

Article

Refuge size variation and potential for sperm competition in Wellington tree weta

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Abstract

Ecological variation in resources can influence the distribution and encounter rates of potential mates and competitors and, consequently, the opportunity for sexual selection. Factors that influence the likelihood that females mate multiply could also affect the potential for sperm competition. In Wellington tree weta (*Hemideina crassidens*, plural “weta”), the size of tree cavities (called galleries) used as refuges affects weta distribution and thus the opportunity for sexual selection and selection on male weaponry size. We examined the predicted effects of gallery size and male weaponry size on the potential for sperm competition. We asked if gallery size influenced the potential for multiple mating by females and potential for sperm competition, if male weaponry size was associated with relative expected sperm competition intensity (SCI), and if estimated male mating success was correlated with potential SCI. To quantify relative competitive environments of males, we created and analyzed networks of potential competitors based on which males could have mated with the same females. We found that small galleries had higher potential for female multiple mating and higher potential for sperm competition. Size of male weaponry was not associated with expected relative SCI. Regardless of gallery size, males with more potential mates were expected to face lower expected relative sperm competition. Thus, in this system, variation in the size of available refuges is likely to influence the potential for sperm competition, in a way that we might expect to increase variation in overall reproductive success.

Key words: ecological variation, mating dynamics, opportunity for sperm competition, polyandry, sexual selection

Exploring the mechanisms that generate variation in the strength and opportunity for sexual selection is fundamental in ecological and evolutionary studies (Andersson 1994; Shuster and Wade 2003; Jennions et al. 2012). One major mechanism is ecological variation, which can determine the distribution of resources and the distributions and likely encounter rates of animals. In particular, the distribution of females in response to resources and the ability of males to monopolize females are important factors generating different social and mating structures at a broad level (Emlen and Oring 1977; Wade and Kalisz 1990; Shuster and Wade 2003). Recent work has also emphasized the importance of accounting for fine-scale

environmental heterogeneity in sexual selection studies. Even within the same population, individuals are likely to encounter local ecological variation generating variable selective pressures, and failing to account for this variation can lead to an incomplete picture or seemingly inconsistent results (Gosden and Svensson 2008; Cornwallis and Uller 2010; Kingsolver et al. 2012). Traditionally, studies have measured the strength of or opportunity for sexual selection by variation in mating success (Bateman 1948; Andersson 1994; Shuster and Wade 2003; Krakauer et al. 2011), but sperm competition can also be important whenever females mate with multiple males and sperm from multiple males compete for fertilization

of eggs (Parker 1970; Birkhead and Pizzari 2002; Evans and Garcia-Gonzalez 2016). Thus, any ecological factors that influence the likelihood that females will mate multiply and that multiple males will mate with the same female could also affect the opportunity for sperm competition (Evans and Garcia-Gonzalez 2016).

Sperm competition between 2 males can be viewed as an indirect connection between them through a mutual mate, and these indirect connections can be modeled as a sexual network (Sih et al. 2009; McDonald et al. 2013; McDonald and Pizzari 2016). Within this framework, we can then ask questions about what environmental factors structure sexual networks and if individual traits or behaviors predict network connections. For example, the number of connections that an individual has (its “degree”) in a mating network is its mate number, the degree of correlation is the correlation between male and female promiscuity, and a male’s indirect connections are his potential sperm competitors. Theoretical work has proposed the broad utility of sexual network analysis to inform studies on aspects of sexual selection including mating success, sperm competition, polyandry, and assortative mating in selection gradients (McDonald and Pizzari 2016), and empirical work is testing many of these aspects. Recent studies of animal sexual networks have been used to investigate effects of predation risk and habitat complexity on intersexual dynamics (Edenbrow et al. 2011), the form and consequences of male mating tactics (Oh and Badyaev 2010; Muniz et al. 2014), characterization of mating systems (Inghilesi et al. 2015), and the relationship between the pre- and post-copulatory environments of male–male competition (Wey et al. 2015; Fisher et al. 2016).

Weta (common names for families Anostomatidae and Rhabdophoridae, plural also “weta”) include a number of insect species endemic to New Zealand (Field 2001). This group includes some of the largest insects in the world, which inhabit a variety of habitats and also exhibit varied mating systems. The Wellington tree weta (*Hemideina crassidens*; hereafter, weta) is a sexually dimorphic, nocturnal species that is relatively widespread in New Zealand (Moller 1985; Spencer 1995). Male *H. crassidens* exhibit striking variation in head morphology due to a genetic polymorphism (Lagueux-Beloin A and Kelly CD, unpublished data) for precocial male maturation (Spencer 1995). While females mature at the 10th instar, males can mature at the 8th, 9th, or 10th instar and exhibit a trimodal distribution in head size as a result (Spencer 1995; Kelly 2005). Mandible size is positively correlated with ultimate instar number. Male tree weta use their enlarged head and mandibles as weapons in combat for tree cavities (hereafter referred to as “galleries”) containing 1 or more adult females, and galleries are important resources affecting weta distribution and movement (Moller 1985; Kelly 2006a, 2006b) (although galleries can contain solo males or 1 or more females without a resident male, Kelly 2008b). Consequently, the size of male weaponry can be under strong directional selection in some environments (Kelly 2005, 2006a, 2006b, 2006c, 2008a, 2008b; Kelly and Adams 2010). Both sexes use tree cavities as daily refuges from predators, and the great majority of mating interactions occur at or in galleries, where male tree weta are more successful at forcing matings (Spencer 1995; Field and Jarman 2001; Kelly 2006b, 2006c). Adult female tree weta typically resist mating attempts and prefer to enter unoccupied galleries over galleries already occupied by a male (Kelly 2006b). Tree weta do not create their own galleries and instead depend on cavities of appropriate entrance sizes being created by other insects.

Experimental manipulation of the size (i.e., internal volume) of available galleries has shown that this environmental factor modifies the pattern of predicted mating success and, consequently, the

opportunity for sexual selection (Kelly 2008b). Larger galleries can hold more females, and at sites dominated by larger galleries, males with larger weaponry had higher expected mating success than males with smaller weaponry, resulting in stronger directional selection on larger male weaponry (Kelly 2008b). At the same time, the opportunity for sexual selection is actually higher in sites dominated by smaller galleries, due to a larger proportion of unsuccessful males (Kelly 2008b). Adult male and female weta do not differ on average in the number of galleries visited per night or in the distance traveled per night, although males showed increased distances traveled and galleries visited in small-gallery sites (Kelly 2006a). Tree weta do not appear to hold home territories, and instead both sexes regularly change galleries, with adult males seeking out galleries with adult females and defending females temporarily rather than defending specific galleries (Kelly 2006a, 2006b). Female tree weta store sperm (Kelly 2008a) and commonly mate with multiple males on consecutive days, while weeks can pass between bouts of oviposition (Kelly CD, personal observation), and just recently, genetic work has confirmed that mixed paternity clutches are common (Nason S and Kelly CD, unpublished data). Thus, sperm competition is likely to be frequent and a potential source of sexual selection. However, the opportunity for sperm competition and how it is influenced by the structure of mating interactions has not been examined in detail in this system.

In this study, we extend the research on sexual selection in tree weta to explore the structure of connections among potential sperm competitors and ask if this structure was influenced by 2 factors known to affect mating dynamics: gallery size and male morphology. For the purposes of this study, we were interested in how gallery size could affect the likelihood of mating events; thus, we focus on a measure of relative estimated mating success, where male–female associations in galleries were considered likely mating events (more details in the “Materials and Methods” section). We first asked if gallery size would influence the potential for multiple mating by females and potential for sperm competition among males. In larger galleries, a subset of males are expected to be more effective at controlling access to females; thus, we predicted that potential for sperm competition would be lower in larger galleries and higher in smaller galleries. We then asked if male morph (a determinant of male weaponry size) was associated with expected relative sperm competition intensity (SCI) experienced by individual males. We predicted that larger morph males (with larger weaponry) would be associated with lower expected relative SCI, but only in larger galleries where larger weaponry allows males to gain and control access to more females. Finally, we asked if expected relative SCI increased with estimated mating success. A positive correlation would suggest that predicted competition could reduce between-male variation in reproductive success, whereas a negative correlation would suggest that predicted competition would amplify between-male variation in estimated mating success. We predicted a positive correlation in small-gallery sites, where the trade-off between finding and guarding mates might reward different male mating strategies, whereas we predicted a negative correlation in large-gallery sites, where a subset of males are expected to be more successful at both obtaining mates and preventing other males from accessing females.

Materials and Methods

Study site and data collection

Data for this study were collected during the austral fall seasons (March–May) of 2003 and 2004 on Te Pakeka/Maud Island, New Zealand, a 309-ha scientific reserve that is free of non-native

predators. While this species does not appear to have a set mating season and have been observed mating throughout the year (Stringer and Cary 2001; Kelly CD, personal observation), the austral fall coincides with the main mating and laying season observed from some captive breeding (Barrett 1991). Tree weta readily occupy artificial galleries, whose volume can be manipulated to allow different numbers of occupants, and mimics naturally occurring group sizes (Kelly 2006a, 2006b, 2008b). In 2002, artificial galleries (hereafter, galleries) of 2 different sizes were installed at 2 sites (200 m apart) of similar area, vegetation, and topography, with each site containing only galleries of one size. All galleries had 20 mm diameter openings, which allowed males of all sizes to enter, but differed in volume and thus the number of possible occupants. Small galleries had a cavity volume of 53.84 cm³ (holding up to approximately 3 adult individuals), whereas large galleries had twice that volume (107.68 cm³) and held up to approximately 6 adult individuals. Galleries were designed to mimic the shape of natural cavities found in different habitat types, with varying lengths to allow different numbers of weta to co-occupy, and they were installed over the sites of natural cavities that were observed to house weta. Data were not collected the first year, during which galleries were artificially seeded with weta and allowed to be naturally occupied to develop odor and other cues to encourage natural use (Kelly 2006a). Both sites had similar density of galleries (approx. 1 gallery/5 m²), although Site A (approx. 24 × 4 m) had 19 small galleries and Site B (approx. 22 × 3 m) had 13 large galleries. More details on gallery design are provided in Kelly (2008b).

Galleries were opened and adult occupants identified every third morning in 2003 and every morning in 2004. Any new (unmarked) occupant was measured for head length as a proxy for size of male weaponry (Kelly 2005) and marked with a colored and uniquely numbered bee tag (E. H. Thorne Ltd., Market Rasen, UK) to allow individual identification. All individuals were immediately replaced into the gallery after handling. This handling does not appear to influence weta behavior or tenure at the gallery (Kelly 2006b). Due to the differences in numbers of galleries between sites and differences in sampling between years, our analyses focus on the emergent patterns seen in each site-year (see the next section). Although we do not have a complete census of every individual on every day, previous research based on this dataset indicates that these methods captured a range of all male morphs and consistent mating dynamics by gallery size, across years, sites, and sampling schemes (Kelly 2006b, 2008b). We were only able to use data from 2003 to 2004 in the current study due to data constraints for network analysis, resulting in the same sites having the same gallery size treatments in both years. However, the gallery size treatments were switched between sites in 2006–2007, and previous studies using all 4 years of data show that gallery size treatment drove differences in animal movements, gallery use, and sexual selection on size of male weaponry, while site ID had no effect (Kelly 2006b, 2008b). Thus, we believe the gallery size treatments are valid in the current study.

While detailed data on animal movements or on the spatial layout of galleries are not available in this system, we expected animal movements and exchange among galleries to be major determinants of patterns of occupancy and co-occupancy that in turn determine the opportunity for multiple mating and for sperm competition. Preliminary analyses supported this by confirming that rates of gallery occupancy were highly heterogeneous and that patterns of animal exchange among galleries, and therefore potential for co-occupancy and mating, differed between small- and large-gallery sites (Appendix 1 and the “Discussion” section).

This work was completed under a research permit issued by the New Zealand Department of Conservation and was done in accordance with the ABS/ASAB guidelines for the ethical treatment of animals. While no specific ethics permits were required for work with invertebrates, the experiment involved noninvasive procedures and handling of animals was limited to the minimum required. Indeed, our goal was to minimize possible interference with natural behaviors, and no adverse effects of handling were observed. Animals were replaced where they were found and free to move naturally throughout and after the experiment.

Analysis

Gallery size and potential for multiple mating by females

We calculated each female tree weta's potential mate number as the number of unique males with which she was found. This variable was right-skewed with substantial zeros because female weta were frequently found alone in galleries (41–55% of observations in these years; indeed female weta prefer to occupy galleries singly to avoid males, Kelly 2006b). A score test for excess zeros (Van den Broek 1995; Yang et al. 2010) indicated that there our data were not zero-inflated. Therefore, we modeled the predicted fixed effects of gallery size and year on potential mate number using a generalized linear model with quasipoisson error distribution to account for some underdispersion. Results were qualitatively similar if we used a Gaussian distribution on a transformed variable or a Poisson distribution. The 2-way interaction between gallery size and year was not significant, so it was not included in the final model. We also ran a model with only females that had at least one potential mate (i.e., excluding 0s) because these are the key females in the network of potential sperm competitors.

Gallery size, male morph, and potential for sperm competition

We created potential mating networks for each site in each year based where a male and female were connected if they were found together in a cavity on the same day. This estimate of mating success is comparable to measures used in previous studies; male weta generally attempt to mate with all females in a gallery, and male–female gallery co-occupancy significantly predicted relative male mating success in a laboratory setting (Kelly 2008b). In the rare event where 2 males were found in the same gallery with females [only 4 times out of 186 observations of co-occupied galleries (2.2%) and 943 observations of occupied galleries (<1%)], both males were assigned connections to females in the gallery. In creating potential mating networks, we only included data from the subset of individuals with at least 4 observations that year, in order to omit poorly sampled individuals.

To create networks of potential sperm competitors, we projected the potential mating networks (which are bipartite networks with connections only between 2 different categories of nodes) into networks of male–male connections, based on potential matings with the same female. In other words, we considered any 2 males that were connected with the same female to have the opportunity for sperm competition with each other, which represents the maximum sperm competition likely to be faced, given the observed pairings. The sampling period is also within the timeframe that females will lay fertilized eggs using stored sperm (Kelly CD, personal observation). We assigned males in our dataset to morphotype based on Kelly and Adams (2010) and examined if males differed in the number of potential sperm competitors based on morphotype. We calculated the expected relative SCI of each male as the harmonic mean

of his partners' number of partners (McDonald and Pizzari 2016), where the harmonic mean is the reciprocal of the arithmetic mean of the reciprocals of the given observations. This can also be thought of as the inverse of the average proportion of paternity of a given male across all of his mates. Shuster and Wade (2003) noted that, with sperm mixing, male fertilization success will be heavily influenced by the harmonic mean promiscuity of his mates and that the least promiscuous females should contribute disproportionately to a male's fitness.

We then ran a linear mixed model (LMM) with the predicted fixed effects of male morph and gallery size on expected relative SCI (log₁₀-transformed to improve residual diagnostics). We included a random intercept for group (gallery size treatment within year). Since network measurements such as SCI potentially violate the assumption of non-independence of observations (Wasserman and Faust 1994; Croft et al. 2011), we checked the *P*-values obtained from this model using 10,000 restricted permutations of observations within years and re-running the model to generate a distribution of parameter coefficients obtained from the randomized data. We then computed significance as the proportion of coefficients from permuted data that were greater than or equal to the observed value (from the real data). Significance values were qualitatively similar from both methods, so we report results from the LMM for simplicity. We then ran a similar model with a weighted version of expected relative SCI (McDonald and Pizzari 2016), accounting for repeated interactions between the same male and female and thus estimating the expected relative SCI faced by a male based on the proportion of times he was found with females. We again checked significance of model results using restricted data permutations and obtained similar results. Results were very similar for unweighted and weighted versions of estimated SCI, so we only report results for the weighted version. We initially included a 2-way morph-by-gallery size interaction, but dropped it from the final models because it was not statistically significant. We ran an ANOVA of the LMM to extract *F*-values and *P*-values based on type III sums of squares. We calculated *P*-values for random effects using log-likelihood ratio tests (LRTs) of nested models with and without the factor of interest.

Potential SCI and estimated mating success

We calculated 2 measures of the correlation between estimated mating success and expected relative SCI experienced by each male. We chose measures simulated to be robust across a range of demographic parameters (McDonald and Pizzari 2016). The first measure was the directed degree assortativity coefficient (Newman 2003) as a measure of how male and female number of connections were related. Assortativity coefficients range from -1 to 1 and reflect the extent to which connections in the network are formed between individuals based on similarity (or dissimilarity) in a characteristic. Degree assortativity is a correlation (*r*) between the degree values (number of connections) of each pair of individuals with a connection. As a measurement of statistical error, we calculated the standard deviation of *r* (σ_r) using a jackknife method suggested by Newman (2003), where *r* is recalculated sequentially with each edge removed and the squared sum of deviations from the original value caused by each removal calculated. The second measure was SCI correlation (SCIC; McDonald and Pizzari 2016), which correlates estimated mating success with the average number of potential sperm competitors that a male faces, based on his expected relative SCI. We also calculated a weighted version of SCIC, which again accounts for repeated observations between the same male and

female. Because results were similar for both versions, we only report results from the weighted version. We report a version of SCIC standardized for population means and standard deviations to facilitate comparisons across different populations (McDonald and Pizzari 2016).

Because estimated mating success was correlated with number of times an individual was observed ($r \sim 0.36$), we ran alternate versions of the above analyses with a measure of estimated mating success per day. We performed all analyses in the R statistical environment (R Development Core Team 2018). We ran mixed effects models with the package "lme4" (Bates et al. 2015) and ran the score test for excess zeros with the package "vcdExtra" (Friendly 2017). We constructed and analyzed networks with the package "igraph" (Csardi and Nepusz 2006). Node permutations were conducted with the package "permute" (Simpson 2015). We modified code provided in McDonald and Pizzari (2016) to calculate SCI and SCIC.

Results

The complete dataset encompassed 211 unique individuals in 2003 (106 in the small galleries, 105 in the large galleries; 95 males and 116 females) and 149 unique individuals in 2004 (70 in the small galleries, 81 in the large galleries; 92 males and 57 females). Although sex ratios and proportions of male morphs varied between sites and years, galleries of both sizes contained males of all morphs and substantial numbers of both sexes, suggesting that the size manipulation itself did not prevent any particular individuals from using specific galleries. Further details on the dataset are provided in Table 1 and on effects on weta distribution in Appendix 1.

Gallery size and potential for multiple mating by females

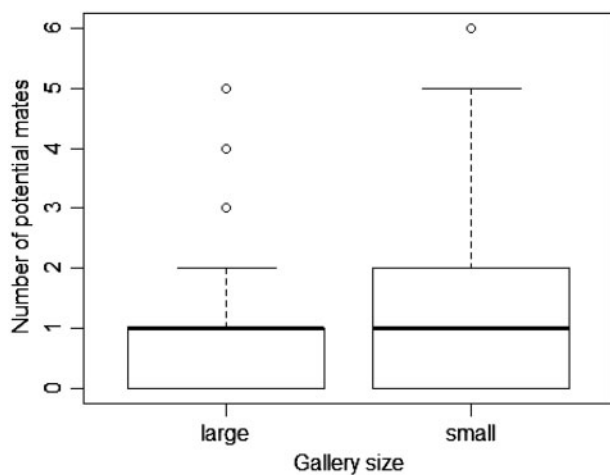
Female tree weta in small galleries tended to have higher potential for multiple mating at large galleries ($\chi^2_1 = 11.048$, $P = 0.001$), when using the potential mate number (Figure 1). Year had no effect ($\chi^2_1 = 1.451$, $P = 0.228$). This pattern remained when we examined only females that had at least 1 potential mate (gallery size: $\chi^2_1 = 5.191$, $P = 0.023$; year: $\chi^2_1 = 1.888$, $P = 0.169$). When females with no potential mates were included in the analysis, female tree weta did not have higher potential mating rate in small galleries (gallery size: $\chi^2_1 = 0.347$, $P = 0.556$; year: $\chi^2_1 = 1.262$, $P = 0.261$), but females that had at least 1 potential mate showed higher potential mating rate in small galleries (gallery size: $\chi^2_1 = 6.198$, $P = 0.012$; year: $\chi^2_1 = 8.710$, $P = 0.003$).

Gallery size, male morph, and potential for sperm competition

In potential sperm competition networks (Figure 2), male morph was not associated with differences in potential SCI, when SCI was calculated from potential mate number ($F_{2,98} = 0.156$, $P = 0.700$), but small galleries had higher potential SCI ($F_{1,98} = 10.013$, $P = 0.010$). The random effect of group accounted almost none of the variance (<0.001 , $SD <0.001$), suggesting that there were no systematic differences among groups in average potential SCI. Full model results from the LMM are presented in Table 2. When SCI was calculated from potential mating rate, male morph was not associated with relative SCI ($F_{2,98} = 0.275$, $P = 0.872$), and small galleries showed a nonsignificant trend for higher potential SCI ($F_{1,98} = 3.407$, $P = 0.065$).

Table 1. Summary statistics for unique individuals included in the study

		Small	Large	Overall
2003	<i>N</i> males	60	35	95
	(% 8th, 9th, and 10th instar)	(47, 28, 24)	(37, 43, 20)	(44, 34, 22)
	<i>N</i> females	46	70	116
	Sex ratio (M/F)	1.3/1	0.5/1	0.8/1
	Mean <i>N</i> obs/ind (SD, max)	3.0 (2.8, 19)	2.2 (2.7, 22)	2.6 (2.8, 22)
	Mean <i>N</i> cav/ind (SD, max)	1.8 (1.2, 6)	1.2 (0.5, 5)	1.5 (1.0, 6)
2004	<i>N</i> males	30	29	59
	(% 8th, 9th, and 10th instar)	(51, 25, 24)	(40, 40, 20)	(46, 32, 22)
	<i>N</i> females	40	52	92
	Sex ratio (M/F)	0.8/1	0.6/1	0.6/1
	Mean <i>N</i> obs/ind (SD, max)	5.4 (5.2, 27)	3.2 (3.3, 21)	4.4 (4.6, 27)
	Mean <i>N</i> cav/ind (SD, max)	2.4 (1.5, 7)	1.2 (0.4, 3)	1.8 (1.3, 7)

**Figure 1.** Box plot of number of potential mates for female weta in large and small galleries. The box spans the interquartile range (IQR), and bolded lines indicate medians. Whiskers indicate 1.5(IQR), and points indicate outliers.

Expected relative SCI and estimated mating success

Potential mating networks all exhibited negative correlations between estimated male mating success and estimated female mating success [assortativity coefficients, $r(\sigma_r)$: 2003, small galleries = -0.240 (0.121); 2003, large galleries = -0.327 (0.169); 2004, small galleries = -0.199 (0.222); 2004, large galleries = -0.321 (0.170)]. However, large errors around this value for small galleries in 2004 suggest this result might not be robust for that year. SCIC values also showed consistent negative correlations, when relative SCI was calculated from potential mating success ($r = -0.247$, $P = 0.014$) (Figure 3). When relative SCI was calculated from potential mating rate, the correlation was weaker but still negative ($r = -0.181$, $P = 0.019$). Together, negative degree assortativity and SCIC values indicate that males with high estimated mating success were expected to face lower relative SCI.

Discussion

We examined the predicted effects of variation in an ecological variable, gallery size, and male morphotype on potential for sperm competition in tree weta. Gallery size influenced the potential for multiple mating by females and consequently the opportunity for

sperm competition. Size of male weaponry did not influence expected relative sperm competition for individual males, and regardless of gallery size, estimated mating success and expected relative SCI were negatively correlated across sites. Our study provides insight into how environmental heterogeneity could influence sexual selection and highlights the utility of considering indirect interactions in mating networks.

As predicted, our results suggest that small galleries will likely create situations with higher potential for sperm competition, in conjunction with the higher opportunity for sexual selection previously measured in small galleries (Kelly 2008b). When considering only female weta that had at least 1 potential mate (which are the females that would affect the potential sperm competition network), females at small gallery sites tended to have more potential mates and higher potential mating rate. This is notable as the conditions that create the most disparity in male mating success (i.e., small galleries) also increase potential sperm competition. Variation in gallery size thus could have implications for sperm competition through its predicted effects on multiple mating by females. Interestingly, while larger galleries create larger groups of females, the shorter tenures and greater movement among small galleries (Kelly 2006a; Appendix 1) appear to create greater mating competition in small galleries. The dynamics of population density and operational sex ratios are well known to affect competition for mates and are predicted to similarly influence sperm competition (Parker 1970; Simmons and Kvarnemo 1997; Wedell et al. 2002; Knell 2009; Weir et al. 2011), but it remains difficult to test the latter effects, particularly in wild populations. In our study, small gallery sites might generally support larger or more dynamic effective mating populations with higher potential for sperm competition. However, we did not manipulate population density or composition directly, and this remains an important direction for future research.

The consistent negative correlations between expected male and female estimated promiscuity and between estimated male mating success and expected relative SCI further indicated that males predicted to have relatively high mating success were likely to face fewer sperm competitors. This suggests that there are not strong trade-offs between acquiring mating success and guarding paternity in this system and that post-copulatory processes might further exaggerate male variance in reproductive success, potentially increasing Bateman's gradients (Jones 2009; McDonald et al. 2013). Our results might be consistent with patterns observed in some other species where the males with the highest mating success were also likely

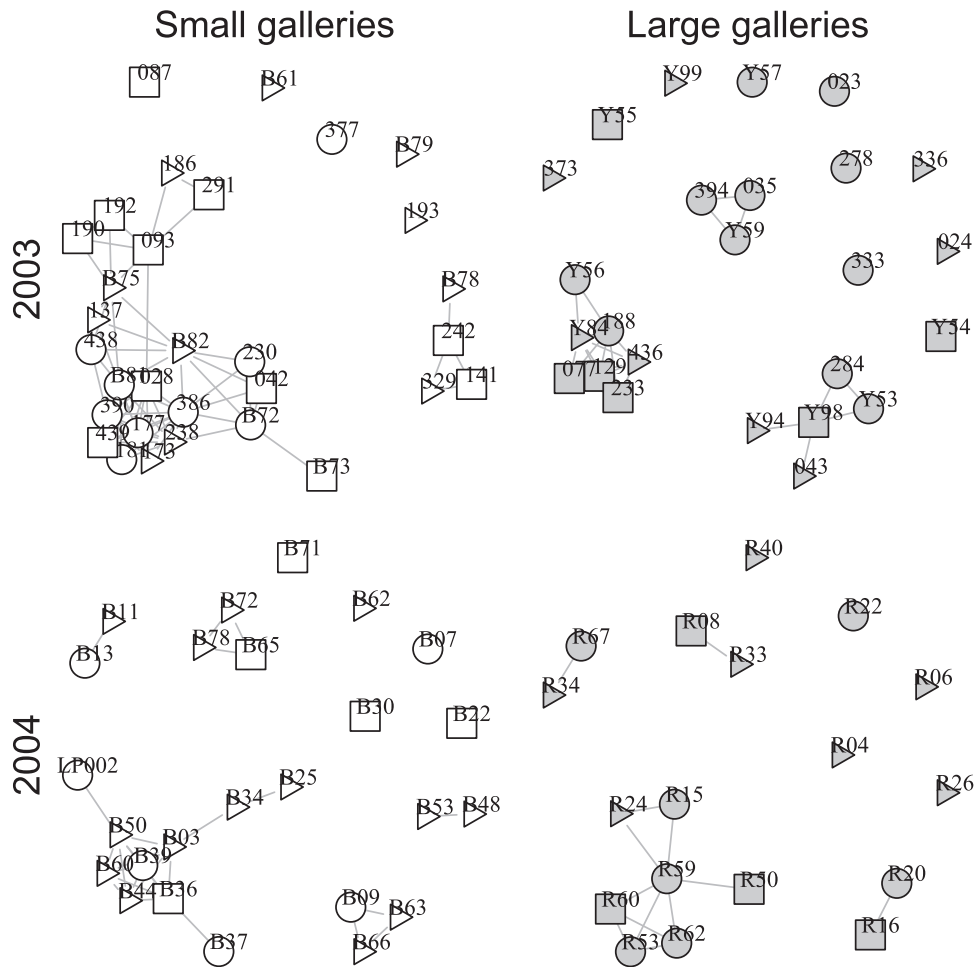


Figure 2. Potential sperm competition networks created from bipartite projections of potential mating networks. Nodes represent male tree weta. Connections represent associations with the same female. Nodes in small-gallery treatments are in white, while nodes in large-gallery treatments are in gray. Squares, 10th-instar males; circles, 9th-instar males; triangles, 8th-instar males. Note that the network layout does not represent spatial proximity; instead better-connected nodes are placed closer together.

Table 2. Results from a LMM for the predicted effects of male morphotype and gallery size on expected relative sperm competition intensity

Random effects	Variance		
Year (Intercept)	<0.001		
Residual	0.078		
Fixed effects	Estimate	SE	t-value
Intercept	0.221	0.057	3.875
Morph 9	0.025	0.067	0.377
Morph 10	-0.036	0.071	-0.513
Gallery size (small)	0.182	0.057	3.164

Notes: The dependent variables were the log₁₀-transformed predicted SCI. Significant results are in bold.

to face relatively little sperm competition. For example, more intense male competition resulted in a subset of males having both high mating success and high mating exclusivity in stream water striders *Aquarius remigis*, which have high levels of male–male competition (Wey et al. 2015). In red palm weevils *Rhynchophorus ferrugineus*, despite a seemingly highly promiscuous mating system, just a few males accounted for the great majority of matings and

maintained this priority over time (Inghilesi et al. 2015). A recent study combining detailed behavioral and molecular data to confirm paternity also showed that postcopulatory sexual selection exaggerated precopulatory selection in male red junglefowl (*Gallus gallus*; McDonald et al. 2017). However, other systems can exhibit a different pattern. In common field crickets *Gryllus campestris*, more promiscuous males tended to mate with more promiscuous females, representing a likely trade-off between success in pre- and post-copulatory male competition (Fisher et al. 2016). Additional empirical tests of when pre- and post-copulatory sexual selection are likely to trade-off or coincide are needed to examine how ecological and evolutionary factors drive these patterns more generally.

Counter to our predictions, male morph did not affect the expected relative SCI experienced in either small or large galleries. This was unexpected since the size of male weaponry is associated with differences in harem size in large galleries (Kelly 2008b), and we had expected this to translate into differences in potential mate sharing. It also contrasts with a study in harvestmen *Serracutisoma proximum*, which found that alternative male mating tactics resulted in different levels of SCI (Muniz et al. 2014). In particular, sneakers faced higher average sperm competition than territorial males, and males with larger harems experienced less sperm competition than males with smaller harems. In tree weta, it is possible

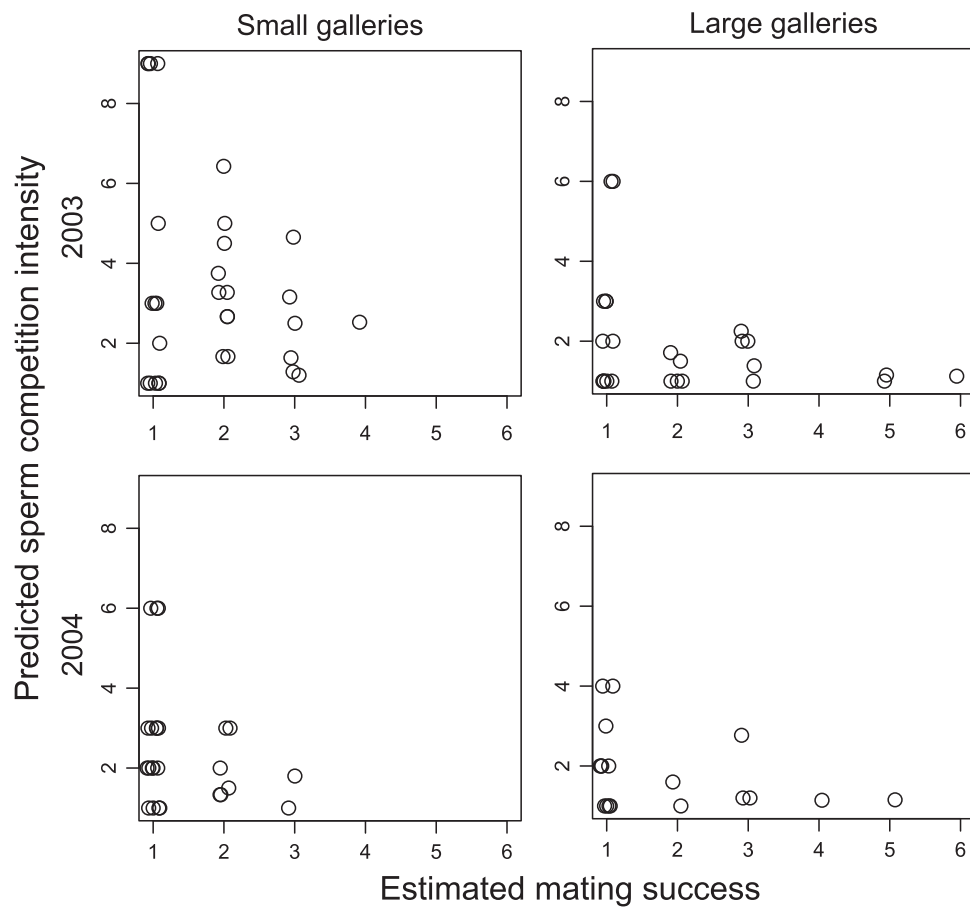


Figure 3. Relationship between male estimated mating success and expected relative sperm competition intensity. Mating success is estimated as the number of females with which a focal male was associated, and sperm competition intensity is related to the number of other males with which the focal male's female partners were associated. For plotting purposes, we added a small amount of noise to estimated mating success values to avoid overlapping points. 2003, small galleries: $r = -0.192$; 2003, large galleries: $r = -0.290$; 2004, small galleries, $r = -0.379$; 2004, large galleries, $r = -0.352$.

that behavioral strategies are more important for determining mating success, which is likely the largest determinant of overall reproductive success. Variation in the opportunity for sexual selection is largely driven by the proportion of unmated males (Kelly 2008b), which varied widely in the years observed (17–48%, although these are likely overestimates due to sampling limitations). Additionally, the relationship between individual traits and reproductive success is likely to be modified by social context. Outcomes of social interactions, such as mating interactions, necessarily depend on the phenotypes of social partners, and indirect effects of selection on social partners can play a role in the evolution of both social and nonsocial behaviors (Moore et al. 1997; Santostefano et al. 2016). The effects of male traits on fitness could also be influenced by correlational selection on associated traits, their development, or the social environment experienced (e.g., Montiglio et al. 2017). Male tree weta with smaller weaponry tended to have larger ejaculates (Kelly 2008a), suggesting that males invest physiologically in pre- and post-copulatory competition consistent with their own phenotype. If male weta are expected to experience similar numbers of sperm competitors regardless of weaponry, it would further reinforce other mechanisms maintaining alternative male mating strategies.

Further investigation is needed to elucidate the mechanisms underlying the difference in expected levels of sexual selection due to ecological variation, in this species and in general (Gosden and Svensson 2008; Cornwallis and Uller 2010). In our study,

differences in potential for sexual selection might arise from ecological factors through changes in animal movements and/or demographic changes. Smaller galleries exhibit shorter gallery tenures and higher rate of movement of individuals (Kelly 2006a), and, consistent with this, we also noted that there was a greater exchange of individuals among small galleries and that some galleries were better connected than others (Appendix 1). While we could not examine these factors in detail with the current dataset, these are possible mechanisms leading to social and sexual dynamics, and thus warrant future study. The structure of exchange of individuals among refuges has important implications for social dynamics and conservation, and identifying environmental factors besides gallery size that determine tree weta movements and why some galleries are used more are important future directions. Physical “hubs” or hotspots can play critical roles in ecological processes such as maintaining metapopulation dynamics or spreading information, for example in tree-roosting bats (Kerth and König 1999; Fortuna et al. 2009; Johnson et al. 2012). Unfortunately, we did not have information on other characteristics of galleries (indeed they were chosen to be as similar as possible), but it is possible that aspects of microhabitat variation could drive preferences for certain locations or movements among them. Nor did we have exact locations of all galleries mapped, so we cannot directly test hypotheses about physical orientation; however, shortest distance between galleries did not predict the amount of exchange of individuals among galleries (Wey TW

and Kelly CD, unpublished data), suggesting that the patterns that we observed are not only a direct consequence of physical proximity. Variation in demographic factors, such as density, sex ratio, and frequency of male phenotypes, could also result in variation in patterns of sexual selection (Le Galliard et al. 2005; Kasumovic et al. 2008). Potential frequency-dependent effects of male phenotypes in tree weta remain to be determined and would permit intriguing comparisons with other systems having variable male morphs (Shuster and Wade 1991; Sinervo and Lively 1996; Simmons et al. 2007; Rowland and Emlen 2009).

There are, of course, limitations to the inferences that can be made from the purported sexual networks constructed here. We could not specifically disentangle treatment effects from potential uncontrolled site effects in the current analysis, but we believe treatment effects are not likely to be site-specific. In previous analyses where the treatments were switched between these sites, gallery size had consistent effects across sites on gallery use, animal movements, and sexual selection on male morphology (Kelly 2006b, 2008b). We also expected any noise from uneven sampling of individuals and uncontrolled variation in population parameters to have affected all groups similarly, and we used measures of assortativity and sperm competition that should be robust to population fluctuations. Another limitation is that our measure of likely mating interactions based on gallery co-occupancy does not capture actual rates of copulations, nor do we currently have more information on fertilization rates or patterns of sperm precedence in this species. Thus, our analyses of the opportunity for sperm competition modeled equal fertilization rates for all males, which is likely inadequate in capturing total sperm competition processes (Kelly 2008a). The genetic underpinnings of tree weta traits also require further investigation, and this and relative contributions of environment and genetics to expression of male weaponry size are subjects of ongoing work. The most recent results indicate that mixed paternity clutches are likely to be common, with variable proportions of offspring sired by the most recently present male (Nason S and Kelly CD, unpublished data), but factors influencing these proportions are unknown. Overall, our general results were consistent when analyzed in multiple ways, so, while caution is needed in extending conclusions to other populations and systems, we believe they are likely to reflect fundamental processes within this system. These questions about demographic and environmental effects on the post-copulatory sexual selection present promising directions for future research.

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APPENDIX 1

GALLERY OCCUPANCY AND CONNECTEDNESS

We expected that differences in gallery occupancy and co-occupancy that affect likelihood of multiple mating and sperm competition are heavily driven by animal movements. While we did not have detailed enough data on animal movements or gallery spatial layouts to test this specifically, we used available data to demonstrate that the distribution of gallery occupancy by weta, and in particular by male–female pairs, was heterogeneous and that small- and large-gallery differed dramatically in the pattern of exchange of individuals among galleries.

ANALYSES

Distribution of gallery occupancy and male–female pairs

We examined the distribution of occupancy across galleries and examined if galleries differed significantly in occupancy and male–female co-occupancy (MFC). For galleries that were occupied at least once in the year (i.e., excluding galleries that were never used), occupancy was tabulated as yearly counts of individuals using a

given gallery, regardless of overlap with other individuals, whereas MFC was tabulated as yearly counts of instances with male–female pairs occupying a gallery on the same night. First, we used separate Chi-squared goodness-of-fit tests (with 10,000 Monte Carlo simulations) on occupancy and MFC at each site in each year to determine if distributions were skewed. Second, we ran LMMs on occupancy and MFC at both sites in both years with random intercepts for year and gallery and a fixed effect of gallery size. We tested for significant variance among galleries in occupancy and MFC using a log-LRT with 1 degree of freedom. Third, a linear model tested whether occupancy predicted MFC, controlling for year and cavity size, to see if highly occupied galleries also contained more male–female pairs.

Structure of gallery networks

Next, for each site in each year, we created gallery networks, with galleries as nodes and connections between galleries if the same individual used both of them (on different days). These networks were intended to capture the effect of gallery size on the structure of movement and exchange of individuals between refuges and on the potential creation of “hotspot” galleries. They included all observations of individuals seen at the galleries in a season. Because results were qualitatively similar for both unweighted networks (where any

Table A1. Goodness-of-fit tests for cavity occupancies

Year	Cavity size	Occupancy					Male–female co-occupancy				
		Range	χ^2	<i>P</i> -value	Skew1 ^a	Skew2	Range	χ^2	<i>P</i> -value	Skew1	Skew2
2003	Small	4–30	61.044	<0.001	0.016	1.319	2–13	28.000	0.005	0.972	1.739
2003	Large	2–40	85.425	<0.001	0.534	1.596	1–19	32.600	<0.001	0.698	1.903
2004	Small	4–49	92.853	<0.001	0.489	1.375	1–12	41.652	<0.001	1.456	2.188
2004	Large	4–44	102.083	<0.001	0.303	1.651	2–15	22.577	0.001	0.252	1.806

^aSkew1 is uncorrected for sample bias, while Skew2 is corrected for sample bias (i.e., sample skewness).

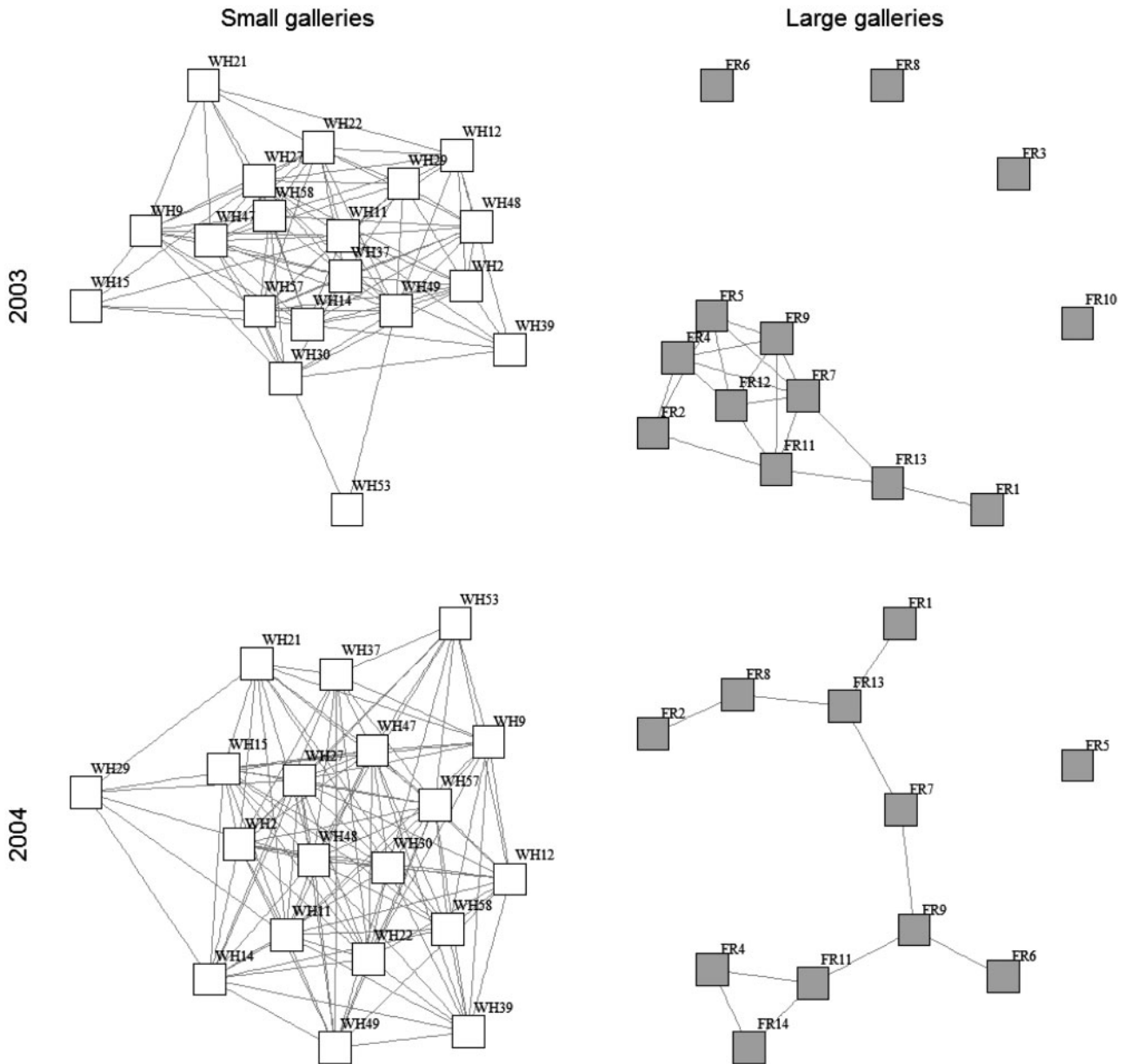


Figure A1. Gallery networks, where nodes represent galleries and connections represent individuals that used both galleries. Small galleries are in white, while large galleries are in gray. Note that the network layout does not represent spatial proximity; instead better connected nodes are placed closer together.

exchange of individuals between 2 galleries counted as a connection with weight 1) and weighted networks (where the connection between 2 galleries was given a weight based on the count of individuals that moved between them) and some measures are less

well-defined for weighted networks, we only report results for unweighted networks.

For each network, we quantified the density, number of components, average degree, degree centralization, and skew of the degree

Table A2. Structural measures of gallery exchange networks

Year	Gallery size	Nodes/ cavities	Ties/cavity exchange	Density (<i>P</i> -value) ^a	Components (<i>P</i> -value)	Average degree	Degree centralization (<i>P</i> -value)
2003	Small	19	96	0.561 (0.063≥obs)	1 (1 = obs)	10.105	0.216 (0.598≥obs)
2003	Large	13	19	0.244 (0≤obs)	5 (0≥ obs)	2.923	0.244 (0.408≥obs)
2004	Small	19	119	0.696 (0≥ obs)	1 (1 = obs)	12.526	0.249 (0.171≥obs)
2004	Large	11	10	0.182 (0≤obs)	2 (0.525≤obs)	1.818	0.118 (0.358≤obs)

^a Simulated distributions were non-symmetrical, and *P*-values reported are the more extreme 1-tailed values. Values that differ significantly from random at a level of $P < 0.025$ are bolded.

distribution. The density is the number of connections that exist in the network divided by the number possible, given the number of nodes, and is a basic measure of overall connectedness. The number of components is the number of disconnected subgroups in the network and is a basic measure of network fragmentation. The degree of each node is the number of other nodes to which it is connected, and the average degree in a network gives a sense of the average node connectedness. The degree centralization of the network is a measure of the inequality or variance in distribution of degree, where the maximally centralized configuration is a “star” network with one node connected to all other nodes, who are otherwise disconnected. The degree centralization is standardized to a value between 0 and 1 by dividing by the theoretical maximum value for a network of that size. We also used a linear model to test whether the most connected galleries (degree centralization) were the ones that were the most frequently occupied, while controlling for year and cavity size. Significance of network structure measures was assessed by comparing observed values against values against a distribution of values from 10,000 randomly generated networks of the same size (for density, where each pair of nodes has a probability of 0.5 of being connected, drawn from a Bernoulli process) or both size and density (for number of components and degree centralization) as the observed network. Significance of the relationship between gallery occupancy and degree was assessed by comparing the real coefficient value against a distribution of coefficient values obtained from linear models run on 10,000 restricted (within year and site) permutations of node degrees, where the *P*-value is the number of coefficients obtained from permutations that are as or more extreme than the real value.

RESULTS

Distribution of gallery occupancy and male–female pairs

Chi-squared tests were all highly significant (all $P < 0.005$; Table A1), indicating that occupancy and MFC were unevenly

distributed across galleries within each site in each year. All occupancy and MFC distributions showed moderate to heavy positive skew (Appendix 1, Table A1). Gallery identity explained a significant amount of variation in occupancy (LRT: $\chi^2 = 4.656$, $P = 0.031$), indicating that galleries varied consistently across years in the number of times they were occupied by any individuals. Occupancy did not differ significantly between gallery size treatments ($\beta \pm SE: 1.554 \pm 3.274$) or between years (LRT: $\chi^2 = 1.752$, $P = 0.186$). In contrast, gallery identity did not explain significant variation in MFC (LRT: $\chi^2 = 0.008$, $P = 0.930$), suggesting that galleries did not vary consistently across years in the number of times they were occupied by male–female pairs. Year did not explain significant variation (LRT: $\chi^2 = <0.001$, $P > 0.999$) either, but small galleries contained fewer male–female pairs throughout the season ($\beta \pm SE: -3.756 \pm 1.408$). Occupancy significantly predicted MFC, with more frequently occupied galleries also housing more male–female pairs ($\beta \pm SE: 3.069 \pm 0.056$, $P < 0.001$).

Structure of gallery exchange networks

Small and large gallery exchange networks differed in many structural aspects (Figure A1 and Table A2). Small galleries were much better connected overall, forming single connected components, with higher density and higher average degree than large galleries, which were made up of disconnected components. Degree centralization was low in all gallery exchange networks and did not differ between small and large galleries. While differences in network size make them hard to compare directly, the densities of large-gallery networks fall well below the lower end of the distribution of values for small-gallery networks, and simulated small-gallery networks always formed one connected component, whereas simulated large-gallery networks often formed multiple components. These differences suggest that the properties of the 2 types of networks are generated from different processes. The most highly occupied galleries also tended to be the ones that were best connected to other galleries ($\beta \pm SE: 0.279 \pm 0.093$, $P = 0.002$).