Original Article

Siring success in kangaroos: size matters for those in the right place at the right time

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In polygynous species, male reproductive success is predicted to be monopolized by a few dominant males. This prediction is often not supported, suggesting that ecological and alternative mating tactics influence siring success. The spatiotemporal distribution of individuals and the number of males competing for each receptive female are often overlooked because they are difficult to monitor in wild animals. We examined how spatial overlap of female–male pairs, the time spent by a male on the breeding site, number of competitors, and morphological traits influence siring probability in eastern gray kangaroos (*Macropus giganteus*). We compared home range overlap for 12 208 dam–male pairs and 295 known dam–sire pairs to define local competitive groups and to estimate every male's opportunity to sire the young of each female. We compared models considering morphological traits relative to the entire population or to local competitive groups. Including local competition improved model performance because it estimated the intensity of competition and compared each male's morphological traits to those of its competitive group. Regardless of size, males can increase their probability to sire a young by increasing their *mating opportunity* relative to the mother. We underline the importance of considering spatial structure to assess the intensity of competition in species where males cannot equally access all females in a population. The estimation of mating opportunity and intensity of local competition improves our understanding of how morphological traits affect siring success when each mating event involves a different set of competing males, a characteristic of most wild species.

Lay Summary: In polygynous species, large males have higher mating success but, to mate with a given female, they also need to be in the right place at the right time. In kangaroos, males do not share space with all females in a population. Thus, a male can increase his reproductive success by increasing the overlap between his home range and that of a female, regardless of body size and condition.

Key words: kangaroo, local competition, mating opportunity, sexual selection, siring success, spatial overlap.

INTRODUCTION

"I been in the right place, but it must have been the wrong time" from the "Right Place, Wrong Time" (1973) song by Dr. John

Sexual selection shapes the evolution of secondary sexual traits (Andersson 1994). Selection on male traits, when variability in those traits exists, should be stronger in polygynous systems where a few males can monopolize paternities (Andersson 1994). Those systems often involve conspicuous male-biased sexual dimorphism (Soulsbury et al. 2014). The relationship between the intensity of competition for mates and strength of sexual selection, however, is complex (Clutton-Brock 2007). Several studies of mating systems thought to be highly polygynous have reported weak mating skew in mammals (Cerchio

et al. 2005; Newbolt et al. 2017), birds (Riehl 2012; Sousa and Westneat 2013), amphibians (Mangold et al. 2015), and fishes (Garant et al. 2001). Furthermore, male morphological and behavioral traits often explain little variation in reproductive success (Vanpé et al. 2010; Olsson et al. 2019), suggesting that other factors are also important (Emlen and Oring 1977; Ims 1988; Cornwallis and Uller 2010).

Several ecological and demographic factors influence the opportunity for sexual selection (Emlen and Oring 1977; Cornwallis and Uller 2010). For instance, Ims (1988) showed how the potential for sexual selection varies with the spatiotemporal distribution of receptive females: synchronous receptivity reduces mating skew irrespective of female spatial distribution. When reproduction is asynchronous, however, the potential for sexual selection is higher if females are uniformly distributed. The number of males competing for receptive females at a given time and place (operational sex ratio) (Emlen and Oring 1977) has also been regarded as an important determinant of the opportunity for sexual selection

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(Emlen and Oring 1977; Clutton-Brock and Parker 1992; but see Shuster 2009). The density of competitors can increase the strength of sexual selection (Kokko and Rankin 2006) and change between years (Martin et al. 2016) or within a year (Kasumovic et al. 2008). Resource dispersion influences the distribution of females, and males are expected to distribute themselves in relation to females (Emlen and Oring 1977). Nonrandom spatial distribution of males with respect to traits affecting reproductive success could generate local differences in the strength of male–male competition.

Most studies of sexual selection assume that all males in a population have equal access to all females (e.g., Vanpé et al. 2010): males compete for receptive females, and females can sample all males (Andersson and Simmons 2006). In many species, however, males have limited home ranges and, thus, only compete with a fraction of other males for access to nearby females. In these cases, siring success is likely based on a *best-of-n* order, where *n* represents the males competing for each female (Janetos 1980). In this case, if dominant males are spatially clumped in areas with many females, subordinate males may reproduce in areas of low female density, potentially moderating the total strength of sexual selection. The number of competitors (*n*) also affects the perceived strength of sexual selection at the population level: the more the males sampled by a female, the stronger the correlation between male traits and mating success (Benton and Evans 1998).

In many species, it is difficult to define local competitive groups (McDonald et al. 2013). Selection will operate within each group, where individuals compete for matings or are sampled by females (Schlicht et al. 2015). Therefore, information on social interactions and space use is critical in the definition of these groups. Recently developed sexual networks use social interactions to measure sexual selection in structured populations (McDonald et al. 2013; Muniz et al. 2017). With these methods, there is no need to define local competitive groups a priori (McDonald et al. 2013). Sexual networks have been used to investigate mating tactics (Oh and Badyaev 2010; Muniz et al. 2015), to assess the effect of environmental heterogeneity on precopulatory and postcopulatory competition (Cramer et al. 2017; Wey and Kelly 2019), and to compare precopulatory and postcopulatory competition (Fisher et al. 2016). An alternative method, based on space use by individuals, allows consideration of the effects of both individual and pairwise predictor variables on mating success (Schlicht et al. 2015), such as distance or overlap between two individuals, time spent together, or the number of males competing for a given female. Both approaches, however, have received little attention in studies of sexual selection in mammals.

Here, we investigated how ecological parameters (spatial overlap between potential mates and time spent on the breeding site by males), intensity of competition (the number of males competing for the same female), and morphological characteristics influence the probability that each male eastern gray kangaroo (*Macropus giganteus*, Shaw 1790) has to sire the young of a specific female. We used information on individual space use to characterize male *mating opportunity*, defined as the opportunity a male has to mate with a specific female based on their encounter probability, and *effective competition*, the number of males competing for access to that female. We sought to compare traits of males actually competing for each female, instead of using a global approach pooling all males of the population in one competitive group (*global competition*). The rationale behind estimating mating opportunity is that a male must be present to ascertain when a female is ready to mate and, all else being equal, his chances should increase with his spatial overlap

with the female. We fitted spatially explicit individual-based models (Schlicht et al. 2015) and compared their performance in predicting the siring probability of individual males.

Eastern gray kangaroos are nonterritorial and polygynous (Jarman 1983). Because estrous females mate with multiple males (Montana L, personal observations), however, the mating system is polygynandrous. Kangaroos are sexually dimorphic (Jarman 1989), with the largest males almost four times heavier than primiparous females. Semicaptive populations reveal a positive relationship between male size and dominance rank, with the largest male siring the majority of offspring (Miller et al. 2010). Males compete for females in contests, sometimes escalating fights with lethal consequences (Toni 2018). Selection should, thus, favor large body size for males, which enhances their performance in intrasexual competition and mate guarding (Jarman 1983). The contribution of female mate choice in selecting large males is unclear. However, despite the strong sexual dimorphism, long breeding season, and stable male dominance hierarchy, Rioux-Paquette et al. (2015) found that mating skew in eastern gray kangaroos was low and similar to that of some monomorphic polygynous or monogamous species. This surprising result suggested that traits linked with dominance, such as size and mass, are not the only determinants of reproductive success. Kangaroos are ideal to compare methods to define local competitive groups because they exhibit fission–fusion dynamics (Jarman and Coulson 1989) and competitive groups are not obvious. Moreover, our study system offers a rare opportunity to test the performance of spatially explicit models to identify drivers of male reproductive success.

To explain the probability of siring, we compared population-wise (global) models, which consider absolute male traits, with models considering male traits relative to local competitive groups. We predicted that spatiotemporal parameters and competition intensity would improve model accuracy regardless of morphological traits. We also predicted that models considering male mating opportunity and effective competition would perform better than global models where all males were assumed to have equal access and, thus, equal opportunity to mate with all females. Furthermore, we expected that a model that considered mating opportunity and effective competition by weighing a male's contribution to the competitive pool would be more precise and, thus, favored to one that just used a spatial threshold to define which males were part of a local competitive group. Finally, we expected large males in good condition to have the highest chances to mate with a female, especially if they widely overlapped her home range. We also expected that the number of competitors would reduce a male's chances to mate with a female by either increasing the chances that other males would thwart his mating attempts (Hogg 1984) or through sperm competition (Møller and Birkhead 1989).

METHODS

Study species

Eastern gray kangaroos are large, common marsupial grazers that feed in open-membership groups (Jarman 1987). They are sexually dimorphic and, like most Macropodidae, have indeterminate skeletal growth (Karkach 2006). Sexual maturity is at about 18 months for females and at least 42.5 months for males (Poole and Catling 1974). Kangaroos may mate throughout the year (Poole 1983) but, in our study area, most matings occur between November and January (MacKay et al. 2018). Females produce one young per reproductive event (Eldridge and Coulson 2015). During autumn

and winter (March–August), most females are philopatric and sedentary (King, Garant, et al. 2015), whereas most males move away from the "breeding site" (Coulson et al. 2014). Because of the long breeding season, estruses are asynchronous (Supplementary Figure S1); thus, males usually do not face a strong trade-off between guarding a female and searching for new females.

Field work and study population

We monitored kangaroos at the Wilsons Promontory National Park (38°56'S, 146°17'E), Victoria, Australia. The study site is a 1.1 km² shrub-encroached grassland around an emergency landing strip. Kangaroos on the site are habituated to observers and easily identified. Monitoring started in 2008 (Gélin et al. 2013), and kangaroo density has varied from approximately 2–7/ha (Glass et al. 2015). Since the start of the study, 1160 individuals have been identified.

Adult kangaroos were immobilized by injection of Zoletil (King et al. 2011) and marked using unique combinations of Allflex colored ear tags and collars (Gélin et al. 2013). Every year, about 90% of marked individuals were recaptured. At each capture, we measured hind leg length (hereafter, referred to as leg length) to the nearest millimeter, as a proxy for skeletal size, and mass to the closest 250 g. Leg length and mass were used to estimate body condition through the relative condition index (K_n; Peig and Green 2010), the ratio of observed individual mass (M_i) and its predicted mass ($M_p = a L_i^b$). The values of the coefficients a and b for predicted mass correspond to the intercept and slope of an ordinary least-square regression of log mass on log leg length (Le Cren 1951). K_n was estimated separately every year, and varied from 0.875 to 1.076 (standard deviation [SD] = 0.024). This index was independent of skeletal size (see Supplementary Appendix II for choice of condition index). We attempted to capture males as soon as they arrived on the study site in September and October. There was no effect of capture date on body condition (Supplementary Figure S2). For pouch young ($n = 295$), we measured hind leg, hind foot, and head length to estimate the date of birth according to Poole et al. (1982). MacKay et al. (2018) showed that this formula accurately estimates birthdates in the population. Poole (1975) estimated that gestation in eastern gray kangaroos lasts 36.4 ± 1.6 days, so conception dates were obtained by subtracting 36 days from the estimated birth date. Ear tissue samples were collected either using a 2-mm biopsy punch or by collecting tissue displaced by ear tags. Samples were stored in 95% ethanol and refrigerated at 4 °C until molecular analyses (see below).

Here, we used data collected from 2010 to 2018, including eight breeding seasons and, thus, eight cohorts. Because less than 2% of births occur in June–September, we identified a cohort as kangaroos born from 1 August one year to 31 July the following year. In 2010–2012, data were collected year-round but, in later years, fieldwork was conducted from late July or early August to mid-December or late January (Supplementary Table S1). Analyses presented here include 295 young born to marked dams caught between 2011 and 2018, representing multiple captures of 151 unique dams (Supplementary Table S2). Only males measured between mid-July and early January were included in analyses ($n = 332$ captures of 146 males; Supplementary Table S2). Median estimated conception date for breeding seasons 2010–2017 was 26 November (yearly range: 21 November–18 December). Fieldwork overlapped annually with 68–75% of conceptions (Supplementary Figure S1; Supplementary Table S1). During fieldwork, we surveyed the study site each morning and evening using binoculars to identify marked kangaroos. Individual locations ($n = 88\ 933$) were recorded from a distance of approximately 15–50 m using a hand-held Global Positioning System unit (GPSmap 62s, Garmin, Olathe, KS). The central point of each group, defined using the 10-m chain rule (King et al. 2017), was used to represent the location of all group members.

Molecular analyses

DNA was extracted as described in Chambers and Garant (2010). The quality and quantity of genomic DNA extracted was verified on 1% agarose gel. We diluted all samples to a final concentration of 5 ng/μL. Each sample was amplified using polymerase chain reaction (PCR, using GeneAmp PCR System 9700 thermocyclers, Applied Biosystem, Foster City, CA) at nine microsatellite loci as reported in King, Garant, et al. (2015). We analyzed microsatellites in two multiplexes where we added 0.15 μL of dye size standard (GeneScan™ 600 LIZ® Size Standard, Applied Biosystem), 8.35 μL of Hi-Di™ Formamide (Applied Biosystem), and 1.5 μL of multiplexed PCR products. Quantities for every locus for each multiplex are in King, Garant, et al. (2015). The amplified products were analyzed in an AB 3130xl DNA sequencer (Applied Biosystem) and fragment lengths were analyzed using GENEMAPPER version 4.1 (Applied Biosystem).

Paternity assignment

Mother–offspring pairs were established by field observations and subsequently confirmed by genetic analyses (King, Forsyth, et al. 2015). Information about maternity was used to identify sires with a likelihood-based approach in CERVUS v. 3.0 (Kalinowski et al. 2007). Paternities were confirmed using the decisional chart in Supplementary Figure S6. Individuals genotyped at less than eight loci were excluded. As in previous studies, we assumed a conservative proportion of mistyped loci of 0.02 (see Rioux-Paquette et al. (2015) for example). Only paternities assigned with 95% confidence were used for analyses. Assignments were performed separately each year because the proportion of adult males sampled and the list of candidate sires varied among years (Supplementary Table S3). Each year, we estimated the proportion of males sampled by comparing the number of marked males to the sum of marked and estimated unmarked males. Candidate sires were those alive near the conception date of the young and at least 42.5 months old at the start of the breeding season (Poole and Catling 1974). We attempted to mark all males regardless of size, and at least 80% of males in the population were marked each year (Supplementary Table S3). Therefore, paternities by unmarked males are unlikely to bias our results. Additional details about the selection of candidate sires are in Supplementary Appendix III.

Spatial and temporal parameters

Home range overlap analysis

Locations from mid-July to late January were used to estimate yearly home ranges (median = 63 locations/individual/year, range = 15–154). Given the limited size of the study site and the presence of at least two observers at most surveys, individuals were seen often enough to estimate their home ranges. For example, resident females were seen on average 20 times per month. We estimated 95% home ranges and their utilization distribution (UD; van Winkle 1975) using fixed-kernel density estimators (Worton 1989) with the adehabitatHR package (Calenge 2006) in R 3.6.2 (R Core Team 2019). UDs are a useful measure of how individuals

use space within their home range because they use a density function to define how areas inside the home range are used. We estimated the UD using grid = 500 and extent parameter = 0.5. The smoothing parameters for each individual were determined by least-square cross validation. To avoid temporal autocorrelation (Swihart and Slade 1985; Noonan et al. 2019), we retained only one location per individual per survey. Individuals with fewer than 15 locations per season were excluded from analyses (Supplementary Appendix IV). Because neither home range size nor body size was normally distributed, we used Spearman's rank correlation to test if larger males had larger home ranges. We estimated the overlap between UDs of every possible dam–male combination within each breeding season using the utilization distribution overlap index (hereafter, referred to as "overlap index") at 95% contour in adehabitatHR (yearly average = 1526 pairs, range = 980–2214, n global = 12 208). This overlap index measures space sharing (Fieberg and Kochanny 2005) and considers jointly the UD of two individuals to quantify overlap, ranging from 0 (no overlap) to >1 (Fieberg and Kochanny 2005). An overlap index of 1.0 describes the perfect overlap of two home ranges when both individuals uniformly use space within their home ranges (uniform UDs). When the overlap index is higher than 1.0, the UDs are nonuniform in a similar way, increasing the opportunity that two individuals will share space (Fieberg and Kochanny 2005).

Temporal variable

We estimated the proportion of time spent by a male on the study site by dividing the number of days an individual was seen by the number of days the field crew conducted surveys between 15 September and 14 December, when 68–73% of young are conceived. Males marked after mid-December were excluded from these analyses.

Mating opportunity, effective competition, and spatial phenotypic structure

Individual mating opportunity ($m_{i,j}$) measured the opportunity of a male i to mate with a specific female j based on the overlap between their home ranges. In the global approach, all males of a population are considered as equal potential mates of all females and vice-versa, and they have $m_{i,j} = 1$ with all females. The distributions of all dam–male pairs (n = 12 208) and those of 295 known dam–sire pairs (Figure 1) were different, suggesting an important role of spatial overlap in male mating opportunity. For this reason, we developed two additional approaches to estimate mating opportunity. In the first "local" approach, mating opportunity was based on a threshold. All males overlapping the home range of a female by an overlap index ≥0.163, which comprised 95% of all dam–sire pairs (Figure 1), had $m_{i,j} = 1$, others had $m_{i,j} = 0$. In the second "weighted" approach, we considered that mating opportunity is related to how the spatial overlap between a male and a focal female affects the likelihood of siring her young. To estimate a male's mating opportunity with each female, we first built density histograms (sum of bins area = 1.0) of the overlap index for all pairs and for parental pairs only (Figure 1). We, then, calculated the ratio of densities of parental pairs over all pairs for each bin. We, then, fitted a function between the ratio of densities and the overlap index weighted for the total number of pairs in each bin (Figure 2). Details on model fitting are in Supplementary Appendix V. Mating opportunity was, thus, proportional to the function built using the ratio between the two distributions. We obtained male mating opportunity by rescaling the values predicted by the curve

for each dam–sire pair to a maximum value of 1 by dividing all values by the maximum value predicted by the curve (2.371; upper red dashed line in Figure 2). Thus, with the weighted approach, $m_{i,j}$ ranged from 0.046 to 1.

As mating opportunity differed depending on the approach used, competition also varied. The global approach assumes that all marked males compete for access to all females, each male had $m_{i,j} = 1.0$, and competition is simply the number of males in a breeding season (global competition). When a spatial overlap threshold defined which males could mate with a female, we defined local competitive groups a priori by including all males with an overlap index ≥0.163 (all males above this threshold with $m_{i,j} = 1.0$) in the effective competition for each female (local approach). With the weighted approach, effective competition was the sum of $m_{i,j}$ estimated with function in Figure 2.

We used correlograms to assess if males displayed spatial phenotypic structure (Valcu and Kempenaers 2010). We built correlograms for each morphometric trait each year using as locations the centroid of each male's home range (Supplementary Appendix VI). All calculations were performed using R 3.6.2 (R Core Team 2019).

Statistical analyses

We used generalized linear mixed-effect models (GLMMs) with a binomial error structure to estimate the probability that each male–dam pair within a breeding season would produce an offspring because kangaroo females are monotocous. Analyses included only young whose sire was assigned. Because each possible dam–male combination was treated as an independent data point (Schlicht et al. 2015), the same males and females contributed to multiple data: on average, dams were repeated 41.5 times and males 36.5 times for each breeding season. Also, on average, females participated in 1.93 breeding seasons and males in 2.27. For this reason,
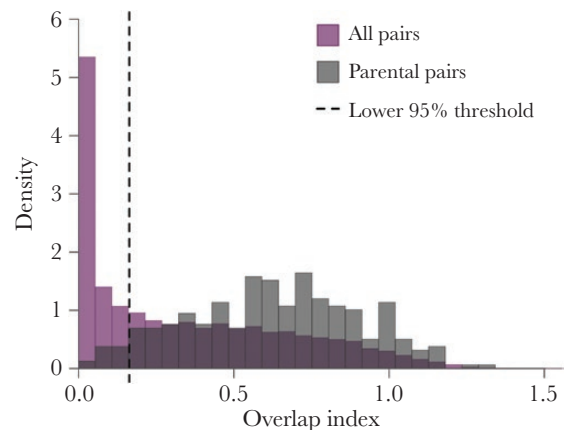

Figure 1

Spatial overlap of dam–male pairs of eastern gray kangaroos, breeding seasons 2010–2017, Wilsons Promontory National Park, Victoria, Australia. Overlap was estimated for each breeding season by the utilization distribution overlap index (Fieberg and Kochanny 2005). The purple histogram represents the distribution of overlap of all 12 208 potential dam–male pairs (i.e., potential mating partners). The gray histogram is the distribution of overlap of 295 parental pairs. To directly compare the shape of these two distributions with different sample sizes, histograms represent the probability densities, and each histogram has a total area of one. The vertical dashed black line at overlap index = 0.163 is the lower 95% threshold used to define local competition groups using the local approach.
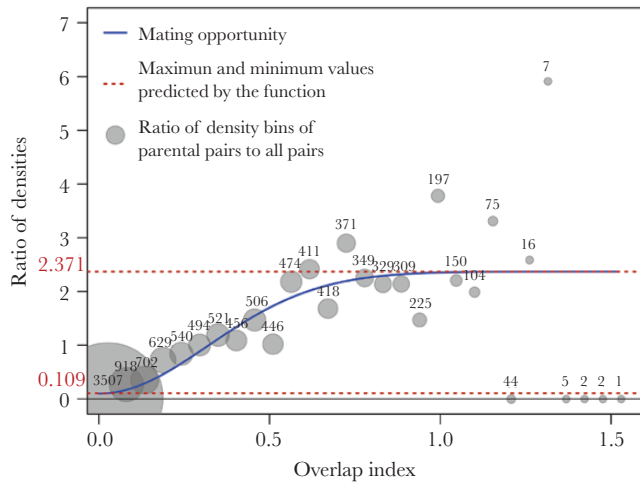
Figure 2
The function used to estimate the mating opportunity of each male using spatial overlap between eastern gray kangaroo dam–male pairs according to the overlap index. The gray circles are the ratios of probability densities of realized over potential mating partners in Figure 1 (gray and purple bins, respectively). Their size represents the number of pairs in each histogram bin, also indicated above every point. These numbers were used as weights to fit the function. The blue curve is the function used to fit these points, which represents the (unscaled) mating opportunity. The lower and upper red dotted lines are the maximum and minimum values used to define male mating opportunity in relation to a given female.

"dam ID" and "male ID" were included as random effects. We also used "year" as a random effect, because environmental conditions and the number of young produced each year differed. All variables were standardized. More specifically, competition was standardized across years for the global approach and within each breeding season for the local and weighted approaches. Similarly, standardization of morphological traits differed depending on the approach used because effective competitors and m_{ij} of each male in the effective competition were estimated differently in the three approaches. Thus, we could compare a male's traits to those of his actual competitors for the local and weighted approaches. Standardization procedures are summarized in Table 1, with details in Supplementary Appendix V.

We fitted two models using the global approach, one using the local approach and one using the weighted approach (Table 1; Supplementary Table S3). The first global model (*Classic*) included as explanatory variables only male size and body condition, testing the hypothesis that morphological traits affect the probability that a male will sire a young, regardless of spatiotemporal overlap and competition intensity. The other global model (*Population*), along with the same morphological parameters, also included spatial (overlap index), temporal (% time on breeding site), and competitive (global competition) variables, but all males in the population were considered to have the same mating opportunity (see above) for each young. The *Threshold* and *Weight* models included the same variables included in the Population model, but morphological parameters were compared within effective competitive groups. We used a natural cubic spline, with 3 degrees of freedom, to model how overlap index affected siring probability because a linear model led to unrealistically high probability values at high overlap index. Those high predicted probabilities could have been produced by the concentrations of observations at low overlap values (Figure 1), leading

to a greater influence on the shape of the predicted curve. Being more flexible, a spline better represents the predicted probabilities across the range of overlap values. None of the variables showed multicollinearity (maximum generalized variation inflation factor [VIF] value = 1.210). Models were fitted using the "glmmTMB" function of the "glmmTMB" package (Brooks et al. 2017). Finally, we compared models by corrected Akaike information criterion (AICc) using the "MuMIn" package (Bartoń 2019). We estimated marginal and conditional R^2 following Nakagawa et al. (2017). All calculations were performed using R 3.6.2 (R Core Team 2019).

RESULTS

Spatial and temporal parameters

We estimated 624 home ranges (female years = 292, male years = 332), and the data set included 12 208 dam–male pairs years for a yearly average of 1526 dam–male pairs over eight breeding seasons. Males showed a weak positive correlation of body and home range size (r_s = 0.183, n = 332, P < 0.001). The overlap index, which measures space sharing and, thus, the opportunity that two individuals will meet, ranged from 0.000 to 1.557 (median = 0.249). Only 3.8% of dam–male pairs had an overlap index >1, suggesting that a male can rarely keep one female always in sight while in their home range, thus leaving mating opportunity to other males. The proportion of time males spent on the breeding site during the peak of the breeding season ranged from 0 to 0.894 (median = 0.556).

Mating opportunity, effective competition, and spatial phenotypic structure

At the global level, the global competition faced by each male varied from 35 to 45 males (median = 42.0), whereas effective competition ($\sum m_{ij}$) varied from 5 to 39 males (median = 24.0) and from 3.52 to 31.11 (median = 18.08) when estimated by either the local or weighted approach, respectively. Numbers of competitors were strongly correlated between the local and weighted approaches (r = 0.877, 95% confidence interval [CI] = 0.873–0.881).

Correlograms suggested no spatial autocorrelation in male size (Supplementary Figure S8). This finding and the strong correlation among morphological measures at the population and local competition level suggested no size-based spatial structure of males.

Standardized estimates of both leg length and body condition obtained by different approaches were all strongly correlated ($r_{leg length}$ average = 0.953, 95% $CI_{leg length}$ range = 0.928–0.987; $r_{body condition}$ average = 0.974, 95% $CI_{body condition}$ range = 0.961–0.994).

Model comparison

Models including morphological parameters, spatial overlap, the proportion of time spent on the study site, and competition intensity explained at least twice as much variance as the Classic model with only morphological parameters (Table 2). The Weight model was superior according to model selection, although its marginal R^2 was similar to those from the Threshold and Population models (Table 2). The effects of morphological (leg length and body condition) and spatiotemporal (spatial overlap and proportion of time spent on the study site) parameters were similar in Population, Threshold, and Weight models (Figure 3; Supplementary Table S4). Competition had no effect in the Population model, but the number of competitors reduced siring success in both Threshold and Weight models (Figure 3).

Table 1

Variables included in models to explain variation in siring success in eastern gray kangaroos

Variable	Variable class	Definition of raw variable	Centering and standardization			
			Classic	Population	Threshold	Weight
Body size	Morphological	Tibia length (mm) of the focal ♂	Centered and standardized using traits of all ♂ of the population	Centered and standardized using traits of all ♂ of the population	Centered and standardized with respect to the ♂ included in the effective competition	Centered and standardized using the weighted mean and SD. Mean and SD were weighted using the m_{ij}[b] estimated through the function used in the weighted approach (Figure 2).
Body condition	Morphological	Relative condition index of the focal ♂	Centered and standardized using traits of all ♂ of the population	Centered and standardized using traits of all ♂ of the population	Centered and standardized with respect to the ♂ included in the effective competition	Centered and standardized using the weighted mean and SD. Mean and SD were weighted using the m_{ij}[b] estimated through the function used in the weighted approach (Figure 2).
Overlap index	Ecological	Home range overlap between ♀ and ♂ pair	NA	Not standardized	Not standardized	Not standardized
Proportion of time spent on the study site	Ecological	Ratio between no. of days ♂ was on breeding site and no. days the field crew made surveys between 15 September and 14 December	NA	Not standardized	Not standardized	Not standardized
Global and effective competition	Competitive	No. of ♂ competing for access to one reproductive ♀[a]	NA	No. of ♂ competing for access to one reproductive ♀. Standardized and centered pooling all breeding seasons together (*global*)	Standardized and centered using the mean effective competition within each breeding season (*effective*)	Standardized and centered using the mean effective competition within each breeding season (*effective*)

[a]Competition was estimated in three different ways depending on the model approach. Global competition for the Population model (global approach) included all marked males in the population each breeding season. For the Threshold model (local approach), effective competition included only males that overlapped a focal reproductive female by overlap index ≥0.163. Finally, effective competition of the weighted approach was the sum of all weighted mating opportunities ($\sum m_{ij}$) of males for a reproductive female.
[b]Mating opportunity.

Determinants of siring success: Weight model

Morphological, spatiotemporal, and competitive variables in the Weight model had significant effects on the probability of siring a young. All were positive except for the effective competition (Figure 3; Table 3). Body size had a stronger effect than body condition on siring probability. Body size could increase the probability of siring the young of a female by up to 10% for some of the largest males within a competitive group (leg length ≈ 680 mm; Figure 3), whereas good body condition increased siring probabilities by at most 4% (Figure 3). High values of overlap index (overlap index ≈ 1.5) increased siring probabilities by up to 4.4%. However, the effect of spatial overlap reached an asymptote at overlap index ≈1, which already granted a 4% chance to sire the young of a female (Figure 3). An increase in overlap index had a similar effect on all males, regardless of their size. For example, a large male (75th percentile leg length ≈ 630–640 mm) with an average overlap index had a higher probability to father a female's young (2.8% chances) compared with medium-sized (50th percentile leg length ≈ 600–615 mm; 1.5% chance) or

small (25th percentile leg length ≈ 565–580 mm; 0.6% chance) males (Figure 4a,b). Likewise, males of different sizes equally improved their siring chances by spending more time on the study site. For example, increasing the proportion of time spent on the study site from 0.4 to 0.8 doubled their chance to sire a young (Figure 4c,d). This temporal variable had a weaker effect than spatial overlap, both at moderate and high competition intensity (Figure 4). Finally, for any given overlap index between a male–dam pair, males had about 60% more chances of siring a young when they faced moderate (25th percentile effective competition ≈ 14.5) compared with intense (75th percentile effective competition ≈ 19.4) competition (Figure 4a,b).

DISCUSSION

We used information on space, time, and density of competitors to accurately define the effective competitive environment for each reproductive female. We then used spatially explicit individual-based models to show that individual siring success was more accurately

Table 2

Candidate generalized linear mixed models to quantify the effects of morphological, spatiotemporal, and competitive parameters on the probability of siring the young of a focal female for eastern gray kangaroo males, Wilsons Promontory National Park (Australia), 2010–2017. K is the number of estimated parameters in the model, ΔAIC_c measures the difference in AICc between each model and the model with the lowest AICc value, and w_i is the Akaike weight. Marginal R^2 represents the variance explained by fixed effects, whereas conditional R^2 sums the variance explained by both fixed and random effects.

Model	K	ΔAIC_c	w_i	Marginal R^2	Conditional R^2
Weight	11	0.00	0.994	0.535	0.572
Threshold	11	10.10	0.006	0.534	0.573
Population	11	28.64	<0.0001	0.530	0.574
Classic	6	296.93	<0.0001	0.221	0.315
Null	4	390.95	<0.0001	0.000	0.252
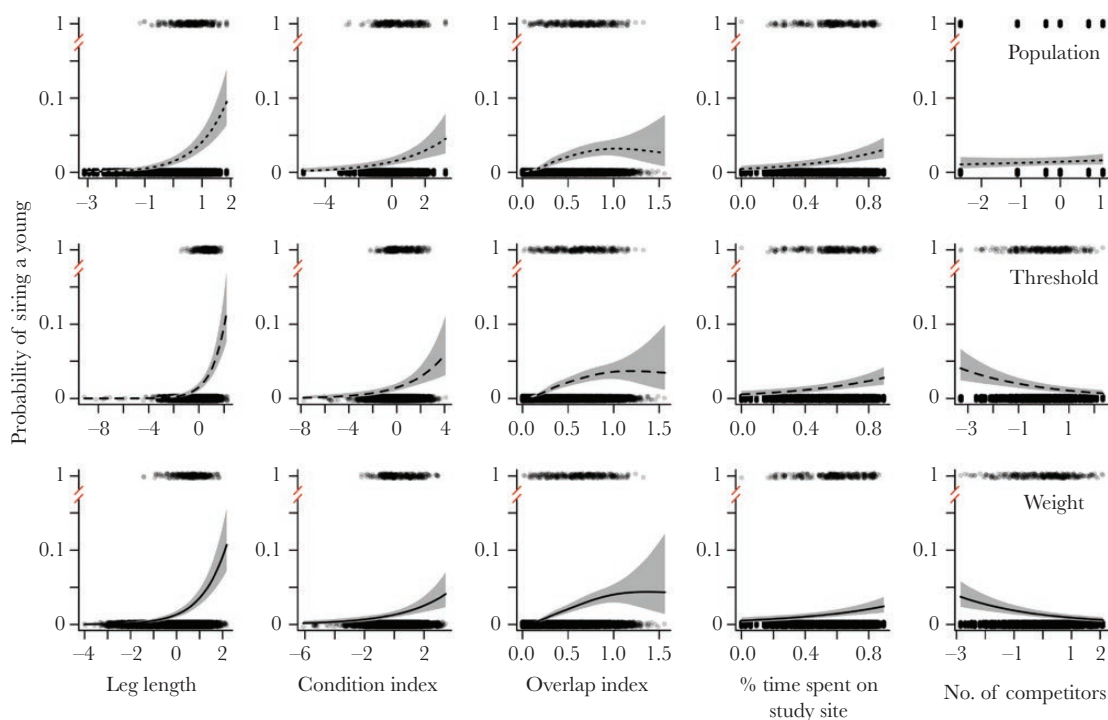
Figure 3

Effects of leg length, body condition, overlap index, residency, and number of competitors in the Population (upper row), Threshold (middle row), and Weight (lower row) models to estimate the probability of siring young with a focal female for eastern gray kangaroo males, Wilsons Promontory National Park. Leg length, body condition, and number of competitors were standardized as specified in the "Statistical analyses" section of Methods, Table 1, and Supplementary Appendix V.

characterized when we integrated individual mating opportunities, which accounted for how males contributed to different competitive pools. Spatial overlap with the dam, proportion of time spent on the study site, leg length, and body condition increased siring probability, whereas the intensity of competition reduced it. Our results, thus, underline the importance of spatiotemporal and competitive factors as drivers of male reproductive success. They also emphasize how males, regardless of body size and condition, can improve their mating opportunity with a given female by being at the right place at the right time.

Research on sexual selection has highlighted the role of temporal and spatial parameters (Ims 1988). The potential for sexual selection increases with asynchrony of estruses. When females breed synchronously, even highly competitive males may be unable to monopolize them (Say et al. 2001). Similarly, when females

are distributed uniformly in space, males with larger home ranges have access to more females, increasing their mating opportunities (Fisher and Lara 1999; Vanpé et al. 2009). To our knowledge, however, no previous study examined the role of spatiotemporal overlap on mating opportunities in polygynandrous species. Regardless of size, we found that a male doubled his probability of siring a female's young by increasing his overlap index from 0.5 to 1. Similarly, studies of ecological factors influencing extrapair mating patterns in birds found that a male's probability of siring extrapair young decreased with breeding distance (Schlicht et al. 2015; Kaiser et al. 2017). We also found that, to a lesser extent, males could improve their siring probability by spending more time on the breeding site. In polygynous species that form discrete breeding groups, all males have access to all reproductive females (Hogg and Forbes 1997; Mainguy et al. 2009) but. in species with

Table 3

Parameter estimates (β) and associated standard errors (SEs) of the Weight model to quantify the importance of ecological, competitive, and morphological parameters on the probability of siring a young with a focal female for eastern gray kangaroo males, Wilsons Promontory National Park (Australia)

Parameter	β	SE	95% CI Lower	Upper
Intercept	−8.523	0.525	−9.552	−7.494
Leg length[a]	1.000	0.109	0.786	1.214
Body condition[a]	0.337	0.080	0.181	0.494
Spline(overlap,1)	3.593	0.409	2.792	4.394
Spline(overlap,2)	6.894	0.978	4.977	8.811
Spline(overlap,3)	3.172	0.594	2.009	4.336
% time spent on study site	1.756	0.446	0.882	2.631
Effective competition	−0.374	0.071	−0.514	−0.235

[a]Morphological traits were standardized weighing the contribution of males within each competitive pool (Table 1).
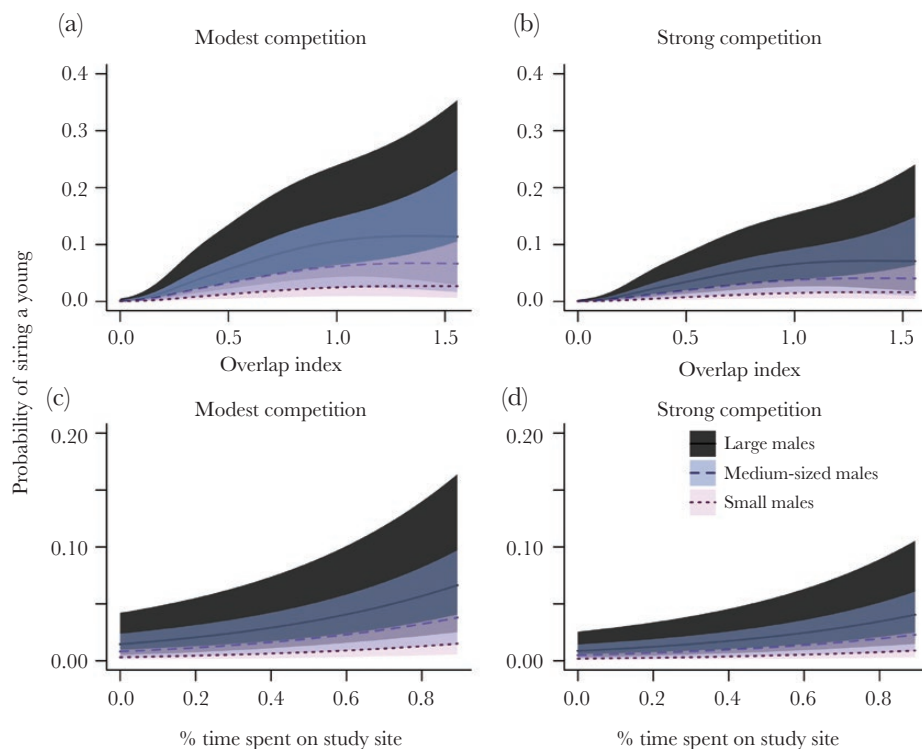
Figure 4
Predicted effects of spatial overlap and residency on the probability of siring a young for males of different sizes ("small"—25th percentile leg length: ≈ 565—580 mm; "medium" —50th percentile: ≈ 600—615 mm; "large"—75th percentile: ≈ 630—640 mm) when (a, c) competing with few (25th percentile number of competitors: ≈ 14.5) or (b, d) many (75th percentile number of competitors: ≈ 19.4) competitors according to the Weight model.

dynamic social structures, as in kangaroos, males only compete for a subset of females in the population. Thus, the knowledge of the whereabouts of individual dams and males was important to detect a positive effect of overlap on siring probability and an indispensable tool to identify local competitive pools.

Accurate measurement of the intensity of competition has been largely overlooked in wild mammals, mostly, because it requires substantial monitoring of individuals during the breeding season. Competitive groups in our population included a median of 15 males, more than twice as many as reported by Miller et al. (2010) in three semicaptive populations. Kangaroo competitive groups were also larger than the average number of males sampled by females in other species, about 4 individuals for 10 vertebrate and 3

invertebrate studies (Benton and Evans 1998). When competition is strong, variation in male reproductive success should increase as dominant males monopolize paternities (Emlen and Oring 1977; but see Kokko et al. 2012). Here, however, we found that increasing the intensity of competition reduced siring success by all males, regardless of phenotype. Facing strong competition, a dominant male may be unable to prevent all mating attempts by other males (Hogg 1984). Also, in a polygynandrous system, sperm competition decreases the probability of siring each young (Møller and Birkhead 1989).

The probability of males siring a young was better explained by models that accounted for the contribution of males to different competition pools and that included morphological,

spatiotemporal, and competitive parameters. The assessment of male mating opportunity compared a male's phenotype to that of actual competitors (local/weighted approaches vs. global approach). The similarity in the variance explained by the Weight and Threshold models, however, suggests that, in this population, how local competition was assessed and, thus, how a male's phenotype was compared with that of his competitors made little difference. We also expected that the effect of body size and condition on the probability of siring a young would differ between the global, local, and weighted approaches. Instead, morphological traits had similar explanatory power in all models, suggesting that there was no male phenotypic spatial structure in the study population. Male spatial distribution is normally determined by the distribution of females (Ims 1988), and lack of spatial clumping by females could explain why there was no obvious male spatial phenotypic structure (Emlen and Oring 1977). Alternatively, Benton and Evans (1998) suggested that the correlation between a male trait and its fitness approaches an upper asymptote when more than 10 males compete for a female. In kangaroos, effective competition estimated with either local or weighted approaches exceeded 10 individuals, possibly explaining why the trait–fitness relationships were similar using different approaches. Weighing morphological traits according to male mating opportunity should be more important for species where monitored males show nonhomogeneous spatial structures (McDonald et al. 2013; Muniz et al. 2017).

CONCLUSION

Research on the determinants of male reproductive success has traditionally focused on the effects of morphology and behavior (Andersson and Simmons 2006). Only recently, studies have examined how the socioecological environment affects sexual selection (Muniz et al. 2015; Fisher et al. 2016; Kaiser et al. 2017; Wey and Kelly 2019). We highlighted the importance of spatial and temporal overlap with breeding females as ecological predictors on siring probability in kangaroos. Our results are relevant for other polygynandrous or polygynous species with dynamic social structure and help explain how small males obtain some paternities by increasing their mating opportunity with individual females. Spatial and temporal parameters, such as those examined here, could also potentially decrease mating skew, even when breeding is asynchronous (Ims 1988). This could occur if the space occupied by a male and the time spent in a breeding ground were independent of traits that improve competitive abilities. In our study system, for example, body size had little influence on male home range size or on the proportion of time spent on the breeding site during the breeding season. Future studies of sexual selection and male reproductive success should consider spatial overlap to weigh the contribution of each male to effective competition and the actual extent of a competitive group and to test for spatial phenotypic structure rather than use a traditional population-wide approach to estimate sexual selection (Benton and Evans 1998; McDonald et al. 2013). Finally, it would be interesting to estimate the average number of competitors in multiple polygynous mammalian species because current knowledge is mostly restricted to birds and arthropods (Benton and Evans 1998; Muniz et al. 2015; Wey and Kelly 2019).

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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