

## Original Article

Habitat geometry does not affect levels of  
extrapair paternity in an extremely unfaithful  
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Density of potential mates has often been proposed to explain the enormous variation in extrapair paternity. However, density is often confounded by other ecological factors that might affect extrapair paternity in their own way. Furthermore, extrapair mating shows strong phylogenetic inertia, making both meaningful intra- and interspecific comparisons difficult. An extreme way to change density is through habitat fragmentation that reduces connectivity between territories. Recently, habitat connectivity was hypothesized to explain the surprising discovery of a virtually monogamous species among the world's most unfaithful bird genus. The monogamous *Malurus coronatus* lives in narrow riparian strips that limit contact with neighbors to both extreme ends of territories, whereas *Malurus* species with high levels of extragroup paternity typically live in high-connected habitat in which they are surrounded by neighbors. Here, we test the habitat geometry hypothesis by comparing levels of extragroup paternity of *Malurus elegans* living in fragmented low-connected habitat and in high-connected habitat. We found that *M. elegans* does not have lower levels of extragroup paternity in low-connected habitat (68%) than in high-connected habitat (56% of offspring), indicating that connectivity does not limit opportunities for extragroup paternity. Furthermore, there was no evidence that females in low-connected habitat gained extragroup paternity further away or from less sires or that they were more likely to be closely related to their social mate. We conclude that behavioral plasticity in response to density-dependent cost and benefits of mating behavior does not explain intrageneric variation in extragroup paternity in *Malurus*. Furthermore, habitat fragmentation may not strongly affect inbreeding risk in this species.

**Key words:** connectivity, density, extragroup paternity, linear habitat, *Malurus*, promiscuity.

## INTRODUCTION

Genetic monogamy in birds is the exception rather than the rule, despite social monogamy being the dominant avian mating system. Extrapair paternity (EPP), whereby offspring are sired by a male other than the female's social male, has been found in over 70% of the studied bird species (reviewed in Griffith et al. 2002). Strikingly, despite 30 years of research, the enormous amount of variation in the occurrence and levels of EPP both within and between species remains largely unexplained (Petrie and Kempenaers 1998; Griffith et al. 2002). Research attempting to explain this variation in EPP has focused on a wide range of factors including the role of life history (Møller and Birkhead 1993; Arnold and Owens 2002) and ecology (Stutchbury and Morton 1995; Westneat and Sherman 1997). However, few

general patterns have been identified other than that more than 55% of the interspecific variation in EPP rates can be attributed to phylogeny occurring at or above the family level (Arnold and Owens 2002).

With respect to ecological explanations, population density has attracted particular attention (for review, see Westneat and Sherman 1997) because of its clear link to the behavioral mechanisms involved in EPP. EPP can arise, for example, through females making forays to pursue EPP outside her own territory (e.g., Sheldon 1994; Gray 1997; Double and Cockburn 2000) or through interaction with intruding males that make extraterritorial forays to display or steal copulations from the resident male (Sherman and Morton 1988; Westneat 1994). Consequently, extrapair mating behavior is expected to vary with breeding or population density, as higher density increases the encounter rates between individuals (Westneat et al. 1990). Furthermore, females are expected to seek EPP when they can select among males of different quality (Gowaty 1996), which is likely to increase with higher density.

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The density hypothesis has, however, received mixed and confusing support. Several studies have shown that the rate of EPP may increase with increasing population density within species (Gibbs et al. 1990; Yezerinac et al. 1999; Richardson and Burke 2001; Rowe and Weatherhead 2007; Stewart et al. 2009; Ryder et al. 2012; Mayer and Pasinelli 2013), though many other studies found no or negative relationships (Dunn et al. 1994; Fridolfsson et al. 1997; Hoi and Hoi-Leitner 1997; Griffith et al. 1999; Charmantier and Blondel 2003; Westneat and Mays 2005; Lindstedt et al. 2007; Olsen et al. 2008; Moore et al. 2012). Furthermore, a comparative study did not reveal a relationship between density and EPP levels among species (Westneat and Sherman 1997).

Encounter rates between individuals will not only depend on density per se but also strongly depend on habitat connectivity and geometry, which are affected by habitat fragmentation. For example, a linear configuration of territories (i.e., riparian or strip of fragmented habitat) means that an individual only has neighbors at 2 sides of the territory and the number of potential partners encountered increases linearly with progressive distance from the home territory. By contrast, in nonfragmented habitat, territories are typically arranged in a hexagonal structure and consequently the number of potential mates encountered also increases linearly with progressive distance from the home territory, but at a roughly 3 times higher rate. Thus, individuals in linear habitat have to travel further to find unrelated/high-quality mates or to display to a similar number of mates as individuals in hexagonal habitat. Indeed positive correlations between nearest neighbor distance and EPP have been shown in several studies (Hill et al. 1994; Hoi and Hoi-Leitner 1997; Richardson and Burke 2001; Stewart et al. 2009), although other studies found no such correlation at all (Verboven and Mateman 1997; Tarof et al. 1998; Chuang et al. 1999; Casey et al. 2011).

Studying the effects of density on EPP is complicated as the measure of density used might not reflect opportunities for EPP accurately. For instance, although the distance to a neighbor will reflect density, the number of neighbors is more likely to affect the likelihood that an individual will seek EPP and therefore capture EPP opportunities better (Westneat et al. 1990). Another major constraint on studying associations between EPP and ecological factors like density is that there is usually little variation in ecology within populations. Comparing closely related species that differ in ecology can resolve this issue, but such species are rare. Alternatively, one can investigate the variation in ecological factors within different populations of a single species. However, the latter is usually problematic because ecological factors are typically confounded with each other. For example, a higher breeding density is likely to be caused by higher resource availability, and each of these factors can affect EPP in their own way (Hoi-Leitner et al. 1999; Griffith et al. 2002). This latter problem can be resolved by manipulating density directly, for example, through reduction of suitable habitat, as now often occurs as a result of habitat fragmentation.

The cooperatively breeding fairy-wrens (genus *Malurus*) are unusual in the extreme extent to which closely related species vary in their extragroup paternity (EGP) levels. Most fairy-wren species have among the highest levels of EGP recorded, with extragroup fertilizations dominating paternity in 4 of the 5 species subject to detailed study (Cockburn et al. 2013). The striking exception is *Malurus coronatus*, which is virtually genetically monogamous (<5% EGP; Kingma et al. 2009). Unlike other *Malurus*, which typically inhabit hexagonal habitat, *M. coronatus* is generally confined to linear riparian strips of habitat. Habitat connectivity and geometry

have been hypothesized to alter the cost–benefit ratio of extrapair mating in 2 different ways. Kingma et al. (2009) hypothesized that linear habitat limits the availability of fertile males nearby and thus reduces the probability that a female will be able to find a high-quality male. Cockburn (2013) suggested the alternative nonexclusive hypothesis that the benefits of extragroup mating are reduced because both the signaling strategy used by dominant males and the information content that can be gleaned by females collapse in linear habitat. This is thought to occur because any distant extrapair male will lure the female past all the intervening males when she seeks out his territory. This could tip the balance in favor of parasitic strategies by males and undermines the utility of the signaling convention.

Here, we perform the first test of whether habitat connectivity and geometry is associated with levels of EGP. Understanding how environmental heterogeneity affects reproductive strategies is important as recent evidence has shown that human activities might alter evolutionary processes (Shochat et al. 2006; Smith and Bernatchez 2008). We use the red-winged fairy-wren (*Malurus elegans*) as a model system because although this species usually inhabits highly connected hexagonal habitat where it has high levels of EGP (Brouwer et al. 2011), it also occurs in fragmented low-connectivity habitat in which birds are forced to live in narrow linear strips of forest. Our study design not only allows us to investigate whether EGP levels vary between linear and hexagonal habitats but also in relation to the number of neighboring territories. Because EGP in this species has been shown to have a function in inbreeding avoidance, with highly related social pairs being more likely to have extragroup offspring (Brouwer et al. 2011), pairwise relatedness of the social pair was analyzed simultaneously. Additionally, we investigated whether females in linear habitat travelled further to gain EGP than females in hexagonal habitat to compensate for the reduced availability of “high-quality” males. And we investigated whether reduced habitat connectivity resulted in a smaller number of sires.

## MATERIALS AND METHODS

### Data collection

Data were collected in Smith Brook nature reserve (95 ha) and surrounding areas in Western Australia (116°10'E, 34°20'S) during 5 breeding seasons (2008–2012). The red-winged fairy-wren is a cooperative breeder in which both males and females are extremely philopatric and help their parents to rear the next brood (Brouwer et al. 2014). The study area consists of eucalypt wet forest with a dense understory (for more details, see Rowley et al. 1988). The main study area (hexagonal habitat) at the western end of the reserve comprises ~65 territories in which >99% of the adult birds were individually color banded and those territories were checked at least fortnightly for group composition and breeding activity throughout the breeding season (October–January). Additionally, from 2009, sampling was done in the ~20 territories at the eastern end of the reserve. Eighty-eight percent of the border of the reserve is bounded by unsuitable habitat (farmland), but 3 narrow corridors of linear habitat lead away from the reserve. The linear habitat has resulted from habitat loss (>100 years ago) due to clearing of forest for farmland while leaving narrow strips of forest along creeks and roads to connect the reserve to nearby state forests. Territories in linear habitat were sampled opportunistically in 2008–2010, but in 2011–2012, we strongly intensified our nest searches and sampling effort.

To create a territory map (see [Supplementary Material](#)), territory borders were determined (using a Garmin 76 GPS) based on observations of individual fairy-wrens and the outcome of disputes between groups. Using the territory map, a connectivity matrix was created between all territories based on the shortest distance in number of territory borders that would have to be crossed. The mean territory width, defined as the minimum Euclidian distance between the borders of 2 opposing neighbors, was measured for 10 randomly selected territories in each habitat type.

### Parentage analysis and relatedness

Nestlings were blood sampled when at least 2 days old and abandoned clutches and unhatched eggs were collected for genotyping. All blood (ca. 15  $\mu$ L) and tissue samples were stored in 1 mL of 100% ethanol and stored at room temperature. Parentage was assigned with high accuracy using 7 or 8 hypervariable microsatellite markers (mean: 30 alleles) with a parent-pair analysis in program Cervus 3.0 (Kalinowski et al. 2007) as described in Brouwer et al. (2011). Offspring of plural breeding females were excluded from analyses here as well as offspring from groups where one or both dominants or male helpers had not been sampled. For 979 offspring, we were able to determine whether the offspring was sired by an extragroup male or not. Note that in this species, levels of EGP are virtually similar to EPP levels, as within-group male helpers rarely gain paternity (<2%; Brouwer et al. 2011). The genetic sire was successfully assigned to 95% of offspring in hexagonal habitat ( $n = 932$  offspring of 411 nests) and to 72% of offspring in linear habitat ( $n = 47$  offspring of 24 nests), which was likely due to the somewhat lower sampling effort of males in this habitat.

Relatedness measures the proportion of alleles shared between individuals that are identical by descent. We estimated marker-based relatedness by calculating the pairwise  $r$  according to Wang (2002) in program KINGROUP v2 (Konovalov et al. 2004). We used Wang's estimator, as calculating pairwise  $r$  for mother-offspring pairs showed that this measure performed best (Wang's pairwise  $r$ :  $0.47 \pm 0.09$  standard deviation [SD]; expected pairwise due to known pedigree  $r = 0.5$ ) compared with 3 other commonly used estimators (Brouwer et al. 2011). Note that pairwise  $r$  can take on negative values, as it measures how much lower (or higher for positive  $r$ ) the probability of recent coalescence is for a dyad relative to the average probability for all considered dyads (Konovalov and Heg 2008).

### Statistical analysis

To investigate whether EGP levels vary with habitat geometry, the number of extrapair offspring in a brood was fitted as a binomial response in a generalized linear mixed model (GLMM) with the denominator set to the size of the brood (range 1–3, mean = 2.3) and identity of the dominant female included as a random intercept ( $n = 979$  offspring of 435 broods from 180 females). Habitat type (linear or hexagonal), the absence or presence of helpers, and cohort were included as categorical fixed factors, whereas pairwise relatedness of the social pair was included as a covariate in the analyses. In addition to comparing linear (i.e., usually 2 neighboring territories) versus hexagonal habitat (i.e., usually about 6 neighboring territories), we also investigated how EGP depended on the number of neighboring territories (range 2–9).

To investigate whether social pairs in linear habitat are more related than social pairs in hexagonal habitat, pairwise  $r$  for each unique pair ( $n = 216$ ) was analyzed in a GLM with the number

of neighboring territories or habitat type included as a fixed effect. Furthermore, to investigate whether females in linear habitat travel further to gain EGP, the distance to the genetic sire in number of territory widths (minus 1) was analyzed for all assigned extragroup offspring ( $n = 512$ ; 46 offspring could be classified as EGP, but not assigned to a specific EGP sire) in a GLMM using a Poisson distribution with identity of the dominant female included as a random intercept. Similarly, to test whether broods in linear habitat are sired by a smaller number of males (due to reduced habitat connectivity), the number of genetic sires (minus 1) per brood was analyzed in a GLMM using a Poisson distribution with identity of the dominant female included as a random intercept and the number of neighboring territories or habitat type included as a fixed effect ( $n = 276$  broods with at least 1 EGP offspring).

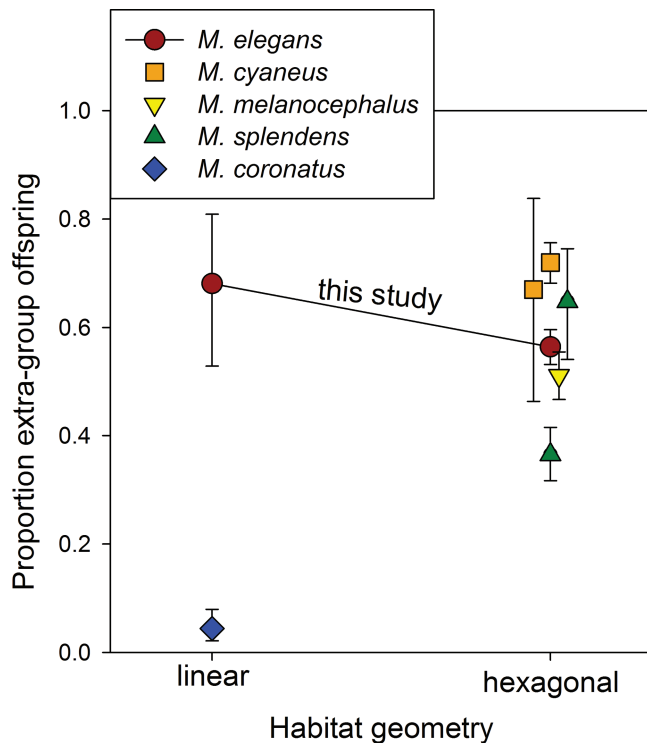
Model selection was based on stepwise backward elimination of nonsignificant fixed terms in order of their  $P$  value. Significance of fixed terms was assessed by a likelihood ratio test. Effect sizes were derived from final models that contain all significant terms. Statistical analyses were performed in R v.2.15.1 (R Development Core Team 2013) using package lme4 (Bates et al. 2011).

## RESULTS

Territories in linear and hexagonal habitats differed less than 10% in group size, productivity, and territory size (respectively  $4.0 \pm 1.7$  SD vs.  $3.8 \pm 1.3$  SD birds/territory; 0.92 vs. 0.92 fledglings per nesting attempt;  $115 \pm 28$  SD vs.  $103 \pm 27$  SD meters territory width).

In contrast to the expectation that habitat connectivity limits opportunity for EGP, the proportion of extragroup offspring per brood in linear habitat was not lower than in hexagonal habitat (Figure 1 and Table 1). Furthermore, there was no evidence that an increasing number of neighboring territories was associated with a higher proportion of extragroup offspring (Figure 2A and Table 1). The proportion of extragroup offspring strongly increases with pairwise relatedness of the social pair (Table 1), with nonrelated pairs ( $r \leq 0$ ) having 51% and highly incestuous pairs ( $r \geq 0.5$ ) having 91% extragroup offspring. However, there was no indication that pairs in linear habitat had a higher relatedness than pairs in hexagonal habitat, as pairwise  $r$  of social pairs was associated with neither the number of neighboring territories (Figure 2B; GLM:  $\beta = -0.010 \pm 0.008$  SE,  $t = 1.3$ , degrees of freedom [df] = 1,  $P = 0.20$ ) nor the habitat type (GLM:  $\beta_{\text{hexagonal}} = -0.037 \pm 0.044$  SE,  $t = 0.9$ , df = 1,  $P = 0.40$ ).

The difference in number of neighboring territories between hexagonal and linear habitats means that the number of neighboring males, which are potential EG sires also differs substantially. Females from hexagonal habitat were able to choose from on average  $9.8 \pm 1.9$  SD neighboring males, whereas females in linear habitat could on average choose from  $3.8 \pm 1.3$  SD neighboring males as potential sires (i.e., dominant and helper males). However, there was no evidence that females in linear habitat travelled further to gain EGP compared with females in hexagonal habitat (Figure 2C; GLMM: number of neighboring territories,  $\beta = -0.016 \pm 0.057$  SE,  $\chi^2 = 0.1$ , df = 1,  $P = 0.79$ ; habitat type,  $\beta_{\text{hexagonal}} = -0.30 \pm 0.47$  SE,  $\chi^2 = 0.4$ , df = 1,  $P = 0.51$ ). Nor did females with less neighboring territories that gained EGP choose a smaller number of males to gain paternity from (Figure 2D; GLMM: number of neighboring territories,  $\beta = 0.069 \pm 0.095$  SE,  $\chi^2 = 0.5$ , df = 1,  $P = 0.47$ ; habitat type,  $\beta_{\text{hexagonal}} = 0.90 \pm 1.07$  SE,  $\chi^2 = 1.0$ , df = 1,  $P = 0.32$ ).



**Figure 1**

Proportion of extragroup offspring for several *Malurus* species and populations in linear and hexagonal habitats. Error bars depict 95% confidence intervals around the means. Data combined for *Malurus elegans* (this study), *Malurus coronatus* (Kingma et al. 2009), *Malurus cyaneus* (Dunn and Cockburn 1998; Colombelli-Négrel et al. 2009), *Malurus melanocephalus* (Webster et al. 2008), and *Malurus splendens* (Brooker et al. 1990; Webster et al. 2004).

**Table 1**

**Results from a GLMM examining the proportion of extragroup offspring in *Malurus elegans* broods ( $n = 428$ ), modelled as a binomial variable using a logit-link function**

Parameter	Estimate $\pm$ SE	df	$\chi^2$	$P$
Final model				
Intercept	0.15 $\pm$ 0.15	1		
Pairwise $r$ social pair	4.4 $\pm$ 0.77	1	35.4	<0.001
Random effects				
$\sigma^2_{\text{female}}$	2.5			
Rejected terms				
Helper presence <sup>a</sup>	0.40 $\pm$ 0.28	1	1.84	0.17
Habitat type <sup>b</sup>	0.56 $\pm$ 0.59	1	0.84	0.36
Cohort		4	3.3	0.51
Habitat type <sup>b</sup> $\times$ Pairwise $r$ social pair	4.8 $\pm$ 5.9	1	0.4	0.53
Number of neighboring territories	-0.051 $\pm$ 0.092	1	0.25	0.62

Reference categories are <sup>a</sup>helper presence: no = 0, yes = 1; <sup>b</sup>habitat type: hexagonal = 0, linear = 1.

## DISCUSSION

Variation in density of potential mates, which is ultimately determined by habitat connectivity, is one of the classic factors proposed to explain inter- and intraspecific variation in EPP in avian mating systems because it promotes encounter rates and thereby

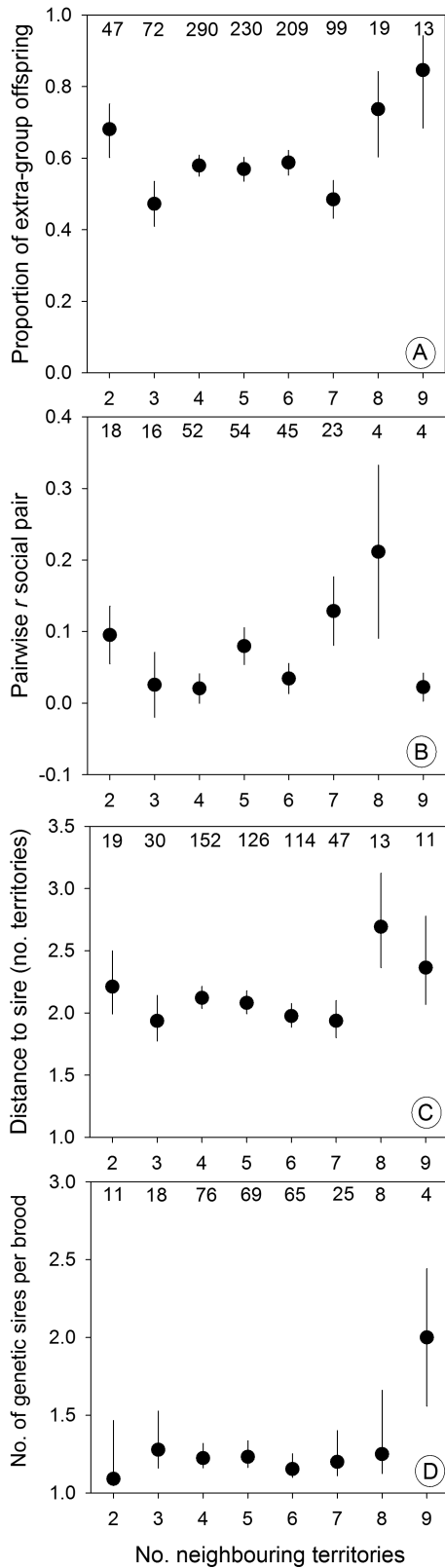
mating opportunities. However, density is often confounded by other ecological factors that might affect EPP in their own way. Here, we tested the role of habitat connectivity on EPP in a species with extreme levels of EGP that usually inhabits hexagonal habitat, but wherein due to habitat fragmentation, birds are also forced to live in narrow linear strips of forest. Furthermore, we tested this in a species from a genus that does not conform to the general pattern of strong phylogenetic inertia in extrapair mating (Arnold and Owens 2002) but instead exhibits striking interspecific variation in levels of EGP that appear to be associated with differences in habitat geometry (Kingma et al. 2009; Cockburn et al. 2013). Our results show that habitat geometry does not limit opportunities for EGP in *M. elegans*. Females from territories in linear habitat did not have lower levels of EGP than females in hexagonal habitat and the number of neighboring territories was not associated with EGP levels. Therefore, our results indicate that variation in density is not a general explanation for variation in EGP.

Despite the enormous attention for the role of ecological factors to explain EPP, only 2 studies have investigated how the alteration of habitat and its accompanying effects on density might affect reproductive strategies. A study on Canada geese (*Branta canadensis*) showed that in anthropogenically modified habitat where densities are extremely high, rates of EPP were higher but not significantly so (Moore et al. 2012). In gray catbirds (*Dumetella carolinensis*), it was found that individuals living in the suburban areas with high population densities, levels of EPP were also higher than in individuals inhabiting parks (Ryder et al. 2012). However, these results could also be due to some other ecological factor (e.g., habitat quality) affecting both density and EPP rate. For example, if food availability is high, males might be able to spend less time on parental care and more time on seeking EPP (Hoi-Leitner et al. 1999). Our study design did not suffer in an obvious way from such confounding effects, as 1) the linear habitat was the result of removal of suitable habitat, 2) both types of habitat had very similar group size, productivity, and territory size, which are often proxies of habitat quality, and 3) birds in both types of habitat were part of a single population with even a few individuals dispersing between the habitat types.

The *Malurus* genus is well known for its extreme infidelity (Cockburn et al. 2013), with 4 of the 5 species tested thus far showing that the majority of females engages in extragroup mating. To explain the absence of high EGP in *M. coronatus*, Kingma et al. (2009) proposed that habitat linearity limits opportunities for EGP. However, this idea is not supported by our findings in the closely related *M. elegans*. At a distance of 2 territories, which is the median distance females travel to gain extrapair paternity in *Malurus cyaneus* and *M. elegans* (Double and Cockburn 2003; Brouwer et al. 2011), 7.6 males were still available as potential extragroup partners in *M. coronatus* (Kingma et al. 2009). Here, we have shown that for *M. elegans* in linear habitat, the number of available males within 2 territories distance is the same ( $2 \times 3.8 = 7.6$ ) but apparently still sufficient to maintain high rates of EGP.

The alternative, but nonmutually exclusive, hypothesis as proposed by Cockburn (2013) suggested that the benefits of EGP for both males and females might be lost in linear habitat. This is because males advertising from beyond immediately neighboring territories can only be accessed by females flying past males on intervening territories, which sharply increases the risk of parasitism to the advertising males and reduces the benefits for the





**Figure 2**  
 The relationship between the number of neighboring territories and (A) the proportion of extragroup offspring, (B) pairwise relatedness of the social pair, (C) distance to the genetic sire of extragroup offspring, and (D) number of genetic sires per brood. Numbers on top indicate sample sizes in terms of no. of offspring (A), no. of social pairs (B), no. of EG offspring (C), and no. of broods (D). Error bars show standard error of the mean.

females. However, observations on *M. cyaneus* showed that most males (>70%) display in neighboring territories (Mulder et al. 1994), suggesting that male display behavior may not necessarily be affected by habitat linearity. Indeed, here, we found that distances females travelled to gain paternity were not higher in linear than in hexagonal habitat. Although female *M. elegans* have been shown to prefer early molting males and do occasionally travel long distances to gain paternity (Brouwer et al. 2011), it is possible that the number of available males in linear habitat has already exceeded a certain threshold (Westneat et al. 1990) and provides females with ample choice.

Our study suggests that habitat geometry does not play a role in EGP in *M. elegans* and thus that there is no evidence for behavioral plasticity in extragroup mating to changing levels of habitat connectivity. Recent findings in *M. coronatus* show that females—despite their generally low levels of EGP—were more likely to gain EGP when 1) mated to a highly related male and 2) when living in high-density areas (Kingma et al. 2013). However, as discussed earlier, density–EPP relationships are difficult to interpret as they could be due to confounding effects. For example, higher reproductive success will result in both high density and the accumulation of closely related individuals, making it hard to separate cause and effect. Nevertheless, we cannot rule out that habitat geometry explains the low levels of EGP in *M. coronatus*. In *M. elegans*, there is still gene flow between linear and hexagonal habitats, which might counteract any selection to reduce EGP. Possibly, this counteracting gene flow results in too low selection pressures to switch from dependence on EGP to genetic monogamy. This raises an interesting point about the difficulties in studying the question whether density and connectivity explain interspecific variation in levels of extra-pair mating in the wild. Basically, we have compared a riparian-like lifestyle in a species that is—and has been for a long time—predominantly a forest specialist. Being confined to riparian habitat—as *M. coronatus* is—possibly could have led to the selective shift to virtual monogamy over many generations. From this perspective, it is important to note that testing the habitat geometry hypothesis in *M. coronatus* itself (which occasionally occurs in wide strips of creek vegetation that allow for neighbors on more than 2 sides; van Doorn 2007) would basically amount to comparing a forest-like lifestyle in a species that is—and has been for a long time—predominantly a riparian specialist, and such a comparison might also not address all factors affecting the habitat-specific selection pressures acting on EGP.

Finally, what may our results mean for the effects of habitat fragmentation on inbreeding risk? Habitat connectivity is expected to affect the movement of individuals and therefore genetic variation. However, there was no evidence that social pairs in linear habitat were more related to each other than pairs in hexagonal habitat. Additionally, there was no evidence that females in linear habitat mated with a larger number of males to compensate for a possible reduction in genetic variation. These findings suggest that either the available extragroup mating is sufficient to maintain genetic variation or that there are other behavioral mechanisms, like increased dispersal distances, that maintain genetic variation in linear habitat. Although these mechanisms require future study, the current results do suggest that habitat fragmentation may not strongly affect inbreeding risk in this species.

**SUPPLEMENTARY MATERIAL**

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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