories (Charmantier and Blondel 2003). Cooperatively breeding species make ideal systems in which to test these alternative hypotheses because helpers may compensate for the potential loss in paternal care to females for engaging in extrapair fertilizations (Mulder et al. 1994) and because many cooperative breeders often defend large group territories with abundant resources (Dickinson and McGowan 2005).

Here, I examine how ecological and social/demographic factors influence intraspecific patterns of extrapair paternity in cooperatively breeding superb starlings, *Lamprolaima superbus*. Superb starlings live in large social groups with up to 30 individuals and up to 6 breeding pairs per group. Despite relatively low overall rates of extrapair paternity (14% of young and 25% of nests), female superb starling can receive direct (i.e., additional helpers) or indirect benefits (i.e., increased offspring heterozygosity) from copulating with extrapair mates (Rubenstein 2007a). The goal of this study is to determine whether ecological factors related to territory quality (vegetation cover, insect abundance) or social/demographic factors (pairwise relatedness of group members, group size, number of breeding pairs in a group) best explain intraspecific patterns of extrapair paternity in a cooperative breeder living in a heterogeneous landscape where territories of varying quality are separated over small spatial scales of meters to kilometers. According to the constrained female hypothesis, extrapair paternity rates would be predicted to be positively associated with territory quality, whereas according to the Gray's (1997) hypothesis, extrapair paternity rates would be predicted to be negatively associated with territory quality. This study provides new insights into the factors that influence intraspecific variation in extrapair paternity in birds and how habitat heterogeneity influences avian reproductive and mating decisions.

METHODS

Study system and species

A population of starlings have been continuously monitored at the Mpala Research Centre, Laikipia, Kenya (0°17'N, 37°52'E), since April 2001. Breeding activities of 7 social groups were monitored from April 2001 to December 2005. One additional group was added in January 2002, and another was added in January 2003. Many of the groups were immediately adjacent to one another, and all were less than 5 km apart. Groups of 10–35 (mean = 21) superb starlings defended year-round territories of similar geographic size. Birds bred during both the long (March–May) and short rains

(November). Up to 6 breeding pairs per group (mean = 3.5) bred during the long rains, but only up to 4 breeding pairs per group (mean = 1.7) bred during the short rains (Rubenstein 2006). More than 90% of nests had at least one helper (Rubenstein 2006), and although both sexes helped at the nest, males did a greater proportion of the provisioning (Rubenstein 2007c). Helpers included both offspring and other first-order relatives (e.g., parents, siblings), as well as other group members that were less related, or even unrelated, to the breeding pair (Rubenstein 2006). Helpers had a positive effect on parental fitness by increasing the number of offspring fledged (Rubenstein 2007c). Nongroup members were never allowed near the nest and were actively chased from the territory during the breeding season (Rubenstein 2007a).

Superb starlings live in mixed savanna woodland habitat and forage on the ground, feeding primarily on insects but supplementing their diet with fruits during the dry season (Feare and Craig 1999). The area where this study was conducted is composed of semiarid bushland that consists of a mosaic of small grassland glades embedded in an acacia-dominated community (Young et al. 1995). Superb starlings inhabit territories that encompass at least one grassland glade (Rubenstein 2006). Glades are typically found at sites of abandoned pastoralist settlements called bomas, which are also used for overnight containment of livestock (Young et al. 1995). Because large quantities of livestock dung are concentrated in these small areas, both the soil and the vegetation inside glades are nutrient rich and persist in an enriched state for nearly 40 years (Augustine 2003a). Insect abundance inside glades is on average 90% higher (range: 0–276%) than in neighboring bushland patches of similar size (Huntzinger 2005).

Capture, parentage, and relatedness analyses

Starlings were captured annually during the dry season using baited wire traps. Nestlings were captured from active nests between 5 and 8 days after hatching. During the course of the study, 476 birds (including 204 nestlings), or more than 97% of the study population, were captured and given a unique set of color leg bands and a metal leg ring. CERVUS v2.0 software (Marshall et al. 1998) was used to analyze parentage data, and KINSHIP v1.3.1 software (Goodnight and Queller 1999) was used to calculate pairwise relatedness. Parentage analysis assigned paternity to all offspring using 15 microsatellite markers with a combined exclusion probability of 0.999 (Rubenstein 2007a). Pairwise relatedness values are equivalent to coefficients of relatedness and were used as a measure of genetic similarity between 2 individuals (Tarvin et al. 2005; Freeman-Gallant et al. 2006). A negative pairwise relatedness value means that the 2 individuals are less related to each other than are 2 individuals chosen at random from the population.

Because 1) mean group extrapair paternity rates did not differ between the short and long rains (Rubenstein 2007a), 2) there were less than half the mean number of nesting attempts per group during the short rains than during the long rains, 3) no extrapair young were born during the short rains in 7 of the groups, and 4) many groups did not try to breed at all during the short rains in some years, the dataset was restricted to only those nestling born during the long rains breeding period. The proportion of extrapair young as well as the proportion of nests with at least one extrapair nestling were calculated for each group in each year, and these values were averaged across years to get a mean value for each group, as well as across groups to get a mean value for each year. Mean pairwise relatedness values for just males, as well as for both males and females, were calculated for each

group. Separate values were calculated for each year of the study because the coefficients are dependent on the genotypes present in the population.

Behavioral observations

Focal observations at nests (1–2 h) were conducted during the nest building and incubation stages to identify the social breeders. Observers used spotting scopes and were hidden under a tree or behind a blind more than 30 m from the nest. Social mothers were identified as the female at a nest that incubated eggs; social fathers were defined as those that remained near the incubating female while she was on the nest.

Vegetation surveys of habitat quality

Vegetation surveys were conducted on the territories of 7 groups in September 2005, about 1 month after the end of the long rains. Two groups (MRC1 and MRCV) were not surveyed because their territories encompassed areas at the Centre where constant human habitation and building, continuous livestock rearing, and seasonal grass and tree cutting substantially altered the landscape and likely influenced the seasonality of food resources. These groups did not differ from the remaining groups in any other way; group sizes, the number of breeding pairs per group, and extrapair paternity rates were similar to other groups (Rubenstein 2006). Territory boundaries were mapped using a geographic positioning systems, and seven 100-m transects starting at a randomly chosen point and compass direction were conducted at each territory. For each 100-m transect, a metal pin was dropped every 2 m (50 points per transect and 350 points per territory), and whether the pin was touching vegetation or bare earth was recorded (Holmes 1974; Stewart et al. 2001). Habitat quality was quantified for each transect as the percent vegetation cover, or the proportion of pins that were touching a grass or forb species over the total number of pin drops per transect. Each species of grass or forb touching the pin was identified and classified as *Cynadon* spp. or as "other." Percent vegetation cover on each territory was positively correlated with the proportion of *Cynadon* grass (correlation: $F_{1,5} = 14.12$, $P = 0.013$, $r = 0.74$), showing that among-territory differences in habitat quality were mainly due to differences in the amount of *Cynadon*, the dominant grass species in glades and an indicator of nutrient-rich soils (Augustine 2003a) and high insect abundance (Huntzinger 2005).

Although vegetation growth and cover vary seasonally with rainfall at Mpala (Augustine and McNaughton 2004), spatial heterogeneity in vegetation cover is heavily influenced by differences in soil nutrients and topography, which vary spatially but not temporally (Augustine 2003b). To verify the assumption that despite seasonal changes in vegetation cover, some sites are consistently different from others through time, vegetation cover was quantified at 17 sites around Mpala in August and September of 2004 and 2005 (Rubenstein DI, unpublished data). The 17 sites spanned a range of habitats, soil types, and topographies during a period that included one of the driest and one of the wettest months of the year. Percent vegetation cover was estimated at each site from one 50-m transect (25 pin drops per transect) using methods described previously. A general linearized mixed model (GLMM) that accounted for repeated measures showed that although vegetation cover varied among sites and months, there was no interaction (site: $F_{16,34} = 3.95$, $P = 0.0045$; month: $F_{1,34} = 4.81$, $P = 0.043$; interaction: $F_{16,34} = 0.60$, $P = 0.86$). Thus, although there were seasonal differences in vegetation cover within sites driven by rainfall, among-site differences in vegetation cover were consistent across years.

Insect surveys of habitat quality

Grasshopper abundance on each of the 7 territories for which vegetation cover was surveyed was quantified using sweep netting in January 2007, about 1 month after the end of the short rains. Despite being collected in different years and seasons, grasshopper abundance was positively correlated with percent vegetation cover (correlation: $F_{1,5} = 26.40$, $P = 0.0037$, $r = 0.92$). Grasshoppers, Orthoptera, were chosen because they have been shown previously at this study area to vary inside and outside of nutrient-rich glades (Huntzinger 2005) and because they are the single largest type of food fed to nestlings, making up more than 40% of the superb starling's diet (Rubenstein DR, unpublished data). Using a GLMM with glade/nonglade nested within territory and transect as a random effect to account for repeated measures, I confirmed these results and found that grasshopper abundance on superb starling territories was 180% higher inside of glades than outside of them (GLMM: glade/nonglade: $F_{7,65} = 2.81$, $P = 0.013$). Although the number of grasshoppers varies seasonally, the differences inside and outside of glades are consistent across seasons (Huntzinger 2005). Six transects of 100 sweeps (approximately 50 m in length) were conducted inside and 6 outside of each glade by a single person on each territory. A 50-m buffer zone was placed at the edge of the glade to ensure that all sweeps were confined to the interior or exterior of the glade. Transects were spaced evenly around the glade using a compass. Interior transects extended toward the center of the glades from the edge of the buffer zone, whereas exterior transects extended away from the center of the glade. The contents of each transect sweep were sealed in paper bags and frozen at -30 °C before counting.

Statistics

GLMM that accounted for repeated measures at territories over the 5-year study period was used to examine the relationships between habitat quality (both percent vegetation cover and grasshopper abundance) and extrapair paternity (both the proportion of extrapair offspring and the proportion of nests with at least one extrapair offspring). Similar models were used to examine the relationships between both measures of extrapair paternity and prebreeding rainfall, group size, the number of breeding pairs per group, average male pairwise relatedness in the group, and the average pairwise relatedness between males and females in the group. Separate analyses were conducted because many of the independent variables were correlated; a Bonferroni correction was used to account for the multiple comparisons ($\alpha < 0.007$). Data from 2001 were excluded from the analyses of group size and pairwise relatedness because not all the birds in each group were identified in that initial year of the study. Wilcoxon tests were used to determine if extrapair paternity rates varied among years. GLMM that accounted for repeated measures was also used to examine the number of grasshoppers inside and outside of glades, as well as on high- and low-quality territories. The number of grasshoppers was arctangent transformed to improve normality.

RESULTS

Among-territory variation in extrapair paternity

The mean proportion of extrapair offspring in each group ranged from 4% to 32%, and the proportion of nests in each group with at least one extrapair offspring ranged from 7% to 60% (Figure 1).

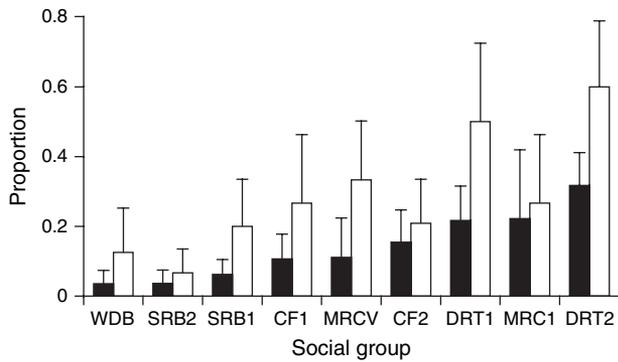


Figure 1
The mean \pm standard error proportion of extrapair offspring per group (filled bars) and proportion of nests with at least one extrapair offspring in each social group (open bars).

Ecological determinants of extrapair paternity

Both measures of habitat quality were significantly related to extrapair paternity rates. There was a negative relationship between percent vegetation cover and the proportion of extrapair offspring in each group (GLMM: $F_{1,31} = 12.75$, $P = 0.0012$, $R^2 = 0.29$; Figure 2A), as well as the proportion of nests with at least one extrapair offspring in each group (GLMM: $F_{1,31} = 8.80$, $P = 0.0058$, $R^2 = 0.22$; Figure 2B), such that territories with less vegetation cover had higher extrapair paternity rates than those with greater vegetation cover. Similarly, there was a negative relationship between grasshopper abundance and the proportion of extrapair offspring in each group (GLMM: $F_{1,31} = 8.51$, $P = 0.0065$, $R^2 = 0.22$; Figure 3A), as well as the proportion of nests with at least one extrapair offspring in each group (GLMM: $F_{1,31} = 6.58$, $P = 0.015$, $R^2 = 0.18$; Figure 3B), such that territories with a lower grasshopper abundance had higher extrapair paternity rates than those with a higher grasshopper abundance. Extrapair fertilizations on the 2 lowest quality territories (i.e., lowest vegetation cover and grasshopper abundance) were primarily with extragroup males, whereas extrapair fertilizations on the 5 higher quality territories (i.e., highest vegetation cover and grasshopper abundance) were mainly with males from within the group; 77% of the extrapair fertilizations on the lower quality territories were with extragroup males, whereas only 20% of the extrapair fertilizations on the higher quality territories were with extragroup males. Extragroup extrapair males were primarily males from nearby territories because there are no floaters in this system (Rubenstein 2007a).

Neither the proportion of extrapair offspring in each group (Wilcoxon test: $\chi^2 = 0.65$, degrees of freedom [df] = 4, $P = 0.96$) nor the proportion of nests with at least one extrapair offspring in each group (Wilcoxon test: $\chi^2 = 3.08$, df = 4, $P = 0.55$), varied among years. Similarly, there was no relationship between prebreeding rainfall and the proportion of extrapair offspring (GLMM: $F_{1,31} = 0.047$, $P = 0.83$, $R^2 = 0.004$) or the proportion of nests with at least one extrapair offspring (GLMM: $F_{1,31} = 1.03$, $P = 0.32$, $R^2 = 0.06$).

Demographic and social determinants of extrapair paternity

The proportion of extrapair offspring was not significantly related to group size (GLMM: $F_{1,32} = 0.0053$, $P = 0.94$, $R^2 = 0.0002$) or to the number of breeding pairs in a group (GLMM: $F_{1,39} = 1.93$, $P = 0.17$, $R^2 = 0.05$). Similarly, the proportion of nests with at least one extrapair offspring was not significantly related to group size (GLMM: $F_{1,24} = 0.24$, $P = 0.63$, $R^2 = 0.008$) or to the number of breeding pairs in a group (GLMM: $F_{1,39} = 2.27$, $P = 0.14$, $R^2 = 0.06$). The proportion of extrapair offspring was also not significantly related to the average male relatedness in the group (GLMM: $F_{1,32} = 0.61$, $P = 0.44$, $R^2 = 0.02$) or to the average relatedness between males and females in the group (GLMM: $F_{1,32} = 0.21$, $P = 0.65$, $R^2 = 0.006$). Moreover, the proportion of nests with at least one extrapair offspring was not significantly related to the average male relatedness in the group (GLMM: $F_{1,32} = 0.0057$, $P = 0.94$, $R^2 = 0.01$) or to the average relatedness between males and females in the group (GLMM: $F_{1,32} = 0.088$, $P = 0.77$, $R^2 = 0.01$).

DISCUSSION

Although extrapair paternity is relatively low in superb starlings (14% of young and 25% of nests) when compared with most other cooperatively breeding species (Rubenstein 2007a), extrapair paternity rates varied greatly among groups, ranging from 4% to 32% of offspring and 7% to 60% of nests. These differences in extrapair paternity rates among groups that were separated by small spatial scales of a few meters to kilometers were related to differences in territory quality (vegetation cover and insect abundance) and not to social or demographic characteristics of the group (group size, the number of breeding pairs, or pairwise relatedness). Although it is not clear in superb starlings whether most extrapair fertilizations are male- or female initiated, limited observations suggest that females can solicit copulations with extragroup males and that females likely play an active role in choosing extrapair males or in allocating paternity (Rubenstein 2007a),

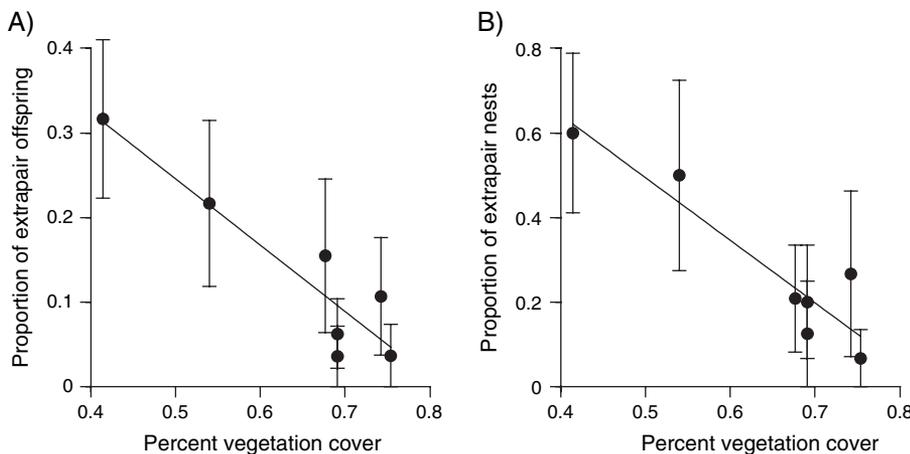
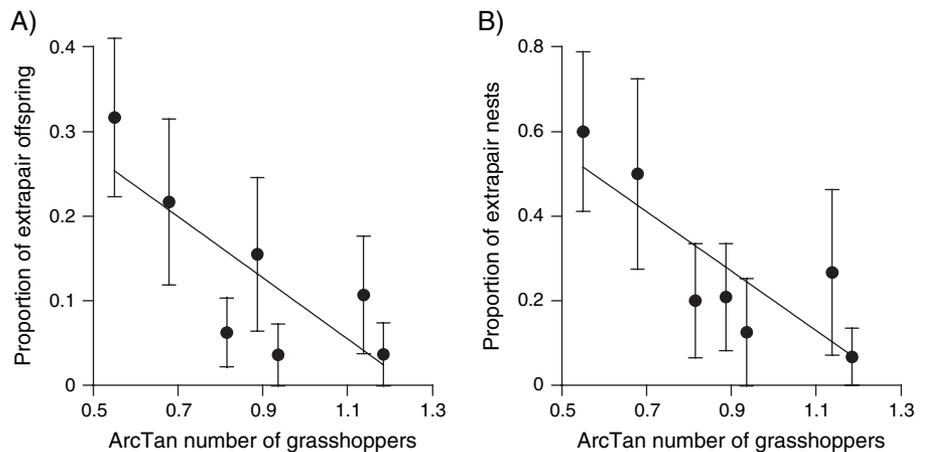


Figure 2
The mean \pm standard error (A) proportion of extrapair offspring per group and (B) proportion of nests with at least one extrapair offspring per group were related to the percent vegetation cover, a measure of habitat quality that is related to insect abundance and food availability. Territories with less vegetation cover had higher extrapair paternity rates than did those with greater vegetation cover.

Figure 3

The mean \pm standard error (A) proportion of extrapair offspring per group and (B) proportion of nests with at least one extrapair offspring per group were related to grasshopper abundance. Territories with a lower grasshopper abundance had higher extrapair paternity rates than did those with a higher grasshopper abundance.



as they do in many avian species (Jennions and Petrie 2000; Griffith et al. 2002; Westneat and Stewart 2003; Mays and Hill 2004; Neff and Pitcher 2005; Safran et al. 2005). It will be important to determine if this relationship between territory quality/food availability and extrapair paternity is directly or indirectly related to food resources and whether food availability influences male or female reproductive strategies or both. That is, does food availability directly influence a female's desire to seek (i.e., female preference for) extrapair fertilizations or does it indirectly influence a female's (or male's) ability to seek them.

Territory quality and food availability could directly influence patterns of extrapair paternity by altering a female's desire to seek extrapair fertilizations if females seek extrapair fertilizations to gain additional resources. Although the results of this study fail to support the constrained female hypothesis, which predicts that females on high-quality territories (high food availability) will be able to resist a male's control efforts better and copulate more with extrapair males than females on low-quality territories (low food availability) (Gowaty 1996), they are consistent with the idea that females on low-quality territories might be expected to seek more extrapair fertilizations than females on high-quality territories in order to gain additional food resources (Gray 1997). Although a previous study in superb starlings has shown that females do not gain direct benefits in the form of increased helpers by copulating with extragroup extrapair males (Rubenstein 2007a), it is at least possible that females could copulate with extragroup extrapair males from neighboring territories to gain direct benefits in the form of additional food resources. Resource availability is known to influence sexual conflict and reproductive decisions in cooperatively breeding dunnocks, *Prunella modularis* (Davies and Lundberg 1984). Moreover, increased food availability led to a similar decrease in extrapair paternity in noncooperatively breeding red-winged blackbirds (Westneat 1994) and house sparrows (Vaclav et al. 2003). Using radio telemetry to follow females and to closely monitor foraging patterns during the breeding season would help determine if female superb starlings initiate most extrapair fertilizations and if they are gaining additional food resources from neighboring territories by copulating with extragroup extrapair males.

Because females are known to receive indirect, genetic benefits in the form of increased offspring heterozygosity by mating with extragroup extrapair males (Rubenstein 2007a), it seems unlikely that territory quality directly influences patterns of extrapair paternity by altering female preference for seeking extrapair fertilizations. In contrast, territory quality and food availability may indirectly influence patterns of ex-

trapair paternity by altering a female's (or male's) ability to seek extrapair fertilizations. That is, if birds on lower quality territories have to go further from the central feeding glades to forage, possibly even to the boundaries of neighboring territories, then females might be able to escape guarding by their social mate, thereby allowing them to copulate with more extragroup males. Preliminary results suggest that birds do go further from active nests and central foraging glades on lower quality territories, even though they feed nestlings at similar rates to those on higher quality territories (Rubenstein 2006). Thus, the effectiveness of mate guarding by males could decrease on lower quality territories, thereby allowing females greater opportunity to seek more extrapair fertilizations with males from outside the territory or extragroup males greater opportunity to gain access to females. This hypothesis makes no assumptions about whether patterns of extrapair paternity are driven by male- or female-initiated reproductive strategies, and it incorporates ideas of how ecological factors might impact patterns of extrapair paternity into a sexual conflict framework (sensu Westneat and Stewart 2003; Griffith 2007). Future studies must use detailed behavioral observations and radio telemetry to examine the role of mate guarding as a potential mechanism constraining female extrapair mating and as a primary factor underlying intraspecific patterns of extrapair paternity in superb starlings and other cooperatively breeding species.

In summary, intraspecific variation in extrapair paternity in superb starlings was related to differences in territory quality (vegetation cover and grasshopper abundance) and not to differences in group structure (group size, the number of breeding pairs, or genetic relatedness), as has been shown in some other cooperative breeders (Durrant and Hughes 2005). Even in heterogeneous landscapes like that of African semiarid savannas, which are characterized by a patchy mosaic of vegetation and bare soil (Aguar and Sala 1999) and a shortage of suitable breeding territories for superb starlings (Rubenstein 2006), subtle differences in vegetation cover and insect abundance in nearby territories (<5 km apart) had profound effects on extrapair paternity rates and mating decisions. Although the mating system of the superb starling appears to be influenced by habitat heterogeneity and subtle differences in territory quality (i.e., spatial environmental variation), the social system is greatly influenced by temporal, or year-to-year, variability (i.e., temporal environmental variation), such that prebreeding rainfall influences breeding roles (Rubenstein 2007b) and offspring sex allocation (Rubenstein 2007c). Understanding the interaction between spatial and temporal environmental variation will be important for determining how complex social and mating systems have evolved,

particularly in semiarid ecosystems where cooperatively breeding species are particularly common (Rubenstein and Lovette forthcoming).

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