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Space, density and extra-pair matings have opposing impacts on male and female reproductive success

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Abstract

Many territorial species have a mating system characterized by males establishing home ranges in the breeding grounds prior to females, resulting in males competing for territories and females choosing a mate upon their arrival. It remains unknown, however, how the outcomes of decisions surrounding territory establishment and mate choice are influenced by the spatial configuration of the breeding grounds. We use a spatially explicit, individual-based model to investigate the sex-specific effects of these decisions on reproductive success. In our model, males that arrive earlier obtain higher quality territories and improve their chances for extra-pair copulations. Females can choose their mate to maximize the quality of the male or to attempt to minimize the density of other females near their nesting site to avoid competition. Females therefore face a tradeoff between high-density regions around high-quality males and low-quality males in areas of low competition. Our model predicts a negative correlation between male and female reproductive success under a wide range of conditions when the majority of the territories are on the margins of the breeding area. Most notably, this sexual conflict arises as an edge effect suggesting that fragmentation of breeding habitats could impact the consequences of mate choice in many species with territorial breeding habits.

KEYWORDS

edge effect, habitat fragmentation, migration, sexual conflict, territoriality

1 | INTRODUCTION

The timing of reproduction and the spatial distribution of individuals shape the mating system of many species. This is particularly true in territorial breeders, in which males establish home ranges early in the breeding season and females choose mates following this establishment. This pattern is perhaps best known in migratory birds (e.g., Canal et al. 2012), but is found across animal taxa. For example, in several lizard species, males maintain home ranges that overlap with multiple female home ranges and females can mate with multiple males (e.g., *Anolis* lizards, Kamath and Losos 2017; *Sceloporus undulatus*, Haenel et al. 2003; *Crotaphytus collaris*, Baird et al. 1996, 2001). Such a reproductive pattern is also seen in some mammals such as the collared pika (Zgurski and Hik 2012; *Ochotona collaris*). Usually males arrive first (a phenomenon called protandry) and the factors underlying the evolution of arrival date at breeding grounds have been investigated using evolutionary game theory (Kokko 1999; Kokko and Rankin 2006). When considering individual condition and biotic interactions, the timing of arrival is dependent on the costs of early arrival (Kokko 1999) and the opportunity for males to gain extra-pair copulations (EPCs; Kokko et al. 2006). A more recent model incorporating seasonal factors showed that arrival date strategy is characterized by a balance between the conditions (both abiotic and biotic) facing early and late-arriving individuals, and may depend on the season length, the resource distribution and the timing and pace of improvement of abiotic conditions early in the season (Johansson and Jonzén 2012). These results show that many factors—including individual quality, intraspecific interactions, territory quality and availability, and seasonal conditions—shape selection on reproductive timing and influence reproductive success. However, the way in which reproductive success is influenced by space, a factor that is ubiquitous when considering territoriality and home ranges, remains understudied.

The spatial distribution of individuals on the landscape is clearly important for determining the reproductive success of individuals that establish and reproduce in discrete home ranges or territories. In the context of population growth and expansion, the ability to disperse must balance with the ability to find a mate—if individuals disperse further than from where they can detect a mate, the population will have difficulty expanding (South and Kenward 2001). The distribution of adult males relative to adult females (the adult sex ratio) has long been recognized as an important factor for breeding systems (reviewed in Székely et al. 2014), but the overall distribution of individuals is also important. Density (a way to describe the spatial distribution of individuals) can drastically affect the strength of sexual selection by altering mate encounter rates or the frequency of interacting with competitors (Kokko and Rankin 2006). These spatial considerations may be additionally important for species that live in fragmented landscapes, where large populations have been subdivided into smaller populations. As this previous work demonstrates, incorporating spatially explicit information about territories or home ranges is key to understanding the factors influencing reproductive success. Understanding this critical factor shaping reproductive success is the primary goal of our model.

An important factor arising from the spatial distribution of individuals is the impact of space on EPCs. Typically, extra-pair matings occur beyond an individual's territorial boundaries (e.g., Yezerinac and Weatherhead 1997), and in the vast majority of passerine species, extra-pair mating is a regular occurrence due to individuals' extra-territorial movements (Whitaker and Warkentin 2010). Thus, the spatial distribution of individuals determines who is likely to have the opportunity for EPC and the potential mating partners that are accessible. Further, in bird species breeding within a dense environment, a decrease in the distances between territories is related to higher rates of male encounters and higher likelihoods of engaging in EPC (Ryder et al. 2012). In this way, space influences both the frequency and opportunity for EPC. Both males and females can benefit from EPC (Foerster et al., 2003), although the sexes have different, and potentially conflicting, motivations for pursuing EPC (reviewed in Petrie and Kempenaers 1998). These conflicting motivations can result in sexual conflict over reproductive traits—meaning that fitness in one sex is increased at the detriment of fitness of the other sex—although our understanding of all of the selective pressures has constrained our ability to fully appreciate what causes these conflicts and to understand the outcomes of these conflicts (Petrie and Kempenaers 1998).

Here, we investigate the sex-specific effects of spatial location on reproductive success in territorial breeders. We use a spatially explicit model to characterize the interaction between space and EPC on the sexes and determine the sensitivity of these results to various population and model structures. We find that, in most cases, females choose territories near high-quality males, resulting in higher quality males engaging in more EPC. This results in sexual conflict that is intensified in smaller habitats, where male and female reproductive successes correlate more negatively among mating pairs. This conflict occurs due to males benefiting from EPC and females suffering from competition. Our model extends previous models by explicitly including space and illuminates a previously unappreciated source of potential conflict between males and females. Furthermore, we provide the insight that such sex-specific responses to density occur as a result of an edge effect, underlining the importance of territory size and habitat fragmentation.

2 | METHODS

2.1 | Overview

Our spatially explicit model considers a system with seasonal breeding and a polygynandrous mating system, where each female has a primary mate but will mate with additional males from neighboring territories. At the start of the breeding season, males establish territories sequentially. We consider scenarios in which males arrive in decreasing order of their quality—modeling condition-dependent or honest arrival orders found in many animals (e.g., Harris 2008; Møller et al. 2003)—or in which males arrive randomly with regard to their quality both to test the importance of this assumption and because other studies have failed to support condition-dependent arrival in at least some years (e.g., Mitrus 2007; Ninni et al. 2004). Females then arrive sequentially in order of their quality and choose where to nest. The choice of nesting location is based on the quality of the male in the territory and the number of females in the neighborhood of the territory. We assume that matings occur only once all individuals have arrived. Each individual will mate with every individual of the opposite sex in their home territory and the neighboring territories. Extra-pair matings are determined from the perspective of females, who have a primary mate (the male in their home territory); thus, extra-pair matings are matings that occur with individuals from neighboring territories. Since females have a limiting number of eggs which they can produce, determined by female quality and the density of females in the neighborhood, additional matings do not result in more offspring to the female, but rather result in a brood with multiple sires. We assume that a greater proportion of the offspring were sired by the home-territory male, as opposed to extra-pair matings, which has been observed repeatedly (Blomqvist et al. 2002, 2005; Graves et al. 1992; Wang and Lu 2011). Additionally, we assume that females compete with neighboring females as well as females within the same territory for resources, resulting in suppressed reproductive success (competition can also occur between individuals on neighboring territories; Sillett et al. 2004). The meaning of all model parameters is summarized in Table 1.

TABLE 1 Summary of parameters

Parameter	Meaning
k	Length of side of breeding grounds
$s_{i,j}$	Number of adjacent territories (sides) of territory (i, j)
$\chi_{i,j}$	Choice function for territory (i, j)
q_M	Quality of male
σ_M	*SD* of male quality
q_F	Quality of female
σ_F	*SD* of female quality
$n_{f_{i,j}}$	Population density of females in neighborhood (i, j)
$N_{f_{i,j}}$	Number of female birds in territory (i, j)
$A_{i,j}$	Attractiveness of territory (i, j)
γ	Stochasticity in female territory choice
p_m	Weight of male quality in female decision
p_N	Weight of population density in female decision
$Q_{i,j}$	Realized quality of male in territory (i, j)
$P_{i,j}$	Reproductive potential of a territory for a male
$w_{F_{\beta_{i,j}}}$	The reproductive success of the βth female for each territory (i, j)
$w_{M_{i,j}}$	The reproductive success of male in territory (i, j)

2.2 | Landscape

We model the breeding grounds of a territorial and seasonally breeding species as a $k \times k$ grid, which is an explicit territory structure where each square represents a distinct, non-overlapping territory. Each territory can hold only one male and arbitrarily many females (with a cost to overcrowding). For computational purposes we take into account the nine possible combinations of adjacent territories (sides) in a von Neumann neighborhood (territories that share a side but not a corner) for a $k \times k$ grid. For example, the neighborhood for the top left territory is composed of itself and its right and bottom adjacent territories. We formalize this by defining a choice function χ that indicates whether the sides of a given territory (i, j) exists,

$$\chi_{i,j} = \begin{cases} 1 & 1 \le i \le k, 1 \le j \le k \\ 0 & \text{otherwise.} \end{cases} \tag{1}$$

As stated, for $k > 1$, the top left territory (which we define as (1, 1), following convention) has two neighbors. The choice functions $\chi_{i,\, j-1}$ and $\chi_{i-1,\, j}$ both take value 0, since there are no territories at locations $(i, j - 1)$ and $(i - 1, j)$. However, the choice functions $\chi_{i,\, j+1}$ and $\chi_{i+1,\, j}$ both evaluate to 1, since there are territories at these locations. In this way, when referring to the neighborhood of a territory, the choice function χ allows for the existence of specific sides to be taken into consideration.

The only distinguishing feature of a territory in our model is its number of neighboring territories or sides $s_{i,\, j}$. We can formally define the number of sides each territory has using χ as,

$$s_{i,j} = \chi_{i-1,j} + \chi_{i+1,j} + \chi_{i,j-1} + \chi_{i,j+1}. \tag{2}$$

Sides are important as they determine the availability of EPC (more sides mean more potential partners for EPC), but also result in more neighbors and competitive interactions. See Figure 1 for a diagram showing $s_{i,\, j}$ for a 3×3 grid.

2.3 | Male arrival

We assume all males establish territories within the breeding grounds before any females arrive (Figure 1). Male quality q_M is quantified as a number between 0 and 1, where 1 indicates the highest possible male quality (see Hunt et al. (2004) for definition and discussion of genetic quality). With all other factors equal, males with

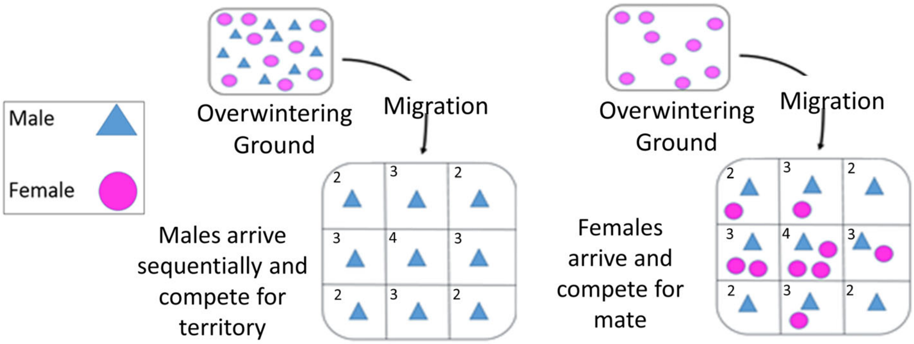

FIGURE 1 Overview of our model. First, males (blue triangles) choose territories attempting to maximize their opportunity for extra-pair copulation. Second, females (pink circles) determine which territory is the most attractive based on their strategy. Small numbers in the top left of each territory (i, j) show its number of sides $s_{i,j}$ [Color figure can be viewed at wileyonlinelibrary.com]

higher quality will have greater reproductive success (see Equation 8). In determining male arrival order, given a $k \times k$ grid, we assume k^2 males will establish territories. The males are modeled by generating their corresponding q_M using a normal distribution with mean of 0.5 and *SD* of σ_M. We assume males choose the unoccupied territory with the greatest number of sides, as this maximizes their opportunities for EPC. Territories that have the same number of sides are filled in random order.

We consider two cases of male arrival order. First, we assume that males arrive in "honest" order of their quality. That is, that the highest quality male arrives first and males then arrive sequentially with decreasing quality. The result is that the highest quality male will always receive a territory with four sides and male quality decreases moving from more central territories to territories along the boundary. We consider this case primarily as honest arrival order has been shown to be adaptive in many cases Kokko (1999).

However, Kokko (1999) also showed that the highest quality males may not evolve to arrive first under all conditions. Thus, we also consider cases where males arrive in random order with respect to their quality to determine the importance of male arrival order to our results. Given random arrival order, there will be no regular spatial pattern of male quality.

2.4 | Female mate choice

Females arrive after all the males have settled at a territory (Figure 1). For most cases, we assumed that the number of females to arrive was the same as the number of males, in other words k^2. However, we also studied sex bias by changing the number of females to be $k^2/2$, $1.5k^2$ and $2k^2$ (rounding up to the nearest integer). Each female has a quality q_F that is drawn from a normal distribution with mean of 0.5 and *SD* of σ_F (here, female quality is the propensity of females to produce viable gametes and is not necessarily genetic). We assume females arrive sequentially in decreasing order of their quality. The territory where a female resides indicates her choice in primary mate, with neighboring males as possible mates for EPCs. Unlike males, more than one female can reside in any given territory, so there may be some territories on which no females reside.

The population density of females in a given neighborhood (i, j) is

$$n_{f_{i,j}} = N_{f_{i,j}} + N_{f_{i-1,j}}\chi_{i-1,j} + N_{f_{i+1,j}}\chi_{i+1,j} + N_{f_{i,j-1}}\chi_{i,j-1} + N_{f_{i,j+1}}\chi_{i,j+1}, \tag{3}$$

where $N_{f_{i,j}}$ is the number of females in a given territory (i, j). Note that since females arrive sequentially, this quantity updates after each female arrival, before reaching its final value.

Females consider the male quality and the surrounding female population density when determining which territory to inhabit. As each female arrives, each territory (i, j) is assigned an attractiveness value $A_{i,j}$ which accounts for the quality of the male occupying the territory, the quality of the male in the territory, $q_{M_{i,j}}$, and the female density in its neighborhood at the time the female arrives, $n_{fi,j}$. Attractiveness is calculated by

$$A_{i,j} = p_m q_{M_{i,j}} + \frac{p_N}{n_{f_{i,j}} + 1}, \tag{4}$$

where p_m and p_N represents the weighting a specific female gives for male quality and female density, respectively, when determining attractiveness. The set of p_m and p_N for a given female thus represents her strategy. Note that the denominator is the population density after the focal individual invades $(n_{f_{i,j}} + 1)$. The attractiveness values of each territory are turned into a distribution of where a female will select nesting in territory (i, j) with probability

$$\frac{A_{i,j}^{\gamma}}{\sum_{i=1}^{k}\sum_{j=1}^{k} A_{i,j}^{\gamma}}. \tag{5}$$

From the distribution of territory selection probabilities, the actual territory to which the female goes is determined stochastically and γ controls the females' propensity to enact their preferences and choose a more attractive territory (larger γ results in less stochasticity in female choice).

2.5 | Determining reproductive success

Female choice influences mating success for males. Males and females have the opportunity for EPC only with their surrounding neighbors. Each mating is assumed to result in higher reproductive success for both males and females with increasing male and female quality. Each individual mating produces fewer offspring as the density around the female increases, due to intraspecific competition. Reproductive success is taken to be relative to a mating in ideal conditions, when male quality and female quality are maximized and females do not have to compete with any neighbors. Thus, all reproductive success values are less than 1, which has the biological interpretation of reproductive success relative to the maximum possible reproductive output of a single mating. We assume that all females successfully mate and that each possible mating that can occur will occur (i.e., opposite sex individuals in each neighborhood always mate), so broods are of mixed paternity. Since females can produce a limited number of eggs (i.e., have a limited gametic investment), we must calculate mating success in a way that does not bias our model in favor of females that partake in more EPC. To do this, we assume that matings will occur most frequently and produce the most offspring between a female and the male residing in the same territory. Conversely, all matings between individuals from adjacent territories are scaled based on the number of neighbors that are available for EPC (i.e., the reproductive outputs from these matings are multiplied by the inverse of the number of sides to the female's territory $\frac{1}{s_{i,j}}$; see Equations 7,8). Thus, a female with four EPC partners will have each of these extra matings scaled by $\frac{1}{4}$ and a female with two EPC partners will have each of these extra matings scaled by $\frac{1}{2}$. Note that this implies that females are advantaged by EPC if, and only if, her partners are of higher quality than her primary mate.

The realized quality of male in territory (i, j) is

$$Q_{i,j} = q_{M_{i,j}}\chi_{i,j}. \tag{6}$$

This is the male's quality in territory (i, j) accounting for its existence. Given this, the reproductive success of the βth female in territory (i, j), denoted $w_{F_{\beta_{i,j}}}$, is

$$w_{F_{\beta_{i,j}}} = \frac{q_{F\beta_{i,j}}}{n_{f_{i,j}}+1}\left(Q_{i,j} + \frac{Q_{i-1,j}+Q_{i+1,j}+Q_{i,j-1}+Q_{i,j+1}}{s_{i,j}}\right), \tag{7}$$

for $1 \le \beta_{i,j} \le N_{f_{i,j}}$. Given Equation (7), accounting for the fact that each territory can contain multiple females and that each territory may not exist, an equation for male reproductive success in territory (i, j), $w_{M_{i,j}}$, is derived as

$$w_{M_{i,j}} = Q_{i,j}\left(P_{i,j} + \frac{P_{i-1,j}}{s_{i-1,j}} + \frac{P_{i+1,j}}{s_{i+1,j}} + \frac{P_{i,j-1}}{s_{i,j-1}} + \frac{P_{i,j+1}}{s_{i,j+1}}\right), \tag{8}$$

where $P_{i,\,j}$ is the reproductive potential of each territory for a male (accounting for its number of females and their quality) calculated as

$$P_{i,j} = \frac{\sum_{\beta=1}^{N_{f_{i,j}}} q_{F_\beta}\chi_{i,j}}{n_{f_{i,j}}+1}. \tag{9}$$

Note that we use $n_{f_{i,j}}+1$ to control density dependence as this allows for weaker competitive effects at low neighborhood sizes, as has been reported empirically (Sillett et al., 2004).

Both $w_{F_{\beta_{i,j}}}$ and $w_{M_{i,j}}$ are reproductive success values prior to rescaling. To give stronger biological meaning, reproductive success is then converted to be relative to the population's mean reproductive success. Henceforth, reproductive success should be taken to mean relative reproductive success.

2.6 | Model analysis

For the initial analysis, all females in the population had the same strategy, which we will refer to as a homogeneous population. This scenario can be considered as analogous to mate choice by sensory drive (Ryan and Rand, 1990) in a population where all females are predisposed to prefer some particular trait value. We simulated female strategies of (p_m, p_N) with (0, 1), (0.25, 0.75), (0.5, 0.5), (0.75, 0.25), and (1, 0) and repeated each simulation 500 times. Heterogeneous populations, in which each female can have different preferences, were simulated by randomly assigning one of the five discrete strategies listed above to each female, with strategies having equal probabilities of being assigned to a given female. These heterogeneous populations result in populations with distributions of female preferences, analogous to populations with preference functions (e.g., Lande 1981). Using the averages from these 500 runs per strategy and the 500 runs from heterogeneous populations, we determined the spatial layout of male reproductive success, male quality, female reproductive success, female quality and female density on our simulated landscape. We repeated all analyses with both random and honest male arrival order.

In the homogeneous population model, we also tested our results for their sensitivity to various assumptions and parameters in the model. For the grid size, we used k equal to 3, 5 and 9 to study how limited space affects reproduction. At these three grid sizes, we calculated density and tested three factors: the type of neighborhood, the variance in male quality and the number of females in the breeding ground (i.e., the sex ratio). The two types of neighborhoods we tested were the von Neumann neighborhood described above and a Moore neighborhood, which counts territories that share a corner as neighbors. We tested four variances in male and female quality (σ_M and σ_F): 0, 0.05, 0.1 and 0.15. We also tested the effect of stochasticity in female territory choice using γ of 0.1, 0.5, 1, 2 and 10. To vary the sex ratio, we also altered the number of females in the breeding ground from $k^2/2$ to $2k^2$ in steps of $k^2/2$ (Supporting information 1). Unless otherwise specified $\gamma = 1$, σ_M, $\sigma_F = 0.05$, there are k^2 females, and males arrive in honest order of their quality. Finally, to determine the extent to which our results were driven by an edge effect resulting from the spatial structure of the model rather than the dynamics of the male and female strategies, we simulated a grid which we wrapped on a torus such that the top row is included in the von Neumann neighborhood of the bottom row, the left-most column is included in the von Neumann neighborhood of the right-most column and so on. In other words, a "wrapped grid" (i.e., a torus) was created so that each territory had exactly four von Neumann neighbors. Although unnatural, such a grid provides the most straightforward way of understanding the effect of the grid's edge on simulations. All simulations and analysis were carried out numerically using Wolfram Mathematica (Wolfram Research, Inc. 2017).

3 | RESULTS

As females choose their nesting territory with more emphasis on male quality (p_m increases and p_N decreases), females become more concentrated in territories with the highest quality males and not as widely distributed. When males arrive in honest order of their quality and females choose their nesting territory considering male quality, this means female density tends to be highest at the center of the breeding ground (Figure 2). Resulting from the distribution of females, the most central males have the highest reproductive success when females choose where to nest based on male quality. Alternatively, when females focus on density, there is less variation across male reproductive success and males along the edge of the grid, who are of lower quality, often have higher reproductive success (Figure 2). These results, as well as all results described below, are qualitatively insensitive to whether a von Neumann neighborhood (neighbors sharing sides) or a Moore neighborhood (neighbors sharing sides and corners) is used (Supporting information 2).

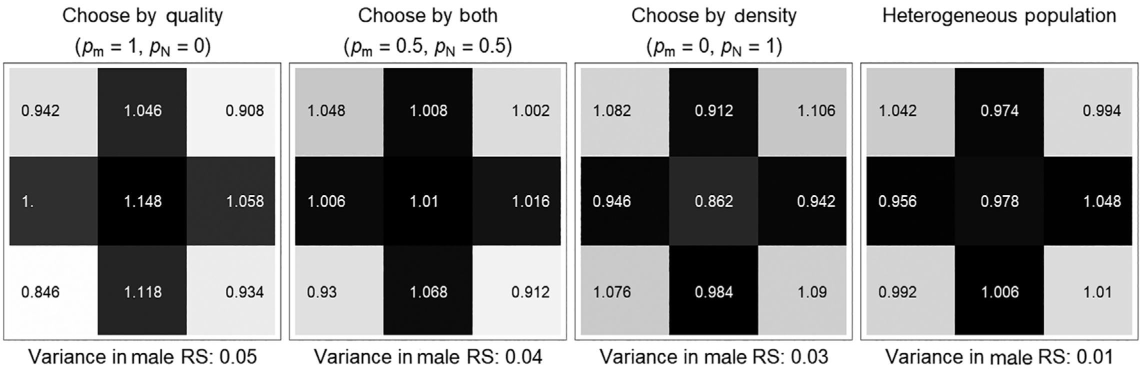

FIGURE 2 The spatial effects of female strategies on male reproductive success and density. Shading represents male reproductive success with darker territories indicating males have higher reproductive success in that territory on average. Notice that the uncertainty in which territory maximizes male reproductive success increases from left to right (multiple territories with the darkest shading along the right). This can also be seen as the variance in male reproductive success decreases moving from left to right due to increased uncertainty in which territory will produce the male with the highest reproductive success. Numbers within each territory is the average number of females in a given territory. Each 3 × 3 grid represents a different strategy, with the labels displayed above. The results presented are averages from 500 simulations with honest male arrival. Parameter values: $\sigma_m = \sigma_f = 0.05$, $\gamma = 1$

3.1 | Opportunity for male EPCs

Female strategy determines whether male arrival location benefits or harms a male's reproductive success. Given honest male arrival order in the homogeneous population, when females care exclusively about male quality, females pursue the higher quality males that occupy the territories with more opportunities for EPC (i.e., the center of territories). Conversely, when females care exclusively about neighborhood density, females choose territories with fewer sides (Figure 2), which have limited opportunities for EPC and therefore are occupied by lower quality males. When females prefer to avoid high density regions as opposed to choosing high-quality males, male reproductive success tends to vary less. For these populations, there is higher uncertainty in the location of the male with the highest reproductive success (seen in the approximately equal shading when females choose based on avoiding density in Figure 2). As with the case in which all females choose territory solely due to female neighborhood density, there is a great deal of uncertainty in which territory maximizes male reproductive success in heterogeneous populations (Figure 2). The location of the male with the greatest opportunity for EPC is therefore not a general result in heterogeneous populations. Interestingly, even with random male arrival order, the clumping of females at regions with high-quality males can produce a negative correlation between male and female reproductive success even without the regular spatial pattern described above.

3.2 | Opposite effects of density on males and females

In our simulations, a negative correlation between male and female reproductive success often emerges due to the opposite effects of increased female density on males and females (e.g., Figure 3, top row). Note that each point represents a female and her primary mate. Since each male need not have a female in his territory, some males are not represented here (but the reproductive success of all males is depicted in Figure 3, middle row). A better understanding of the model dynamics can be gained by looking at the reproductive success of females and males as a function of the number of females in the neighborhood of an individual's home territory. Due to an increase in number of mates resulting from EPC, male reproductive success increases as the number of females in the neighborhood (the number of females which they have access to mate with) increases (Figure 3, middle row). On the other hand, female reproductive success decreases as the number of females in surrounding territories increases due to density dependent reproductive success (Figure 3, bottom row). A benefit to males resulting from multiple matings and negative density dependence in reproduction (both common ecological features; Rodenhouse et al. 2003; Sillett et al. 2004) can lead to opposing fitness effects in males and females. Female-biased sex ratios increase female density and exaggerate this effect (Supporting information 1). These trends are not sensitive to whether a population is homogeneous or heterogeneous.

The magnitude of the negative correlation between male and female fitnesses becomes weaker as grid size increases. This negative correlation is strongest when females choose a territory based on male quality and weakest when females choose a territory based on female density. On a 3 × 3 grid, males and females have opposite fitness consequences regardless of strategy. On a 5 × 5 grid, the negative correlation is still strong when females focus on male quality, but does not occur when females focus on avoiding competition. On a 9 × 9 grid, a negative correlation between male reproductive success and female reproductive success occurs when females focus on male quality, but a positive correlation between male reproductive success and female reproductive success occurs when females focus on female density. Still, of the nine combinations of grid size and strategy shown in Figure 3, most result in a negative relationship between male and female reproductive success. Comparing these grid sizes suggests a trend towards a positive correlation between male and female reproductive success with larger grid sizes, which we indeed observe in a 15 × 15 grid (Supporting information 3).

3.3 | Presence of edge effect

To explore the potential of an edge effect in driving the negative correlation between male and female fitnesses, we modeled a variety of grid conformations beyond the square grids of sizes 3 × 3, 5 × 5 and 9 × 9. Removing edge territories entirely, by wrapping the grid on a torus, resulted in the less negative—and often positive—correlation coefficients between male and female reproductive success, regardless of grid size (Figures 4, 5). These results demonstrate that large negative correlations in reproductive success is exacerbated by an edge effect and does not simply result from the dynamics of the male and female strategies. Further, this provides an explanation as to why the negative correlation is weakened with increasing grid size. In larger grids, exponentially more territories are centralized, rendering the edge less important. The fact that there is still a grid size effect with the wrapped grid can be understood because the boundary condition which we use here does not fully remove the influence of the small population.

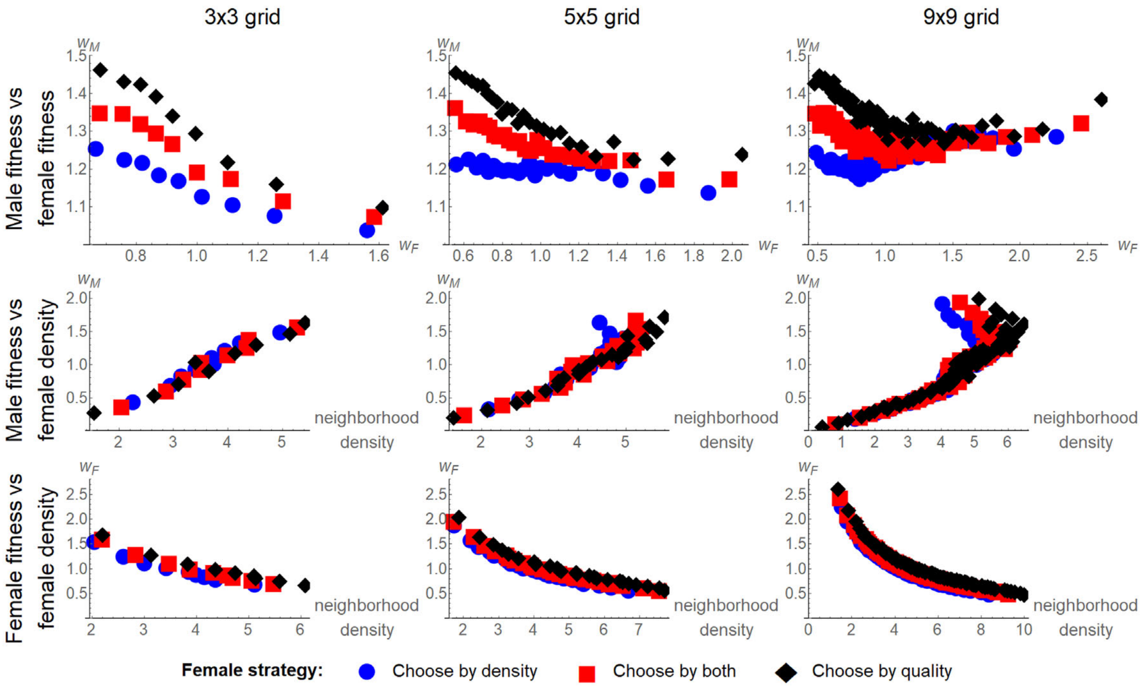

FIGURE 3 When the density of females around a territory is high, females have low reproductive success but males have high reproductive success. The first column shows 500 simulations from 3 × 3 grids. The second column is from 5 × 5 grids and the third column is from 9 × 9 grids. The first row plots male reproductive success w_M on the y-axis and female reproductive success w_F on the x-axis. Each point represents a female paired with her primary mate, thus if a male does not have any females nesting in his territory, his reproductive success will not appear in the first row and a single male can be factored in multiple times for a given simulation. The second row plots male reproductive success on the y-axis and the density of females within the male's home neighborhood on the x-axis. The third row plots female reproductive success on the y-axis and the density of females within the female's home neighborhood on the x-axis. In all panels, different colors and shapes correspond to the means of simulations with different female strategies (as indicated by the legend) with error bars representing *SE*s present when larger than the plotted data point. Females from each simulation were sorted by their reproductive success, then the average is computed over all of the females with the same reproductive success rank (i.e., the female with the highest reproductive success, the female with the second highest reproductive success, etc.) in a given simulation and their primary mate. Parameter values: $\sigma_m = \sigma_f = 0.05$, $\gamma = 1$. Strategy parameters: choose by quality ($p_m = 1$, $p_N = 0$), choose by both ($p_m = p_N = 0.5$), choose by density ($p_m = 0$, $p_N = 1$) [Color figure can be viewed at wileyonlinelibrary.com]

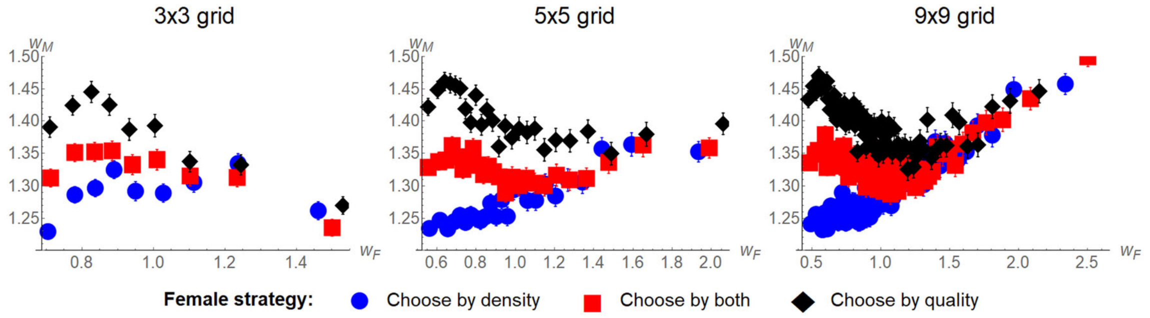

FIGURE 4 Male and female fitnesses are more similar when there is no edge to the grid. Again, the figure shows male reproductive success w_M on the y-axis and female reproductive success w_F on the x-axis for three grid sizes (3 × 3, 5 × 5 and 9 × 9), but wrapped on a torus (territories on the borders of the grid were treated as each others' neighbors), eliminating edge effects. Different markers indicate different female strategies as shown in the legend. The correlation coefficients of these lines are shown in Figure 5 for clearer comparison with the unwrapped grids. Parameter values: $\sigma_m = \sigma_f = 0.05$, $\gamma = 1$. Strategy parameters: choose by quality ($p_m = 1$, $p_N = 0$), choose by both ($p_m = p_N = 0.5$), choose by density ($p_m = 0$, $p_N = 1$) [Color figure can be viewed at wileyonlinelibrary.com]

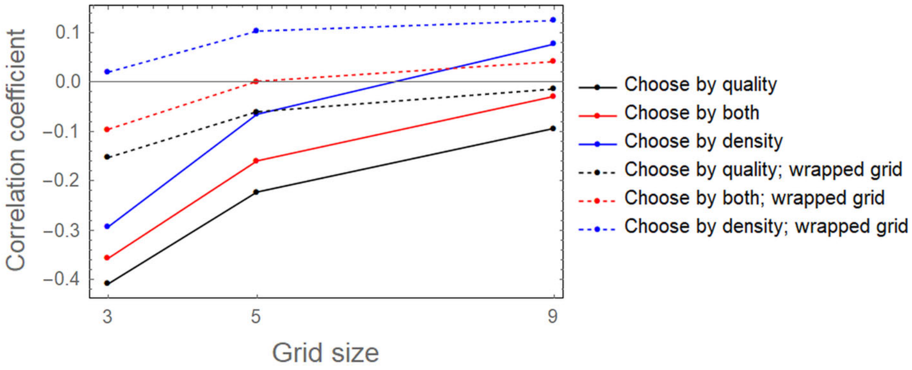

FIGURE 5 The relationships in Figure 4 can be summarized by the correlation coefficients between male and female reproductive success, and allows a clear comparison between the grids with edges and the torus (dashed lines). Clearly, wrapping the grid on a torus reduces the negative correlation between w_M and w_F. Parameter values: $\sigma_m = \sigma_f = 0.05$, $\gamma = 1$. Strategy parameters: choose by quality ($p_m = 1$, $p_N = 0$), choose by both ($p_m = p_N = 0.5$), choose by density ($p_m = 0$, $p_N = 1$) [Color figure can be viewed at wileyonlinelibrary.com]

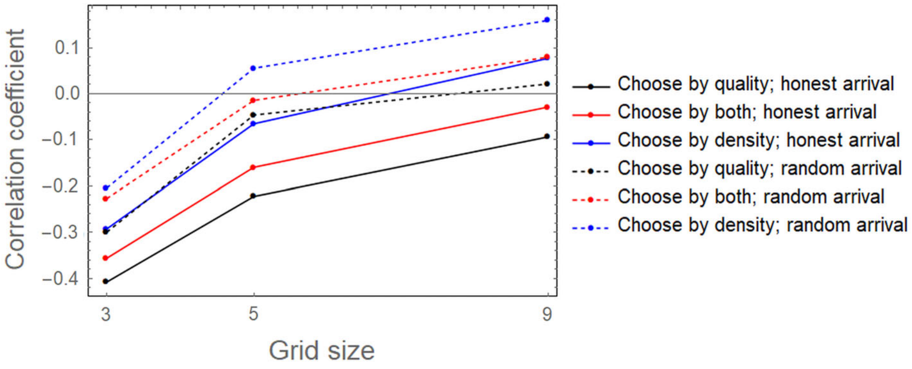

FIGURE 6 Plot shows correlation coefficient between male and female reproductive success at a range of grid sizes for both honest and random arrival. Dotted lines show random male arrival with solid lines from the original analyses also plotted for comparison. Random arrival results in less pronounced or no negative correlations between male and female reproductive success. Parameter values: $\sigma_m = \sigma_f = 0.05$, $\gamma = 1$. Strategy parameters: choose by quality ($p_m = 1$, $p_N = 0$), choose by both ($p_m = p_N = 0.5$), choose by density ($p_m = 0$, $p_N = 1$) [Color figure can be viewed at wileyonlinelibrary.com]

3.4 | Effect of male arrival order

The analyses described above assumed that males arrived in honest order of their quality. We explored the same scenarios when males arrived randomly with respect to their quality to determine the importance of male arrival order in our model. We find that when males arrive in random order, the negative correlation between male and female reproductive success is weaker than when males arrive in honest order (Figure 6). Nevertheless, in small populations and when females choose their territory by male quality, a negative relationship between male and female reproductive success can still be found even with random male arrival. This result shows that the existence of explicit spatial structure is enough to lead to sex-specific fitness effects even without the presence of a regular and predictable pattern in this spatial structure.

3.5 | Influence of stochasticity and interactions with female strategy

Interestingly, the effect of stochasticity in female territory choice interacts strongly with female strategy. When females choose their territory solely based on male quality, less stochasticity exacerbates a negative relationship between male and female reproductive success (Figure 7). This is because females more reliably choose the highest quality males and the density in the highest quality territories becomes higher. With other female strategies, however, less stochasticity in female choice results more similarity in male and female fitness outcomes (Figure 7). In these cases, females are more reliably choosing to avoid high density and are better able to spread themselves around the breeding ground.

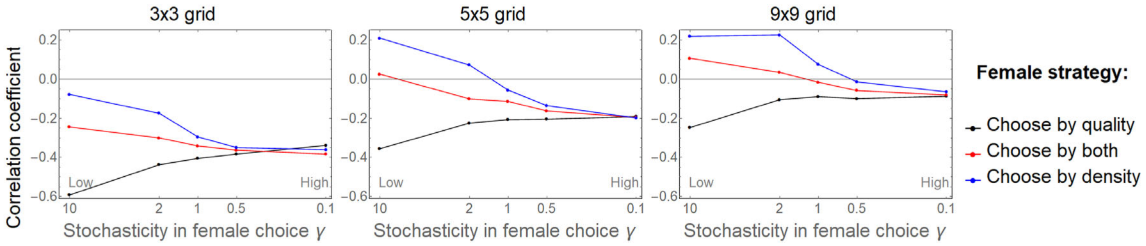

FIGURE 7 Plots show correlation coefficients between male and female reproductive success at a range of stochasticities in female territory choice. Note that larger γ corresponds to less stochasticity in female territory choice. Different panels show different grid sizes. When females choose territories primarily based on male quality, less stochasticity in their choice increases makes the correlation coefficient more negative. Otherwise, less stochasticity in female choice reduces the negative relationship between male and female fitnesses. Parameter values: $\sigma_m = \sigma_f = 0.05$. Strategy parameters: choose by quality ($p_m = 1$, $p_N = 0$), choose by both ($p_m = p_N = 0.5$) and choose by density ($p_m = 0$, $p_N = 1$) [Color figure can be viewed at wileyonlinelibrary.com]

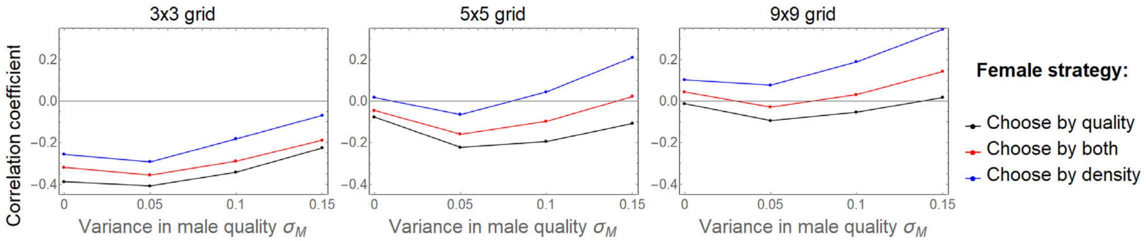

FIGURE 8 Plots show correlation coefficients between male and female reproductive success at a range of variances in male quality. Different panels show different grid sizes. High variance in male quality overwhelms the effects of density, reducing the negative correlation between w_M and w_F. Parameter values: $\sigma_f = 0.05$, $\gamma = 1$. Strategy parameters: choose by quality ($p_m = 1$, $p_N = 0$), choose by both ($p_m = p_N = 0.5$), choose by density ($p_m = 0$, $p_N = 1$) [Color figure can be viewed at wileyonlinelibrary.com]

3.6 | Influence of variation in individual quality

Increasing the variation in male quality (σ_M) weakens the negative correlation in reproductive success (Figure 8), because when variance in male quality is high, the difference between the gains from the highest-quality male and the lowest-quality male in the population are larger than the costs of high density. Although the highest-quality males are often in the territories with the highest densities of females, so females would be expected to suffer a cost of density, the trade-off for females between a high-quality male and density disappears when the highest-quality males provide such better gains than the low-quality males. Therefore, when variance in male quality is sufficiently high, the negative correlations between male and female reproductive success are reduced or disappear. When there is no variation in male quality, there is less of a contrast in male and female reproductive success in the population than when there is a low amount of variation (e.g., $\sigma_M = 0.05$) in male quality (Figure 8). The effect of variation in female quality result in similar outcomes and can be found in Supporting information 4.

4 | DISCUSSION

By incorporating the effect of space on the reproductive success of a territorial breeder, we found a negative correlation between male and female reproductive success. This negative correlation can be considered to be a form of sexual conflict over reproductive success as a result of spatial clustering. Previous theoretical results have suggested that sexual conflict should intensify with increased population sizes and high population densities (Gavrilets 2000; Kokko et al. 2006), and empirical work has revealed trade-offs between male and female fitnesses at high densities (Smith 2005), but our results suggest that even if the overall population density remains the same, if the number of connected territories on a fine spatial scale are small, sexual conflict may emerge.

Sexual conflict emerged from our model as a result of considering the effects of space on territorial breeders, which is a major advancement on previous related studies (see Kokko 1999; Kokko et al. 2006). Sexual conflict over reproductive success emerges due to differential effects of female density on males (positive effects) and females (negative effects). When most territories are edges, females must choose between territories containing high-quality males and the cost of high female density or territories with low-quality male and low densities of females. This creates a negative relationship between male reproductive success (which is exacerbated by high female density; Supporting information 1) and female reproductive success (which is reduced by high female densities; Supporting information 1). The negative relationship is enhanced when many territories have edges, the female territory choices are determined more by male quality than density, and the sex ratios are female-biased. Removing the effects of edges relaxes this trade-off—even when females make decisions based on male quality—by allowing high-quality males to avoid concentrating in the center territories. Therefore, females no longer require the density refuges provided by edges, removing the sexual conflict.

Stochasticity, which we modeled in several ways, influenced when sexual conflict arose. One way we incorporated stochasticity was by randomly generating female strategies in heterogeneous populations (where individuals differed in their strategies) and comparing these results to those from homogeneous populations (where all individuals had the same strategy). Since we generated female strategies randomly in heterogeneous populations, they experienced an additional source of stochasticity. Heterogenetity in female strategy caused the location of the male with highest reproductive success to be unpredictable (Figure 2), but did not remove sexual conflict because females who chose territories based on male quality continued to cluster around high-quality males. We also allowed arrival order to be random, which resulted in weaker sexual conflict, although conflict still existed in small populations where females preferred male quality (Figure 6). It is worth noting that the mechanism behind this effect is similar to why wrapping the grid on a torus reduces sexual conflict. Additionally, we incorporated a stochasticity parameter that mediated the extent to which females could act on their preferences. This stochasticity parameter greatly impacted the sexual conflict outcomes—high stochasticity in female choice removed sexual conflict when females chose territories based on male quality, but increased sexual conflict with other female strategies (Figure 7). These results highlight the importance of stochasticity in determining fitness outcomes, particularly in small populations, a factor that is critical to incorporate into evolutionary models (Uyeda et al., 2009). Indeed, patterns of reproductive success of gopher frogs *Rana sevosa* in small populations (approximately 100 individuals) appear to be mainly stochastic (Richter et al., 2003). Our model suggests that randomness may in fact generate sexual conflict, and potentially alter the selective landscape, depending on the mate choice mechanisms in these populations.

Another important factor shaping the strength of sexual conflict in our model is the variance in individual quality. Increasing the variance in male quality (Figure 8) and female quality (Supporting information 4) ameliorates the negative effects of high female densities, even in small grids. Large variance in male quality reduces sexual conflict because high-quality males confer such a large fitness benefit to females that the costs of density are offset by male quality, especially when comparing the reproductive success of females mated with high-quality males to the reproductive success of females mated with low-quality males. Because populations with lower variance in heritable traits are less robust to phenotypic disturbance (Houle 1992), our model suggests that sexual conflict emerges when populations are most vulnerable—with low evolvability and in habitats with many edges or exaggerated clustering of individuals (i.e., when populations are in highly fragmented territories).

Sexual conflict often results in a coevolutionary arms race between the sexes over evolutionary timescales (Gavrilets 2000; Gavrilets et al. 2001), but because our model focuses on a single generation we were not able to capture how the territory preferences of the sexes might evolve over time. We also do not allow individuals to exhibit a preference for edges versus interior parts of the grid for the qualities of those sites per se (as opposed to for the opportunities for EPC), which could happen in real populations when edge habitats are inherently of lower or higher quality (e.g., Anderson et al. 2003; Bowman 2003; Buchanan and Catchpole 1997; Candolin 2003; Harris and Reed 2002; Horváth et al. 2000). An extension of our model to incorporate multiple generations would provide insight into the evolution of female strategies and is necessary to generate evolutionary predictions. Nevertheless, simply by incorporating space, we show that density dependence and mate choice can lead to sexual conflict over a broad range of conditions. This message stands regardless of our model being a single generation. Future evolutionary studies would determine when we should expect this result to be evolutionarily stable. For instance, many generations with high variance in individual quality could increase the synchrony of breeding (Knowlton 1979), or could impact the dynamics of sexual selection. Particularly if generations were to overlap, it is possible that the optimal female strategies may change over time, as has been demonstrated theoretically for cryptic female choice (Jones 2002), or sex-specific habitat preferences could evolve (e.g., Hillen et al. 2011).

The observed sexual conflict might be driven in part by how we modeled EPC. We considered that all males viewed the opportunity for EPC as a benefit. However, each EPC that a male gains is a loss of paternity for another male. Therefore, although males residing in territories with many neighbors have more possible females to mate with, they also have more males attempting to steal paternity from them—so in the real world both the number of potential mates and potential competitors could impact male strategy (Wong and Candolin 2005) and therefore sexual conflict. That being said, we observed sexual conflict even when males arrived in a random order, and we reduce the effect of competitors by assuming that the territory-holding male obtains a majority of the offspring from the females in his own territory (note in Equation 8 that the reproductive success derived from the male's own territory is not weighted by its number of sides). Furthermore, our model does not incorporate any mechanisms for EPC, which in real systems could impact individual strategies. For example, a good genes model would allow females paired with low-quality males to seek more EPC than females paired with high-quality males (reviewed in Petrie and Kempenaers 1998), whereas in our model the rates of EPC are constant. Our constant-rate EPC model is more analogous to a situation where EPC is sought to avoid the costs of mate loss, where a population might have high search costs associated with finding a primary mate, and/or a system where forced copulations are frequent (for a review of EPC mechanisms see Petrie and Kempenaers 1998). Future work could explicitly incorporate different EPC mechanisms to identify how mechanisms affect when sexual conflict emerges.

We considered male territory choice to be only related to the potential for EPC, but territory choice in real-world systems is likely determined by additional aspects of the other individuals in the area and the intrinsic qualities of his territory such as food availability and nesting habitats or refuges (Candolin 2003; Bowman 2003; Buchanan and Catchpole 1997; Flanagan and Bevier 2014; Nagy and Holmes 2004). Our results apply whenever territory quality is random with respect to spatial location and males seek EPCs. Of course, territories on the margins of the breeding grounds could be of lower intrinsic quality than central territories (other than opportunity for EPC), such as when smaller clutches are produced in edge territories (e.g., Suarez et al. 1997) or offspring have reduced survival or growth in edge territories (e.g., Flaspohler et al. 2001; Harris and Reed 2002; Huhta et al. 1999; Leighton et al. 2008; Ries and Fagan 2003; Suarez et al. 1997). This is only likely to exacerbate sexual conflict, however. On the other hand, there are potential benefits of edges, such as higher abundance of food (e.g., Horváth et al. 2000), fewer predators (e.g., Harris and Reed 2002), or increased habitat complexity (e.g., Anderson et al. 2003; Horváth et al. 2000), which we do not include in our model. Furthermore, the quality of individuals is likely condition-dependent, in contrast to how we modeled male quality as a fixed trait (analogous to a "good genes" model). For example, overwintering grounds can impact male and female quality, impacting male arrival dates and female mate choice (Drake et al. 2014; Norris 2005; Reudink et al. 2009). Future models could explore the impact of mate or territory choice on suites of traits on the emergence of sexual conflict due to edge effects, leading to insights for species with different mate choice strategies.

For computational reasons, our model has been restricted to small populations, containing only 18 (3 × 3 grid), 50 (5 × 5 grid), 162 (9 × 9 grid) or 225 (15 × 15 grid) individuals. Although these population numbers are small, they are not entirely unrealistic, particularly for species that are threatened. For example, the hihi (*Notiomysts cincta*) is an endangered New Zealand bird with few breeding adults, who form breeding pairs but commonly have EPCs (Castro et al., 2004). Similarly, the endangered Brazilian Jabiru stork (*Jabiru mycteria*) has a socially monogamous mating system with EPCs (males and females build nests together) and small effective population sizes (approximately 35 reproductively active adults) (Lopes et al., 2013). Beyond birds, lizards such as chuckwallas (*Sauromalus obesus*) often maintain home ranges, and can have population sizes around 100 individuals (Kwiatkowski and Sullivan, 2002). Males generally have non-overlapping territories, but female home ranges may overlap the ranges of males and other females, though it is unknown whether matings with males in non-overlapping home ranges occurs. The model could also be extrapolated to consider pack animals and consider packs as analogous to territories in our model with extra-pack copulations being equivalent to EPCs. In this case, our model could be relevant to the Ethiopian wolf, a population of which has approximately 100 interacting adults with female dispersal and mating with extra-pack members (Sillero-Zubiri et al., 1996). These threatened animals are not alone in that they form small breeding colonies (i.e., collared pika, Franken and Hik, 2004; western gull [*Larus occidentalis wymani*], Harper 1971; fieldfare [*Turdus pilaris*], Wiklund and Andersson 1994; and other colonial bird species, Brown et al., 1990). Importantly, it is in small populations when we would expect the effect of stochasticity to be greatest. Stochasticity in female territory choice is expected to be mediated by how well females are able to obtain information on male quality and female density. As such, our results might have implications for the evolution of male signaling (Holzer et al., 2003; Zahavi, 1975).

Indeed, the emergence of sexual conflict as a consequence of habitat edges has important implications for conservation. Habitat fragmentation of breeding grounds is a critical concern for many species because it eliminates overall breeding ground area and creates more edges (Murcia 1995; Wilcove et al. 1986), and can result in widespread population declines (Donovan and Flather 2002). Given the potentially detrimental ecological consequences of sexual conflict (Galliard et al., 2005; Rankin and Kokko, 2006; Rankin et al., 2011), our model suggests that this could become an additional potentially negative impact of habitat fragmentation. Alternatively, habitat fragmentation may alter sexual conflict in other ways; for instance, in livebearing fishes in the genus *Gambusia*, habitat fragmentation resulted in reduced predation and decreased salinity, factors which reduced the strength of sexual conflict (Heinen-Kay et al. 2014). Regardless, incorporating mating dynamics into predictions regarding species' responses to habitat fragmentation will be key for accurately capturing all of the evolutionary forces shaping species distributions.

In conclusion, we find that spatial clustering due to edge effects can lead to sexual conflict over reproductive success in a model of territorial breeders. This new result only emerges because we explicitly incorporated space into territoriality. Our results could have implications for populations of territorially breeding species that are experiencing habitat fragmentation. Empirical work on the interaction between habitat fragmentation and the effects of density on reproductive success would provide more insight regarding the conservation of territorial breeders such as songbirds. Relaxing the assumptions of our model, such as no female choice of EPC partners, will also improve our understanding of how space and mate choice interact to produce differential reproductive success. Our work highlights the tight interplay between space and territoriality, which has remained surprisingly understudied in theoretical models, and provides a specific example (sexual conflict) of how this interplay can manifest itself in a species' ecology.

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