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The impact of mating systems and dispersal on fine-scale genetic structure at maternally, paternally and biparentally inherited markers

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31 Running Title: Impact of mating and dispersal across markers

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33

34 **Abstract**

35

36 For decades, studies have focused on how dispersal and mating systems influence  
37 genetic structure across populations or social-groups. However, we still lack a thorough  
38 understanding of how these processes and their interaction, shape spatial genetic  
39 patterns over a finer-scale (tens – hundreds of metres). Using uniparentally inherited  
40 markers may help answer these questions, yet their potential has not been fully  
41 explored. Here, we use individual-level simulations to investigate the effects of  
42 dispersal and mating system on fine-scale genetic structure at autosomal, mitochondrial  
43 and Y chromosome markers. Using genetic spatial autocorrelation analysis, we found  
44 that dispersal was the major driver of fine-scale genetic structure across maternally,  
45 paternally and biparentally inherited markers. However, when dispersal was restricted  
46 (mean distance = 100 m), variation in mating behaviour created strong differences in the  
47 comparative level of structure detected at maternally and paternally inherited markers.  
48 Promiscuity reduced spatial genetic structure at Y chromosome loci (relative to  
49 monogamy), whereas structure increased under polygyny. In contrast, mitochondrial  
50 and autosomal markers were robust to differences in the specific mating system,  
51 although genetic structure increased across all markers when reproductive success was  
52 skewed towards fewer individuals. Comparing males and females at Y chromosome  
53 *versus* mitochondrial markers respectively, revealed that some mating systems can  
54 generate similar patterns to those expected under sex-biased dispersal. This  
55 demonstrates the need for caution when inferring ecological and behavioural processes  
56 from genetic results. Comparing patterns between the sexes, across a range of marker  
57 types may help us tease apart the processes shaping fine-scale genetic structure.

58

59 **Introduction**

60

61 A wide range of biological processes can influence patterns of genetic structure within  
62 and among populations. This has inspired the extensive use of genetic analyses to

63 understand behavioural and ecological patterns (Chesser 1991a; Mossman & Waser  
64 1999; Ross 2001; Banks & Peakall 2012; Parreira & Chikhi 2015). Of particular interest  
65 has been the use of genetic analyses to identify patterns of animal movement (Goudet *et al.*  
66 *al.* 2002; Lawson Handley & Perrin 2007; Banks & Peakall 2012). However, genetic  
67 structure can be influenced by a many behavioural, ecological and molecular processes  
68 other than dispersal, such as social structure and mating systems (Sugg *et al.* 1996;  
69 Storz 1999; Parreira & Chikhi 2015). Furthermore, these processes can influence  
70 genetic structure differently across markers with different inheritance modes (Chesser &  
71 Baker 1996; Petit *et al.* 2002; Hedrick 2007; Greminger *et al.* 2010). Thus,  
72 understanding the impact these factors have on genetic patterns may help us avoid false  
73 conclusions about ecological and behavioural processes.

74 Comparing patterns across different marker types presents an exciting  
75 opportunity for biological inference from genetic data. Until recently, studies using this  
76 comparative marker approach in species other than primates, focused mainly on  
77 comparing autosomal markers with the maternally inherited mitochondria (mtDNA)  
78 (Sunnucks 2000; Petit *et al.* 2002; Prugnolle & de Meeus 2002; Hedrick *et al.* 2013).  
79 However, in mammals mtDNA markers make an ideal comparison to the Y  
80 chromosome, as both are inherited from one parent and are non-recombining, or have  
81 non-recombining regions, which are preserved as haplotypes during sexual reproduction  
82 (Petit *et al.* 2002; Prugnolle & de Meeus 2002; Greminger *et al.* 2010). Alternatively,  
83 while the X chromosome spends less evolutionary time in the male germ-line compared  
84 to autosomal markers, it is not uniparentally inherited. This means that the X and Y  
85 chromosomes are not directly comparable (MacDonald *et al.* 2014). However,  
86 comparing Y chromosome to mtDNA markers may provide a sex-specific genetic  
87 perspective for inferring biological processes (Goudet *et al.* 2002; Petit *et al.* 2002;  
88 Lawson Handley & Perrin 2007). Furthermore, these markers may offer insight into  
89 these processes over greater time-scales, as both uniparental inheritance and the lack of  
90 recombination ensure genetic patterns are maintained.

91 Development of Y chromosome markers in wild populations remains rare, partly  
92 due to low levels of polymorphism at the Y chromosome (Petit *et al.* 2002; Greminger  
93 *et al.* 2010; Evans *et al.* 2014). However, studies using the Y chromosome are  
94 becoming more feasible with next generation sequencing and reference genome  
95 information (Petit *et al.* 2002; Greminger *et al.* 2010; Neaves *et al.* 2013; MacDonald *et al.*  
96 *al.* 2014). In fact, a growing number of studies are using population-level analyses of

97 the Y chromosome in combination with other genome regions to find evidence for sex-  
98 biased dispersal (Hammond *et al.* 2006; Schubert *et al.* 2011; Yannic *et al.* 2012;  
99 MacDonald *et al.* 2014), skewed sex ratios and polygyny (Neaves *et al.* 2013),  
100 population expansion and contraction, and variation in mutation rates between the sexes  
101 (Evans *et al.* 2014).

102 In order to take full potential of uniparentally inherited markers in population  
103 genetic studies, it is fundamental that we understand how these markers are influenced  
104 by ecological and behavioural processes. A number of simulation studies have  
105 investigated the ability of autosomal markers to detect differences in genetic structure  
106 between the sexes, both at an individual- and population-level (Goudet *et al.* 2002;  
107 Banks & Peakall 2012; Parreira & Chikhi 2015). However, the potential to use  
108 uniparentally inherited markers at the individual-level, rather than at population or  
109 social-group levels, has not been extensively explored. This is a major knowledge gap,  
110 as the effect of social behaviours and dispersal are likely to be particularly important for  
111 influencing the distribution of individual genotypes and haplotypes in space (Banks &  
112 Peakall 2012; van Dijk *et al.* 2015).

113 Genetic data provide powerful tools for elucidating processes such as dispersal  
114 and mating behaviour, but any inferences made from such data should be strongly  
115 grounded in an understanding of the genetic patterns expected under the diverse mating  
116 and dispersal strategies that occur (McEachern *et al.* 2009; Blyton *et al.* 2012; also, see  
117 Appendix S1, for an extensive list of mammalian examples). When considering these  
118 processes in mammals, there is a long-held assumption that most species are  
119 polygynous and dispersal is male-biased (Greenwood 1980; Foltz 1981). However, this  
120 assumption tends to overlook small and inconspicuous species, where dispersal and  
121 social behaviours occur over much finer-scales (Foltz 1981; Burda *et al.* 2000; Swilling  
122 & Wooten 2002; Maher & Duron 2010). These processes can vary across species (e.g.  
123 bats show a range of complex social, mating and dispersal patterns, see Kerth 2008), as  
124 well as within single populations (depending on temporal, spatial, demographic or  
125 environmental variables, see: Busch *et al.* 2009; Yannic *et al.* 2012; Keane *et al.* 2015).  
126 It is not surprising then, that patterns detected in genetic investigations often do not  
127 reflect the mating systems or dispersal patterns previously identified in observational  
128 studies (McEachern *et al.* 2009). Thus, to accurately interpret genetic data, it is essential  
129 to understand how mating systems and dispersal influence patterns of genetic structure.

130 Here, we use spatially explicit, individual-level simulations to investigate a  
131 range of dispersal and mating scenarios found across small mammal species (Fig. 1) and  
132 their effect on fine-scale spatial genetic structure as measured by spatial autocorrelation  
133 (Smouse & Peakall 1999; Peakall *et al.* 2003; Smouse *et al.* 2008; Banks & Peakall  
134 2012; Blyton *et al.* 2015). We define fine-scale genetic structure as the non-random  
135 distribution of genotypes and haplotypes in space, over spatial-scales of tens to  
136 hundreds of metres (Banks & Peakall 2012). Simulations provide a powerful and  
137 flexible tool for exploring different biological processes, and can be adapted to  
138 investigate many different ecological and behavioural scenarios.

139 As a starting point, simulations were built around the life history of the agile  
140 antechinus (*Antechinus agilis*), an Australian marsupial with a long history as a study  
141 organism in behavioural, landscape and molecular ecology (Cockburn *et al.* 1985;  
142 Kraaijeveld-Smit *et al.* 2002a; b; c; Banks *et al.* 2005a; Fisher *et al.* 2006a; b; Banks &  
143 Lindenmayer 2013). Simulations were then extended to test hypotheses relating to a  
144 range of dispersal and mating system scenarios observed across small mammal species  
145 (ensuring relevance to a wide range of real world scenarios). Simulations are therefore  
146 broadly representative of mammalian systems where females produce multiple offspring  
147 in a single litter, for a range of common mating and dispersal strategies. We compare  
148 the level of fine-scale genetic structure between females and males to provide insights  
149 into the ecological questions that can be answered using the combination of Y  
150 chromosome, mtDNA and autosomal markers.

151 We explore three key hypotheses related to both mating and dispersal: (1) fine-  
152 scale genetic structure across autosomal, mtDNA and Y chromosome markers will be  
153 strongly influenced by dispersal, with limited dispersal increasing fine-scale genetic  
154 structure and high levels of dispersal reducing this structure. (2) When comparing Y  
155 chromosome with mtDNA markers (paternally and maternally inherited markers),  
156 varying the mating system from promiscuity to monogamy and polygyny will influence  
157 fine-scale genetic structure differently for females and males. (3) Increased reproductive  
158 success under promiscuity (females) and polygyny (males) will lead to increased fine-  
159 scale genetic structure at autosomal, mtDNA and Y chromosome markers.

160

161 **Methods**

162

163 Several life-history traits of the agile antechinus provide rich opportunities for  
164 simulation-based testing (Banks & Peakall 2012). This semelparous dasyurid marsupial  
165 is commonly found in south-eastern Australia. Promiscuous mating occurs in the same  
166 week each year and individuals mate in their first breeding season after birth. All males  
167 die after this breeding season and very few females survive to reach a second breeding  
168 year, resulting in almost completely discrete generations (Cockburn *et al.* 1985; Naylor  
169 *et al.* 2008). Females can have up to 10 young, with most litters sired by two or three  
170 males; however, as many as seven sires for a single litter have been found (Kraaijeveld-  
171 Smit *et al.* 2002b; Banks *et al.* 2005a). After weaning, almost all juvenile males  
172 disperse, whereas females remain strongly philopatric (male-biased dispersal; Cockburn  
173 *et al.* 1985; Banks *et al.* 2005a). Daily movements for most individuals are less than 100  
174 m, although social home ranges vary between the sexes (Lazenby-Cohen & Cockburn  
175 1991; Banks & Peakall 2012). Over a multi-year study, the social range for females  
176 never exceeded 3 ha on average, whereas males could exceed 5 ha on average  
177 (Lazenby-Cohen & Cockburn 1991).

178

179 *Simulation details*

180 Spatially explicit genetic simulations were conducted using an extended version of the  
181 software package GenAIEx 6.5 (Peakall & Smouse 2006, 2012). The simulation process  
182 is well documented in previous studies by Banks & Peakall (2012) and Blyton *et al.*  
183 (2015), and simulations are extensively validated in the supplementary data for these  
184 papers. Here, we added the capability to output haplotypes for mtDNA and Y  
185 chromosome markers and to vary reproductive parameters.

186 After defining parameters, we simulated mating and dispersal to create spatially  
187 referenced, autosomal genotypes and mtDNA and Y chromosome haplotypes for all  
188 individuals within the simulation landscape. Simulations were performed over a  
189 continuous, hypothetical 5.6 x 5.6 kilometre landscape, with a total carrying capacity of  
190 15700 individuals and an equal sex ratio. Density was controlled following Banks &  
191 Peakall (2012) and Blyton *et al.* (2015), with a mean of 5 and maximum of 10  
192 individuals ha<sup>-1</sup>, consistent with findings for density in real populations (Banks *et al.*  
193 2005a). At the end of each simulation, we subsampled 500 individuals for analysis from  
194 the central 100 ha, as previous work revealed that differences in spatial autocorrelation

195 patterns between the sexes are most readily detected at or below the scale over which  
196 dispersal is limited in the philopatric sex (Banks & Peakall 2012). This is also true for  
197 behavioural processes, which are likely to occur over the scale of a home range (Banks  
198 & Peakall 2012; Blyton *et al.* 2015). A focused sampling effort (rather than sampling  
199 spread over many kilometres) is therefore most likely to detect meaningful differences  
200 in spatial autocorrelation patterns between the sexes (Banks & Peakall 2012).  
201 Furthermore, the scaling of dispersal, population density and sampling in our  
202 simulations is likely to be indicative of many empirical studies of small mammals and  
203 represents a feasible sampling design. The relative scaling of these processes should  
204 also be applicable to many molecular ecological studies of similar processes in other  
205 taxa.

206

#### 207 *Overview of the simulation process*

208 Simulations began with the setup of initial allele and haplotype frequency distributions,  
209 drawn at random from an even distribution of 10 autosomal loci with 10 alleles each  
210 and 10 mtDNA and Y chromosome haplotypes. In reality, the number of unique  
211 mtDNA and Y chromosome haplotypes identified varies considerably among studies  
212 and taxa. However, we chose to use 10 haplotypes as this is representative of real  
213 situations, with many population-level studies finding between 1–18 mtDNA and Y  
214 chromosome haplotypes within populations, at the sequences analysed (e.g. in birds:  
215 Johnson *et al.* 2003; Pierson *et al.* 2010, mammals: Eriksson *et al.* 2006; Nietlisbach *et*  
216 *al.* 2012, and reptiles: Ujvari *et al.* 2008). Furthermore, exploratory analyses revealed  
217 that variation in the number of loci, alleles and haplotypes did not dramatically alter  
218 patterns of genetic structure, but did influence the power of spatial autocorrelation  
219 analysis (Appendices S2 – S3). This is particularly important for directly comparing  
220 mtDNA and Y chromosome markers, since the number of haplotypes generally differs  
221 between markers in empirical data.

222 Genotypes and haplotypes were randomly constructed from pre-defined allele  
223 and haplotype frequency distributions and sex and XY coordinates were randomly  
224 allocated. The first generation was obtained by random mating among all individuals in  
225 the population (establishing Hardy-Weinberg equilibrium), with offspring becoming  
226 parents in the following generation. After this initial random generation, mating  
227 included nearest neighbours only. Sires were drawn from a list of potential nearest  
228 neighbour mates (calculated from pairwise geographical distances among individuals),

229 with a mean of 72–76 m, approximating the distance over which females select male  
230 antechinus in the wild (0–200 m; Banks *et al.* 2005b). When simulating polygyny, this  
231 distance was reduced to an average of ~30 m, owing to the parameter set changes  
232 required to represent the harem structure usually associated with this mating system (for  
233 detailed information on mate search distances across all mating systems, see Appendix  
234 S4). Inbreeding avoidance mechanisms were not included in simulation parameters  
235 (with the exception of sex-biased dispersal, detailed below). These mechanisms are  
236 unlikely to be important for our results given that we measured fine-scale genetic  
237 structure within same-sex individuals (and only then compared between the sexes).  
238 However, this could be investigated by comparing opposite-sex pairs (see Blyton *et al.*  
239 2015). Following mating, female and male offspring were dispersed.

240 In a genetic mark-recapture study, Banks (2005) found that juvenile males  
241 dispersed 1250 m on average (median 274 m; maximum 6000 m). However, males of  
242 the closely related *Antechinus stuartii* only dispersed a mean distance of 387 m (median  
243 303 m; maximum 1230 m; Fisher 2005; Banks *et al.* 2011). In both studies, female  
244 mean dispersal was <100 m. Therefore, in our simulations dispersal distances were  
245 drawn from an exponential distribution with a mean dispersal distance of 100 m  
246 representing philopatry or restricted dispersal, and a mean dispersal distance of 500 m  
247 representing high dispersal (2.5–97.5 percentiles of dispersal distances: restricted  
248 dispersal = 2.6 m – 407.5 m; high dispersal = 12.8 m – 1864 m. For distributions of  
249 dispersal distances, see Appendix S5). The direction in which an individual dispersed  
250 was decided by drawing a random angle from 0° to 360°. If the resulting coordinates  
251 were already at maximum density, this process (allocating dispersal distance and  
252 direction) was repeated until an available location was found, for a maximum of 20  
253 search loops.

254 We ran all simulations for 100 generations, as exploratory analyses indicated  
255 that fine-scale genetic structure develops quickly, but can take 10–15 generations to  
256 fully stabilise (Appendix S6 and Banks & Peakall 2012). Female and male genetic  
257 (autosomal, mtDNA and Y chromosome) and geographical distance matrices were  
258 output at the 100<sup>th</sup> generation, after dispersal had occurred. This process was repeated  
259 for 100 simulations, with a new population created at the beginning of each simulation.  
260



261 *Simulation parameters*

262 Simulation parameters were divided into two categories, those that were fixed  
263 throughout this study (and drawn from the biology of the agile antechinus) and those  
264 that were varied. Fixed parameters included non-overlapping generations that lasted one  
265 year, an equal sex ratio and a mean population density of five animals per hectare, with  
266 a maximum density of 10. The maximum number of offspring for both sexes was held  
267 at 10 for all simulations (Banks *et al.* 2005b). Several other parameters were varied in  
268 order to ask the following questions:

269

270 ***What is the effect of dispersal on fine-scale genetic structure at autosomal, mtDNA***  
271 ***and Y chromosome markers?***

272 We simulated three different dispersal scenarios by changing the mean exponential  
273 dispersal distance for females and males. Male-biased dispersal (consistent with the  
274 antechinus system) was modelled by setting mean dispersal distance to 100 metres for  
275 females and 500 metres for males (hereafter simplified as F100/M500). Restricted  
276 dispersal (or philopatry) was modelled by setting both male and female mean dispersal  
277 distance to 100 metres (F100/M100). This dispersal scenario was also simulated to  
278 represent sampling individuals pre-dispersal (as individuals within the same litter and  
279 neighbouring litters remained spatially clustered when the mean dispersal distance was  
280 100 m). Finally, high dispersal was modelled by setting the mean dispersal distances for  
281 both sexes to 500 metres (F500/M500). We did not investigate less extreme levels of  
282 sex-biased dispersal as previous research using autosomal markers suggests that when  
283 one sex is strongly philopatric, the signals of sex-biased dispersal develop rapidly, even  
284 when this bias is subtle (Banks & Peakall 2012).

285

286 ***What is the effect of the mating system on fine-scale genetic structure at autosomal,***  
287 ***mtDNA and Y chromosome markers?***

288 We simulated three common mating strategies by varying a range of parameters under  
289 each of the above dispersal scenarios (see Fig. 2 for a detailed infographic describing  
290 this process, with predictions for how these processes influence fine-scale spatial  
291 genetic structure at mtDNA and Y chromosome markers). We simulated promiscuity  
292 (consistent with the antechinus system), monogamy and polygyny. In all three cases,  
293 females could produce an average of three offspring ( $\lambda = 3$ ) with the allocation of  
294 offspring to females following a Poisson distribution with the maximum number of

295 offspring capped at 10. In each generation, females were randomly selected for mating  
296 until the carrying capacity was reached. The number of females contributing to  
297 reproduction and the average number of offspring produced by each female did not  
298 differ substantially between promiscuity ( $\lambda = 3$ ), monogamy and polygyny. Conversely,  
299 the number of males contributing to reproduction and the average number of offspring  
300 produced by each male differed dramatically between mating systems (see below, as  
301 well as Appendices S7 – S9, for detailed parent and offspring data).

302 Promiscuity was modelled by allowing a maximum of five males to contribute  
303 to the paternity of a litter with the mean number of sires per litter approximately 2.75.  
304 Sires were drawn from the 10 nearest neighbours. On average (over all 100  
305 simulations), 4978 females contributed to reproduction compared to 6014 males, from a  
306 total of 15700 individuals. Females produced a mean of 3.15 offspring, whereas males  
307 produced a mean of 2.61.

308 Monogamy was modelled by reducing the number of sires per litter to one and  
309 specifying that males were only able to mate once. An average of 4934 individuals of  
310 each sex contributed to reproduction and both females and males produced 3.02  
311 offspring on average. This meant that the number of males contributing to reproduction  
312 decreased by 18% and the mean number of offspring per male increased by 16%  
313 relative to promiscuity ( $\lambda = 3$ ).

314 To represent polygyny, the maximum number of sires per litter and the number  
315 of nearest neighbours were reduced to one, effectively forcing females to mate with  
316 only one male. However, males could be the nearest neighbour for multiple females,  
317 meaning they were able to mate more than once. Therefore, a smaller number of males  
318 were producing more offspring, across multiple litters. The mean number of offspring  
319 produced by males increased by 74% to 4.55 and the number of males contributing to  
320 reproduction decreased by approximately 43% to 3451, relative to promiscuity ( $\lambda = 3$ )  
321 (females = 3.16 and 4975 respectively). Under polygyny, it was possible for one male to  
322 sire only one litter, thus monogamy could also occur. However, this is also a possibility  
323 in real populations and would weaken any sex-specific differences in fine-scale spatial  
324 genetic structure caused by the mating system, meaning that conclusions were drawn  
325 from conservative estimates of sex-specific differences in structure.

326

327 ***What is the effect of reproductive skew on fine-scale genetic structure at autosomal,***  
328 ***mtDNA and Y chromosome markers?***

329 In many real-world cases, only a subset of individuals successfully reproduce, such that  
330 mating success is strongly skewed. To explore this component of reproductive biology,  
331 we investigated the impact of increasing levels of reproductive skew for both females  
332 and males across all dispersal scenarios. Extreme female reproductive skew was  
333 investigated under promiscuity by changing the mean number of offspring produced by  
334 females ( $\lambda$ ) from 3 to 8, meaning females produced larger litters. By increasing the litter  
335 size, the carrying capacity of the population was reached before the majority of females  
336 reproduced, thus skewing reproduction in favour of a small number of females. This  
337 resulted in a 58% decrease in the number of females contributing to reproduction (mean  
338 = 2070) and the mean number of offspring produced by each female increased by 141%  
339 (mean = 7.58) (compared to promiscuity,  $\lambda = 3$ ). Male reproductive skew also  
340 increased, but only slightly, with the number of males contributing to reproduction  
341 decreasing by 17% (mean = 5008) and the number of offspring produced by each male  
342 increasing by 20% (mean = 3.13; compared to promiscuity,  $\lambda = 3$ ).

343 Moderate male reproductive skew was investigated under polygyny, as in this  
344 mating system reproductive success is skewed towards fewer males (43% fewer males  
345 than under promiscuity ( $\lambda = 3$ ), mean = 3451). Under polygyny, males produced more  
346 offspring than under any other mating system (mean = 4.55).

347

348 *Statistical analysis*

349 We compared simulation results between females and males at autosomal, mtDNA and  
350 Y chromosome markers. Simulations were analysed in GenAlEx 6.5 (Peakall & Smouse  
351 2006, 2012) using the genetic distance based method of multilocus spatial  
352 autocorrelation analysis. This method allows any data type to be used (e.g. multilocus  
353 allelic genotypes, biallelic SNPs or haplotypes) and measures the relationship between  
354 genetic and geographical distance by estimating the autocorrelation coefficient,  $r$ , for  
355 each group of individuals over specified distance classes (Smouse & Peakall 1999;  
356 Peakall *et al.* 2003; Double *et al.* 2005; Smouse *et al.* 2008). This coefficient is bounded  
357 by [-1 +1] and is related to Moran's  $I$ , with high  $r$  values representing high levels of  
358 relatedness over a particular area. Following Banks & Peakall (2012),  $r$  was estimated  
359 for five distance classes of 100 metres each (500 metres in total), as this optimised both  
360 the scale of fine-scale genetic structure and the sample size needed for detecting this

361 structure. We used known home range size and dispersal distances to inform our choice  
362 for these distance classes, however in species where this data is unavailable, exploratory  
363 analyses can be used to determine the most biologically relevant distance classes (as  
364 outlined in Peakall *et al.* 2003; Beck *et al.* 2008).

365 We compared the distribution of male and female  $r$  values over 100 simulations  
366 at all three markers to investigate whether different behavioural and ecological  
367 processes drive sex-specific differences in fine-scale spatial genetic structure. The null  
368 hypothesis predicts no difference in fine-scale genetic structure between the sexes  
369 ( $r_{\text{females}} = r_{\text{males}}$ ). However, if the alternative hypothesis is true, then one sex will show  
370 higher levels of fine-scale genetic structure than the other. To investigate this, we  
371 looked at the distribution of differences in female and male  $r$  values ( $r_{\text{females}} - r_{\text{males}}$ ) in  
372 the first distance class, because genetic structure is more apparent at this finer scale  
373 (Banks & Peakall 2012). Under no difference in fine-scale genetic structure between the  
374 sexes, this distribution is centred on zero. However, differences in fine-scale genetic  
375 structure between the sexes will shift the distribution in a positive or negative direction  
376 (positive =  $r_{\text{females}} > r_{\text{males}}$ , negative =  $r_{\text{females}} < r_{\text{males}}$ ).

377 To test whether differences in spatial autocorrelation patterns between the sexes  
378 were significant, we compared 95% bootstrap confidence intervals (CIs) about the  
379 autocorrelation  $r$  values within each individual simulation, following Peakall *et al.*  
380 (2003). Banks & Peakall (2012) showed by simulation that this approach is consistent  
381 and conservative for both type I (falsely rejecting the null hypothesis) and type II errors  
382 (falsely rejecting the alternative hypothesis). Bootstrap 95% CIs were estimated for  $r$  by  
383 drawing (with replacement) from a set of pairwise comparisons in the first distance  
384 class (Smouse & Peakall 1999). We then tallied the number of simulations in which  
385 female and male Bootstrap 95% CIs did not overlap (indicating a significant difference  
386 in fine-scale spatial genetic structure between the sexes).

387

## 388 **Results**

389

390 Simulation performance was extensively validated and returned the results expected  
391 relative to the parameters set (see Appendices S2 – S9). Spatial autocorrelation  $r$  values  
392 were strongly influenced by varying the mean dispersal distance for females and males  
393 (Fig. 3). This was most apparent at the first distance class (0–100 metres), with genetic  
394 spatial autocorrelation  $r$  values decreasing to zero by the fifth distance class (400–500

395 metres). This was true for all markers and for all dispersal scenarios. Below, our results  
396 focus on the magnitude of  $r$  values in the first 100 m distance class, as this provides the  
397 most informative metric for investigating the effects of the biological processes  
398 modelled.

399

#### 400 ***Male-biased dispersal (F100/M500)***

401

##### 402 *Promiscuity ( $\lambda=3$ )*

403 When simulation parameters were realistic to the antechinus system, autocorrelation  $r$   
404 values were substantially higher in females than males across all three markers [Mean  $r$   
405 for autosomal = F: 0.033 vs. M: 0.004; mtDNA = F: 0.15 vs. M: 0.026; mtDNA vs. Y  
406 chromosome = F: 0.15 vs. M: 0.005 (Table 1; Fig. 4: column b)]. Across all simulations,  
407  $r_{\text{females}} - r_{\text{males}}$  (the distribution of the difference between female and male  $r$ ) was  
408 positive and did not overlap zero, meaning that female  $r$  was always greater than male  $r$   
409 (Fig. 4: column b.). Across the different marker types, female and male 95% bootstrap  
410 CIs did not overlap in 92–99 of 100 simulations (Appendix S10). The correlograms for  
411 all markers showed this typical pattern of male-biased dispersal, with non-overlapping  
412 2.5–97.5 percentiles for the distributions of  $r$  values for females and males (Fig. 3:  
413 column b).

414

##### 415 *Monogamy, polygyny, promiscuity ( $\lambda=8$ )*

416 Varying the mating system from promiscuity ( $\lambda=3$ ) to monogamy and polygyny had no  
417 apparent influence on patterns of genetic spatial autocorrelation when dispersal was  
418 male-biased (Table 1). Females showed higher levels of fine-scale spatial genetic  
419 structure than males across all marker types (Fig. 4: column b). Furthermore, female  
420 and male 95% bootstrap CIs did not overlap in 95–100 simulations (Appendix S10).

421 High male dispersal removed any impact of increased male reproductive skew  
422 under polygyny (Fig. 4: column b). However, in females (where dispersal was  
423 restricted), increasing female reproductive skew under promiscuity ( $\lambda=8$ ) resulted in  
424 higher levels of fine-scale genetic structure at autosomal and mtDNA markers [mean  $r$   
425 for promiscuity  $\lambda=3$  vs. promiscuity  $\lambda=8$ : autosomal = 0.033 vs. 0.058; mtDNA = 0.150  
426 vs. 0.283 (Table 1; Fig. 4: column b)].  $r_{\text{females}} - r_{\text{males}}$  was therefore greater than under  
427 any other mating system (Fig. 4: column b) (with the exception of the difference found

428 under polygyny at autosomal markers, which was similar to promiscuity  $\lambda=8$ ). Non-  
429 overlapping 95% bootstrap CIs were seen in 99–100 simulations (Appendix S10).

430

#### 431 ***Restricted dispersal for both sexes (F100/M100)***

432

433 Reducing mean dispersal distance to 100 metres created strong patterns of spatial  
434 autocorrelation for both females and males, with positive distributions of simulated  $r$   
435 values across all mating scenarios at autosomal, mtDNA and Y chromosome markers  
436 (Fig. 4: column a; Table 1). However, despite equal, restricted dispersal for both sexes,  
437 variation in mating system generated different patterns of genetic spatial autocorrelation  
438 between females and males when comparing Y chromosome with mtDNA markers  
439 (Fig. 4: column a).

440

#### 441 *Y chromosome versus mtDNA markers*

##### 442 *Promiscuity ( $\lambda=3$ )*

443 Under promiscuity ( $\lambda=3$ ), female mtDNA  $r$  values were greater than male Y  
444 chromosome  $r$  values [mean  $r$  for mtDNA = F: 0.137; Y chromosome = M: 0.087  
445 (Table 1)].  $r_{\text{females}} - r_{\text{males}}$  overlapped zero, but was skewed towards positive values,  
446 meaning that in most cases female fine-scale spatial genetic structure was greater than  
447 that of males (Fig. 4: column a). Female and male 95% bootstrap CIs did not overlap in  
448 36 simulations (Appendix S10).

449

##### 450 *Polygyny*

451 Under polygyny, the reverse pattern was found, with males having considerably higher  
452 autocorrelation  $r$  values than females [mean  $r$  for mtDNA = F: 0.148; Y chromosome =  
453 M: 0.214 (Table 1)]. While  $r_{\text{females}} - r_{\text{males}}$  overlapped zero, the distribution was strongly  
454 skewed towards negative values, indicating that male fine-scale spatial genetic structure  
455 was greater than that of females in the majority of simulations (Fig. 4: column a). Of the  
456 100 simulations, 51 showed non-overlapping 95% bootstrap CIs between the sexes  
457 (Appendix S10).

458

##### 459 *Monogamy*

460 Monogamy resulted in similar distributions of simulated  $r$  values between females and  
461 males [mean  $r$  for mtDNA = F: 0.111; Y chromosome = M: 0.096 (Table 1)], with

462  $r_{\text{females}} - r_{\text{males}}$  bounding zero (Fig. 4: column a). In 14 simulations, female and male  
463 95% bootstrap CIs did not overlap (Appendix S10). Given the equal dispersal and  
464 mating opportunities present under monogamy, we would expect no difference in fine-  
465 scale genetic structure between the sexes. However, this skew towards increased female  
466 structure is driven by the dispersal component of the mating system (mate-search  
467 dispersal, see Appendix S4). However, the difference in female and male fine-scale  
468 genetic structure driven by mate-search dispersal is much less pronounced than the  
469 differences driven by the actual mating behaviours (which individuals mate) across each  
470 mating system.

471

#### 472 *Promiscuity ( $\lambda = 8$ )*

473 Increased female reproductive skew under promiscuity resulted in substantially higher  
474 autocorrelation  $r$  values for females than males [mean  $r$  for mtDNA = F: 0.255; Y  
475 chromosome = M: 0.111 (Table 1)], generating a similar pattern to that seen under  
476 male-biased dispersal (Fig. 4: column a). This resulted in a substantial divergence  
477 between female and male distributions of simulated  $r$  values, with  $r_{\text{females}} - r_{\text{males}}$   
478 strongly positive and not overlapping zero (Fig. 4: column a). Female and male 95%  
479 bootstrap CIs did not overlap in 84 simulations (Appendix S10), with these results  
480 approaching those found under male-biased dispersal (where 92–100 simulations  
481 showed non-overlapping 95% bootstrap CIs between the sexes).

482

#### 483 *Autosomal and mtDNA markers*

#### 484 *All mating systems*

485 When comparing females and males at autosomal and mtDNA markers, variation in  
486 mating system influenced the magnitude of simulated  $r$  values, but patterns of fine-scale  
487 spatial genetic structure were consistent between the sexes. Under each of the four  
488 mating scenarios, female and male distributions of simulated  $r$  values mirrored each  
489 other, with  $r_{\text{females}} - r_{\text{males}}$  bounding zero (Fig. 4: column a; Table 1). Only a small  
490 number of these simulations (3–9) showed non-overlapping 95% bootstrap CIs between  
491 the sexes (Appendix S10). At mtDNA markers, increased female reproductive skew  
492 under promiscuity ( $\lambda = 8$ ) created higher levels of fine-scale spatial genetic structure for  
493 both sexes. At autosomal markers, male and female fine-scale spatial genetic structure  
494 increased under both promiscuity ( $\lambda = 8$ , increased female reproductive skew) and  
495 polygyny (increased male reproductive skew) (Fig. 4: column a; Table 1).

496

497 ***High dispersal for both sexes (F500/M500)***

498

499 *All mating systems*

500 When high levels of dispersal were present for both sexes, variation in mating system  
501 had no obvious impact on fine-scale spatial genetic structure (Table 1; Fig. 4: column  
502 c). Genetic spatial autocorrelation was not present for males or females across all  
503 markers and all mating systems. There was no apparent difference between the  
504 distributions of female and male simulated  $r$  values and  $r_{\text{females}} - r_{\text{males}}$  was centred on  
505 zero (Fig. 4: column c). Only 0–2 simulations showed non-overlapping 95% bootstrap  
506 CIs between the sexes, across all markers and mating scenarios (Appendix S10).

507

508

509 **Discussion**

510

511 The impacts of social and behavioural processes on genetic structure are often  
512 overlooked in studies focused on dispersal. Here, we have developed a simulation  
513 framework to help us understand the processes that contribute to patterns of fine-scale  
514 spatial genetic structure across uniparentally and biparentally inherited markers. We  
515 found that dispersal was the major driver of fine-scale spatial genetic structure, with  
516 limited dispersal distances generating strong patterns of fine-scale genetic structure and  
517 high dispersal removing this structure. Sex-biased dispersal is expected to generate a  
518 significant difference in fine-scale genetic structure between the sexes (Banks & Peakall  
519 2012). Indeed, in this study, we found that under male-biased dispersal, females  
520 consistently showed greater genetic structure than males across all marker types and  
521 mating systems. Furthermore, female and male 95% bootstrap CIs did not overlap in  
522 92–100% of simulations. This means, when considering a single point analysis (such as  
523 one would carry out in an empirical study), there was a 92–100% chance that a  
524 significant difference in fine-scale genetic structure would be detected between the  
525 sexes.

526

527

528

529

Along with this compelling evidence that dispersal is a major driver of fine-scale spatial genetic structure, our comparison of male Y chromosome with female mtDNA markers revealed that mating systems can also strongly influence patterns of fine-scale spatial genetic structure under restricted dispersal. Critically, promiscuity ( $\lambda=3$  and 8)



530 and polygyny, while opposite, created a result similar to that expected under sex-biased  
531 dispersal in the absence of any dispersal bias. For example, when considering a single  
532 point analysis there was a 36–84% chance of detecting a significant difference between  
533 female and male fine-scale genetic structure, generated by mating system alone. In  
534 contrast, mtDNA and autosomal markers were fairly robust across different mating  
535 systems, but fine-scale spatial genetic structure increased at both marker types when  
536 reproductive success was skewed towards fewer individuals. These findings have  
537 important implications for any studies intending to infer ecological and behavioural  
538 processes from genetic data, which we discuss in detail below.

539

#### 540 *Mating systems and reproductive skew*

541 When simulated dispersal distance was low for both sexes, the level of fine-scale  
542 genetic structure differed between Y chromosome markers in males and mtDNA  
543 markers in females depending on the mating system, despite identical dispersal patterns  
544 for both sexes. Under promiscuity, higher levels of positive genetic spatial  
545 autocorrelation were present in females than in males. Under polygyny, this was  
546 reversed, with male genetic spatial autocorrelation almost always greater than that of  
547 females. The comparative difference in the level of fine-scale genetic structure between  
548 the sexes was driven by male Y chromosome markers (see Figure 2).

549 An explanation of these patterns is offered by considering the consequences of  
550 each mating system on Y chromosome diversity. Promiscuity (and likely polyandry,  
551 though not simulated here) reduces the probability that Y chromosomes are identical-  
552 by-descent within litters, while polygyny increases the probability of identical-by-  
553 descent Y chromosomes among litters. This increases local Y chromosome diversity  
554 within litters or reduces local Y chromosome diversity among litters, thereby shaping  
555 fine-scale spatial genetic structure in the relevant groups. These results highlight the  
556 influence of mating systems and sociality in driving patterns of genetic diversity,  
557 particularly at uniparentally inherited markers. Indeed, Parreira & Chikhi (2015) used  
558 simulations and comparisons with real data from ecological and population genetic  
559 studies to show that sociality can maintain genetic diversity without the need for sex-  
560 biased dispersal or other inbreeding avoidance mechanisms. This suggests that social  
561 behaviours, such as mating strategies, are an important aspect of genetic structure and  
562 need to be accounted for in genetic studies. It is important to note, however, that mating  
563 systems can also facilitate gene-flow through additional movement in the form of mate

564 searching. The distance over which individuals choose mates can vary considerably  
565 among species and can impact patterns of gene-flow across the landscape (Double *et al.*  
566 2005). Using simulations, Blyton *et al.* (2015) showed that as the spatial scale over  
567 which individuals chose mates increased, spatial genetic structure decreased. Indeed, in  
568 our study, we found that mate-searching movements by males slightly reduced fine-  
569 scale genetic structure (as seen under monogamy). However, mating behaviour (which  
570 individuals were involved in mating) still had a much more pronounced impact on fine-  
571 scale genetic structure than this dispersal component of the mating system.

572         Increasing reproductive skew for females under promiscuity generated  
573 substantially higher levels of fine-scale spatial genetic structure at mtDNA markers in  
574 our simulations. This is likely because the population consisted of a relatively smaller  
575 number of larger litters with identical maternally inherited mtDNA. Similarly, polygyny  
576 increased fine-scale spatial genetic structure for males at Y chromosome markers, due  
577 to fewer males producing more offspring and siring entire litters with identical  
578 paternally inherited Y chromosomes (rather than producing fewer offspring across  
579 litters with multiple sires). Eldon & Wakeley (2006) used simulations and an empirical  
580 study of Pacific oysters to show that reproductive skew is an important factor for  
581 describing levels of genetic diversity across populations. Our results demonstrate that  
582 reproductive skew can also be important over finer-scales, as the effects on genetic  
583 variation described above will be exaggerated by litter size and will vary depending on  
584 the mating system. For example, increased male reproductive skew under promiscuity  
585 may counteract the reduction in genetic structure caused by multiple mating, thus  
586 resulting in similar levels of fine-scale structure for both sexes. Therefore, while the  
587 mating system creates differences in female and male genetic structure, the level of  
588 reproductive skew determines how extreme this difference will be.

589         In species where females only produce one or two offspring every year (or every  
590 few years) and the majority of females successfully reproduce, such as in mountain  
591 brushtail possums (Lindenmayer *et al.* 1998; Blyton *et al.* 2015) or white-tailed deer  
592 (Verme 1965), fine-scale genetic structure at maternally inherited markers would be  
593 expected to be low compared to species with large litters (all else, including dispersal,  
594 being equal). Conversely, in species where females produce thousands of offspring at a  
595 time, such as marine invertebrates (Hedgecock 1994), or in systems where a small  
596 number of females dominate reproduction, such as naked mole rats (Clarke & Faulkes  
597 1997; Patzenhauerová *et al.* 2013), genetic structure at maternally inherited markers

598 would be expected to be very high (in the absence of differences in dispersal). At Y  
599 chromosome markers, promiscuity, polyandry, polygyny and the number of males  
600 contributing to reproduction are all important factors for shaping fine-scale spatial  
601 genetic structure. However, these factors may also have a greater impact when females  
602 can produce more offspring.

603

#### 604 *Dispersal*

605 Dispersal had the largest impact on the magnitude and direction of fine-scale genetic  
606 structure and generally outweighed any influence of the mating system. High dispersal  
607 created low or no positive genetic spatial autocorrelation across all marker types and  
608 removed the effect of mating system on genetic structure differences between Y  
609 chromosome and mtDNA markers. When male dispersal was high, but females  
610 remained mostly philopatric, females always showed higher levels of positive genetic  
611 spatial autocorrelation than males (significant in 95-100% of simulations). Thus,  
612 philopatry plays an important role in allowing the detection of genetic structure  
613 developed under sociality.

614 Previous studies have demonstrated that social dynamics can have a major  
615 influence on the magnitude of population genetic structure, so long as some degree of  
616 philopatry is present (Chesser 1991b; Dobson *et al.* 1997, 1998; Storz 1999). For  
617 example, in greater spear-nosed bats, one successful male may sire over 50 offspring in  
618 his reproductive lifetime, whereas the majority of males will never successfully  
619 reproduce (McCracken & Bradbury 1981). Despite this extreme skew in mating  
620 success, greater spear-nosed bats showed a relatively low level of population  
621 differentiation ( $F_{ST} = 0.031$ ), most likely driven by the fact that juveniles of both sexes  
622 disperse in this species (McCracken & Bradbury 1977, 1981; McCracken 1987).  
623 Conversely, red howler monkeys also exhibit a polygynous mating system, where  
624 females live in harems and a single male usually sires the majority of offspring (Pope  
625 1990). However, in this species among-group differentiation was high ( $F_{ST} = 0.142$ –  
626 0.225), likely driven by the fact that ~33% of female red howler monkeys remain  
627 philopatric (Pope 1992). Therefore, high dispersal in greater spear-nosed bats randomly  
628 distributed genetic variation across the total population, removing any patterns of  
629 population-level genetic structure generated by the mating system. In contrast, female  
630 philopatry in red howler monkeys reinforced the population-level genetic structure  
631 developed under polygyny, creating genetically differentiated groups (Storz 1999).

632 The interplay between dispersal and mating strategies has long been known to  
633 influence patterns of genetic variation (Chesser 1991b; Sugg *et al.* 1996; Storz 1999).  
634 However, it can be difficult to resolve how these processes interact. Previous studies  
635 generally focus at the population-level, using biparentally inherited markers only  
636 (Chesser 1991b; Pope 1992; Dobson *et al.* 1997, 1998; Storz 1999; Parreira & Chikhi  
637 2015). Here, we show that individual-level, fine-scale genetic structure can also be  
638 shaped by social processes at uniparentally inherited markers. Furthermore, dispersal  
639 can potentially remove any genetic signal of mating behaviour.

640 While not assessed here, female-biased dispersal should reduce mtDNA  
641 structure, whereas male philopatry would reinforce mating systems patterns detected at  
642 Y chromosome markers. Additionally, polyandry could potentially bring male and  
643 female structure together, reducing the difference in genetic structure between the sexes.  
644 While polyandry is relatively rare in mammals (although some cases exist), there are  
645 many examples of female-biased dispersal (Dobson 1982; Favre *et al.* 1997; also, see  
646 Appendix S1).

647

#### 648 ***A combined marker approach: implications for the agile antechinus***

649 Our findings demonstrate that both dispersal and mating behaviour impact the patterns  
650 of fine-scale genetic structure in the agile antechinus, as measured at autosomal,  
651 mtDNA and Y chromosome markers. While dispersal has been a primary focus of  
652 previous studies of antechinus, simulation findings highlight that patterns of genetic  
653 structure can be shaped by a range of processes (Banks *et al.* 2005b; Banks & Peakall  
654 2012; Banks & Lindenmayer 2013). Male-biased dispersal reduced genetic structure in  
655 males compared to females across both biparentally and uniparentally inherited  
656 markers. Promiscuity also reduced male genetic structure, but only at Y chromosome  
657 markers, however, this was obscured by high male dispersal. This suggests that the  
658 impact of mating behaviour on genetic structure can only be detected when both sexes  
659 are philopatric, which does not occur in the agile antechinus (although many examples  
660 exist in other wild populations of small mammals, see Appendix S1).

661

#### 662 ***A combined marker approach: implications for studies of other species***

663 There remains potential to use the combined marker approach to learn about both  
664 dispersal and mating behaviour by sampling pre- and post-dispersal individuals, as the  
665 level of genetic structure detected can vary dramatically with temporal sampling

666 (Balloux & Lugon-Moulin 2002). While our simulations were parameterised with  
667 discrete generations, systems with overlapping generations add new dimensions to  
668 spatial genetic patterns, such as inter-generational comparisons (Blyton *et al.* 2015). In a  
669 simulation study, Blyton *et al.* (2015) found that as generational overlap increased,  
670 spatial genetic structure also increased for both sexes. Therefore, in scenarios of  
671 overlapping generations, restricting comparisons of spatial genetic structure to particular  
672 groups of individuals (e.g. adults only or pre- *versus* post-dispersal individuals) will  
673 help to link the observed patterns to the underlying process. However, in the  
674 semelparous antechinus, fine-scale genetic patterns detected in pre-dispersal individuals  
675 will be shaped by mating behaviour (and should reflect patterns shown in our  
676 F100/M100 scenario), while post-dispersal individuals should show a clear pattern of  
677 male-biased dispersal across all marker types (similar to our F100/M500 scenario).  
678 Additionally, our results indicate that it is still possible to detect these patterns when  
679 there are different levels of diversity between marker types (Appendix S3).

680 Comparisons of sex-specific patterns of fine-scale spatial genetic structure at  
681 autosomal, mitochondrial and Y chromosome markers, for both pre- and post-dispersal  
682 individuals, are expected to be of interest for many species. For example, differences in  
683 spatial autocorrelation between the sexes that are congruent across autosomal, mtDNA  
684 and Y chromosome markers would indicate dispersal is the predominant driver of fine-  
685 scale spatial genetic structure. Alternatively, inconsistent patterns across markers would  
686 indicate a mating system influence. If these patterns change between individuals from  
687 different age groups (e.g. pouch young or young at foot *versus* adults) then the impact  
688 of dispersal and mating behaviour on fine-scale genetic structure could be directly  
689 compared and these processes more accurately inferred in wild populations. This is a  
690 powerful approach, as detecting the genetic signatures of mating and dispersal  
691 independently of each other would allow studies to avoid making assumptions about  
692 which processes are shaping these genetic patterns. This is particularly important, given  
693 that mammals span the continuum of mating and dispersal strategies.

694

#### 695 ***Implications for other approaches to measuring spatial genetic structure***

696 Here, we employed spatial autocorrelation analysis to quantify the fine-scale,  
697 individual-by-individual spatial genetic patterns arising from different dispersal and  
698 mating system scenarios. This approach has the advantage of enabling visualisation of  
699 the magnitude and spatial extent of genetic structure at this fine-scale. However, these

700 patterns are also likely to be apparent using population-level statistics. For example, in  
701 our simulations the interactive effects of dispersal and mating system variation were  
702 also detectable at the population-level using an Analysis of Molecular Variance  
703 (AMOVA; Excoffier *et al.* 1992; Peakall *et al.* 1995; Michalakis & Excoffier 1996).  
704 Figure 5 shows an infographic of the AMOVA results obtained from an entire simulated  
705 landscape (5.6 x 5.6 km, under promiscuity  $\lambda=3$  and restricted dispersal), for mtDNA  
706 and Y chromosome comparisons of females and males. At the population-level, this  
707 analysis detected sex-specific differences in genetic structure similar to the patterns  
708 shown by spatial autocorrelation analysis, demonstrating that these analyses can be  
709 complementary. A key difference is that population-level analyses typically involve the  
710 sampling of pre-defined sub-population units (based on spatial scale and location).  
711 Thus, it is important to recognise that the spatial scale of sub-population sampling can  
712 have a large bearing on the results. In our example, the level of genetic structure  
713 detected with AMOVA varied depending on the distance between populations and the  
714 spatial distribution of samples.

715

#### 716 ***Other factors shaping genetic patterns***

717 The majority of studies using markers with different modes of inheritance have focused  
718 on long-term or population-level estimates of gene-flow, using F-statistics, estimates of  
719 effective population size ( $N_e$ ) or assignment tests and comparing these metrics among  
720 markers (Schubert *et al.* 2011; Nietlisbach *et al.* 2012; Hedrick *et al.* 2013; MacDonald  
721 *et al.* 2014; Verkuil *et al.* 2014). However, factors like mutation, genetic drift,  
722 bottlenecks, founder effects and selection are strongly influenced by the evolutionary  
723 history of a species and shape background levels of genetic diversity (Hedrick 2007;  
724 Charlesworth 2009; Banks *et al.* 2013; MacDonald *et al.* 2014). Therefore, when  
725 directly comparing patterns among different markers, these factors must be taken into  
726 account.

727       Here, we use an alternative approach, where the comparison is between the  
728 sexes rather than between marker types. The patterns are then only compared across  
729 markers for congruence, except when comparing mtDNA to the Y chromosome.  
730 However, the effective sizes of mtDNA and Y chromosome markers are expected to be  
731 equal, as both are haploid and lack recombination (Petit *et al.* 2002). Furthermore,  
732 Yannic *et al.* (2012) found that a 100-fold difference in mutation rates between mtDNA  
733 and the Y chromosome in their model had negligible effects on their ability to detect

734 sex-biased dispersal using population-level analyses, as mutation rates were small  
735 compared to other parameters.

736

### 737 **Conclusions**

738 Our computer simulations, initially parameterised for the agile antechinus and extended  
739 to represent a broad range of mating and dispersal strategies found in small mammals,  
740 revealed that dispersal was the major driver of fine-scale genetic structure across  
741 maternally, paternally and biparentally inherited markers. When dispersal was  
742 restricted, the mtDNA *versus* Y chromosome comparison was sensitive to variation in  
743 mating systems. Three aspects of mating behaviour, promiscuity (multiple sires per  
744 litter), polygyny (multiple litters per sire) and reproductive skew, caused changes in the  
745 spatial structure of male Y chromosomes compared to female mtDNA that led to  
746 patterns similar to those expected under sex-biased dispersal in some cases. Thus  
747 caution is required when inferring ecological processes from genetic results.

748 Nonetheless, assessing whether female and male patterns are congruent or different  
749 across markers with different modes of inheritance, and whether these patterns change  
750 when individuals are sampled at different times, may help disentangle the different  
751 ecological and behavioural processes shaping genetic structure within populations.

752

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758

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1013

#### 1014 **Data Accessibility**

1015

1016 Distance matrices and the GenALEx Add-in containing simulation routines are available  
1017 from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.kn8d2>.

1018

#### 1019 **Author Contributions**

1020

1021 RES, SCB and RP designed the study, SCB provided organismal expertise for the  
1022 *Antechinus*, RES ran simulations and downstream analyses and drafted the manuscript;  
1023 RP completed the simulation programming, all authors contributed to editing the draft  
1024 manuscript.

1025

#### 1026 **Figures captions**

1027

1028 **Fig. 1** Mating and dispersal patterns in mammals vary across a continuum, from  
1029 promiscuity to monogamy, and philopatry to high dispersal (for an extensive list of  
1030 examples, see Appendix S1). Mating systems can also differ between social mating  
1031 systems (based on spatial and temporal relationships) compared to genetic mating  
1032 systems (based on the actual parentage of offspring). Here, we show an example of the  
1033 variation in mating systems and dispersal patterns across small mammals, over fine-  
1034 scales (tens – hundreds of meters). We focus on genetic mating systems, with  
1035 definitions based on the number of mating partners involved in a breeding event, with  
1036 definitions following Campbell *et al.* (2006) and McEachern *et al.* (2009). Polyandry is  
1037 not considered in this study, as it is fairly uncommon in mammals (but see Appendix S1  
1038 for some examples). All figures were drawn or edited using Adobe Illustrator CC 2014.  
1039 **Figure References:** <sup>1</sup>Larsen & Boutin 1994 <sup>2</sup>Cockburn *et al.* 1985 <sup>3</sup>Kraaijeveld-Smit *et al.* 2002b <sup>4</sup>Banks  
1040 2005 <sup>5</sup>Zgurski & Hik 2012 <sup>6</sup>Swilling & Wooten 2002 <sup>7</sup>Ribble 1992 <sup>8</sup>Telfer *et al.* 2003 <sup>9</sup>Aars *et al.* 2006  
1041 <sup>10</sup>Nutt 2005 <sup>11</sup>Nutt 2008 <sup>12</sup>Hoogland 1998 <sup>13</sup>McCracken & Bradbury 1981



1042

1043 **Fig. 2** The impact of mating behaviour and dispersal on fine-scale genetic structure for  
1044 females and males, at uniparentally inherited markers. *Step 1:* Females (circles) and  
1045 males (squares) involved in mating are indicated by the solid (promiscuity), broken  
1046 (monogamy) and dashed (polygyny) lines. **Female mtDNA vs. male Y chromosome:**  
1047 *Step 2:* Female offspring share the same mtDNA haplotype as their sisters within a  
1048 litter, but are genetically different to females in other litters. Conversely, male genetic  
1049 structure at Y chromosome markers varies depending on the mating system. *Step 3a:*  
1050 When dispersal is restricted in both sexes, the patterns developed under each mating  
1051 system are maintained. *Step 3b:* Under male-biased dispersal, female structure remains  
1052 high, whereas male dispersal randomly distributes Y chromosome haplotypes  
1053 throughout the population. *Step 3c:* High dispersal in both sexes randomly distributes  
1054 mtDNA and Y chromosome haplotypes throughout the population. **Female mtDNA vs.**  
1055 **male mtDNA:** *Step 2:* No difference in genetic structure is detected when comparing  
1056 both sexes at mtDNA markers. *Steps 3a-c:* Dispersal reduces genetic structure at  
1057 mtDNA markers. Female skew increases the overall magnitude of genetic structure, but  
1058 this impacts both sexes equally (\*exceptions: here, only three haplotypes are  
1059 represented, creating high levels of genetic structure in these examples. With more  
1060 individuals in the population, dispersal would introduce more haplotype variation and  
1061 this structure would also likely be reduced).

1062

1063 **Fig. 3** Correlograms for females and males with mean autocorrelation  $r$  values  
1064 generated over 100 simulations, at the 100<sup>th</sup> generations ( $n = 500$ ), across autosomal,  
1065 mtDNA and Y chromosome markers. Simulations represent restricted dispersal (column  
1066 a: F100/M100), male-biased dispersal (column b: F100/M500) and high dispersal  
1067 (column c: F500/M500), for a promiscuous mating system ( $\lambda = 3$ ). Error bars around the  
1068 autocorrelation  $r$  values represent the 2.5 – 97.5 percentiles of the distribution of  $r$   
1069 values across simulations. Figures were prepared in R 3.2.2 (R Core Team 2015).  
1070 Correlograms were generated in ggplot2 (Wickham 2009).

1071

1072 **Fig. 4** Back to back bean plots showing female and male distributions of simulated  
1073 spatial autocorrelation  $r$  values in the first distance class (0-100 m) across autosomal,  
1074 mtDNA and Y chromosome markers. Different dispersal scenarios are represented in  
1075 panel columns [a) restricted dispersal, b) male-biased dispersal and c) high dispersal].  
1076 Mating systems and levels of reproductive skew are shown on the  $x$  axis. The vertical  
1077 bars in the centre of each bean plot show the 2.5 – 97.5 percentiles of the difference in  $r$   
1078 value distributions between females and males ( $r_{\text{females}} - r_{\text{males}}$ ). When the vertical bars  
1079 shift towards positive values, females generally show greater structure than males, while  
1080 a negative direction means that male structure is generally greater than that of females  
1081 (for the significance of individual simulations see Appendix S10) (R package: Bean  
1082 plot, Kampstra 2008).

1083

1084 **Fig. 5** A visual demonstration of the concordance between individual-level *versus*  
1085 population-level analyses (multilocus spatial autocorrelation analysis *vs.* an Analysis of  
1086 Molecular Variance - AMOVA). Restricted dispersal (F100/M100) was simulated under  
1087 each mating system. Different groups of individuals were then analysed within the  
1088 same, single simulation (for each mating system). **Spatial autocorrelation analysis:**  
1089 This analysis was performed on individuals spread across the entire landscape.  
1090 Significant differences in the level of fine-scale genetic structure were detected between  
1091 the sexes for all mating systems except monogamy (in the first distance class).  
1092 **AMOVA:** This analysis was performed over four “populations”, defined using different  
1093 sampling schemes (with each population made up of a random subset of 125  
1094 individuals). The highlighted section of the pie chart represents the percentage of  
1095 between population differentiation ( $\Phi_{PT}$ , an analogue of  $F_{ST}$ ). AMOVA results reflect  
1096 spatial autocorrelation patterns. However, the level of population structure (as detected  
1097 by AMOVA) varies depending on how populations are defined across the landscape and  
1098 how individuals are sampled. (Analyses were performed in GenAlEx 6.5: Peakall &  
1099 Smouse 2006, 2012)

1100

1101 **Table 1** Means and 2.5 – 97.5 percentiles of female and male  $r$  values under all  
1102 simulation scenarios (dispersal and mating behaviour), for autosomal, mtDNA and Y  
1103 chromosome markers.

1104

1105

1106 **Supporting Information**

1107

1108 **Appendix S1** Mammalian mating systems and dispersal strategies over fine-scales:  
1109 examples from the literature.

1110

1111 **Appendix S2** How does varying the number of loci, alleles and haplotypes impact  
1112 spatial autocorrelation patterns for females and males?

1113

1114 **Appendix S3** What is the effect of having different numbers of mtDNA haplotypes  
1115 compared to Y chromosome haplotypes on spatial autocorrelation patterns?

1116

1117 **Appendix S4** Distributions and summary statistics for mate search distances across  
1118 each mating system.

1119

1120 **Appendix S5** Distribution of dispersal distances under promiscuity ( $\lambda = 3$ ) for mean  
1121 dispersal distances of 100 metres and 500 metres.

1122

1123 **Appendix S6** How many generations does it take for fine-scale genetic structure to  
1124 develop and stabilise?

1125

1126 **Appendix S7** Summary statistics for the number of offspring produced by females and  
1127 males across each mating system.

1128

1129 **Appendix S8** Summary statistics for the number of parents across each mating system.

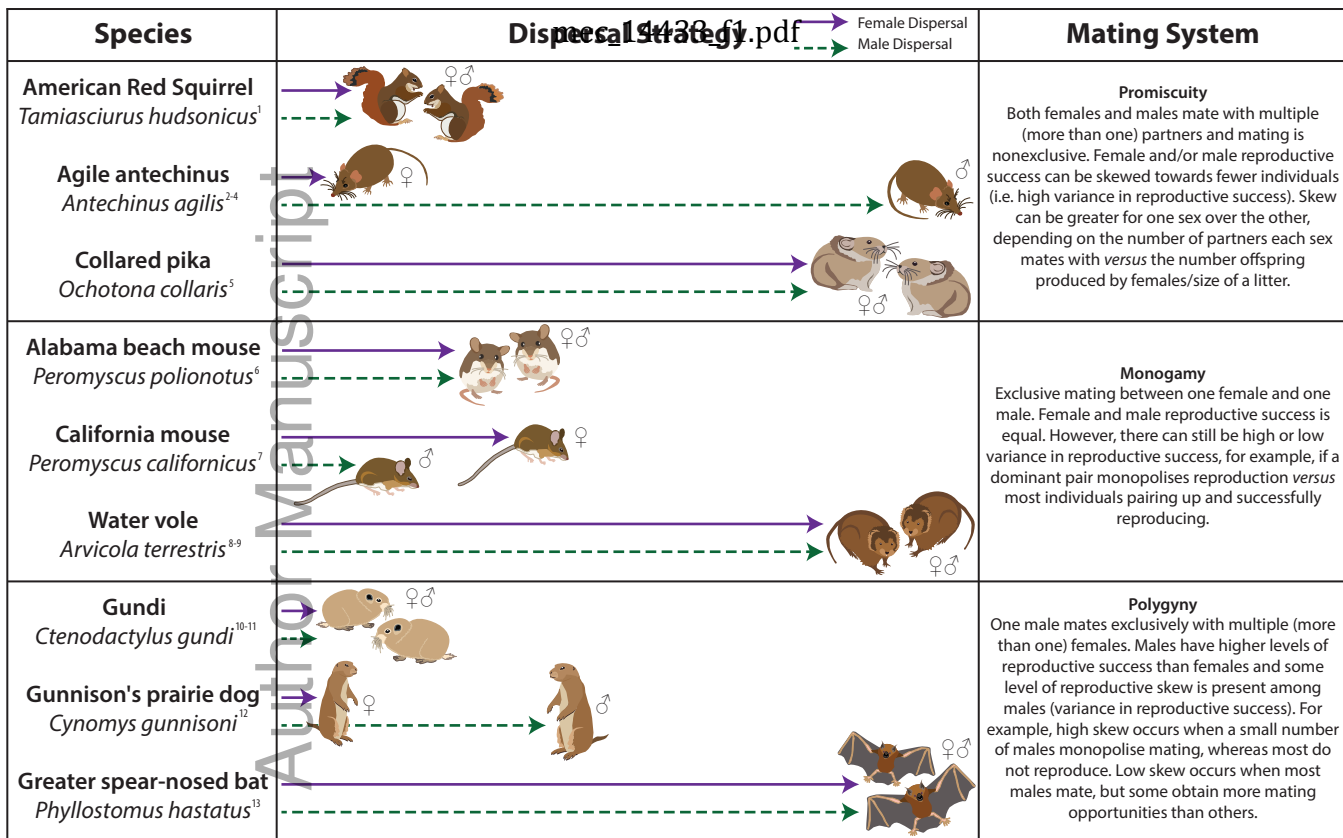
1130

1131 **Appendix S9** Distributions for the number of offspring produced by females and males  
1132 across each mating system.

1133

1134 **Appendix S10** The proportion of simulations where female and male 95% bootstrap  
1135 confidence intervals do not overlap, across all marker types, dispersal scenarios and  
1136 mating systems.

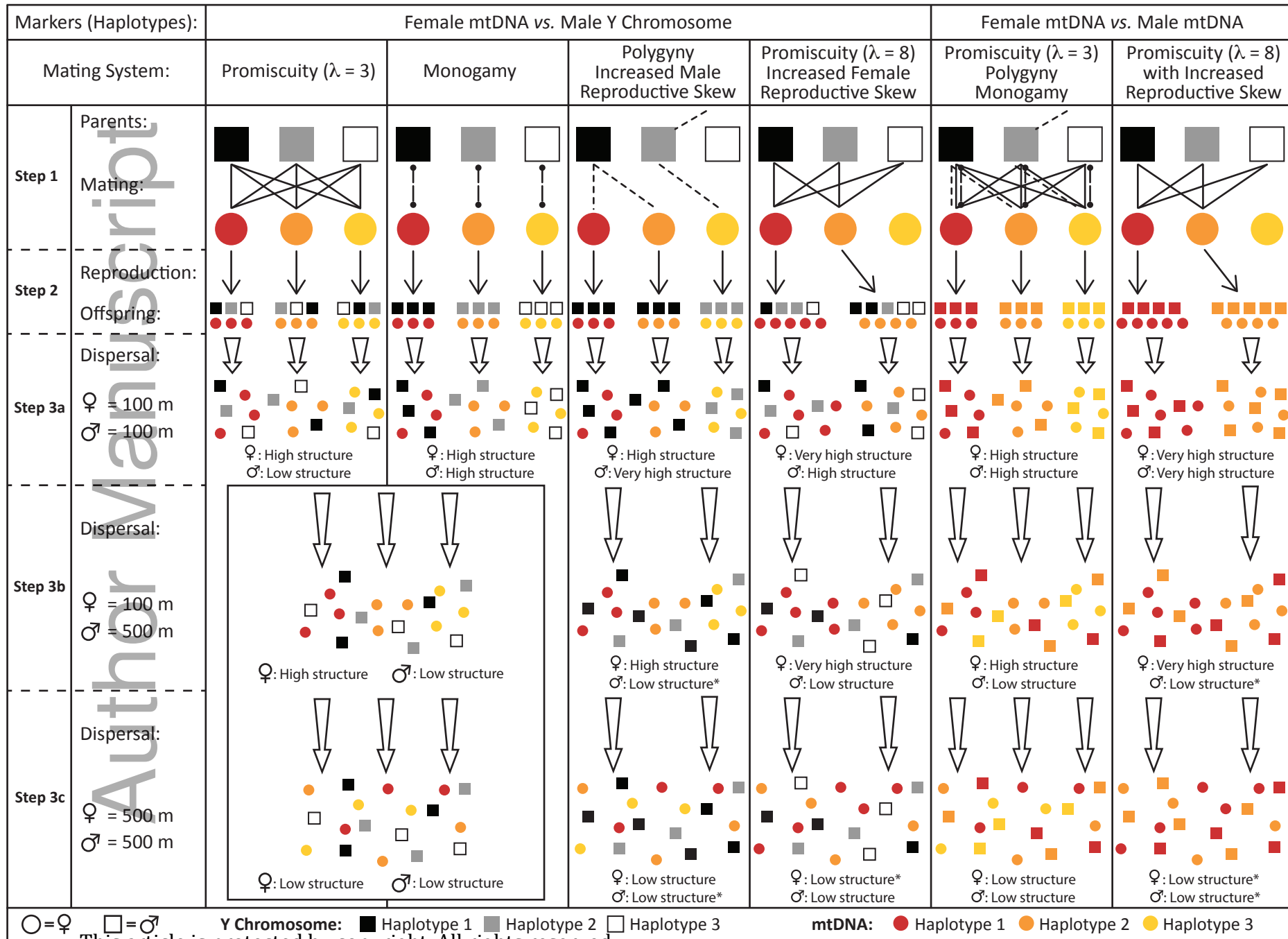
Marker	Dispersal	Mating System	Female $r$ mean ± SE	Male $r$ mean ± SE	Female $r$ 2.5 – 97.5 Percentiles	Male $r$ 2.5 – 97.5 Percentiles
Autosomal	F100M100	Monogamy	0.054 ± 0.001	0.053 ± 0.001	0.038 to 0.074	0.036 to 0.073
		Polygyny	0.103 ± 0.002	0.104 ± 0.002	0.077 to 0.141	0.074 to 0.141
		Promiscuity ( $\lambda=3$ )	0.058 ± 0.001	0.057 ± 0.001	0.04 to 0.08	0.04 to 0.078
		Promiscuity ( $\lambda=8$ )	0.1 ± 0.002	0.1 ± 0.002	0.068 to 0.138	0.07 to 0.143
	F100M500	Monogamy	0.035 ± 0.001	0.003 ± 0	0.023 to 0.051	-0.004 to 0.01
		Polygyny	0.059 ± 0.001	0.007 ± 0	0.039 to 0.088	-0.003 to 0.016
		Promiscuity ( $\lambda=3$ )	0.033 ± 0.001	0.004 ± 0	0.021 to 0.051	-0.002 to 0.012
		Promiscuity ( $\lambda=8$ )	0.058 ± 0.001	0.007 ± 0	0.039 to 0.087	-0.001 to 0.016
	F500M500	Monogamy	0.003 ± 0	0.003 ± 0	-0.003 to 0.009	-0.002 to 0.008
		Polygyny	0.004 ± 0	0.004 ± 0	-0.001 to 0.011	0 to 0.009
		Promiscuity ( $\lambda=3$ )	0.002 ± 0	0.003 ± 0	-0.004 to 0.008	-0.003 to 0.008
		Promiscuity ( $\lambda=8$ )	0.005 ± 0	0.005 ± 0	0 to 0.011	-0.002 to 0.011
mtDNA	F100M100	Monogamy	0.111 ± 0.003	0.107 ± 0.003	0.06 to 0.17	0.06 to 0.181
		Polygyny	0.148 ± 0.004	0.145 ± 0.004	0.079 to 0.246	0.072 to 0.224
		Promiscuity ( $\lambda=3$ )	0.137 ± 0.003	0.142 ± 0.004	0.082 to 0.21	0.071 to 0.234
		Promiscuity ( $\lambda=8$ )	0.255 ± 0.007	0.255 ± 0.007	0.142 to 0.4	0.135 to 0.382
	F100M500	Monogamy	0.113 ± 0.003	0.016 ± 0.001	0.066 to 0.169	-0.002 to 0.039
		Polygyny	0.142 ± 0.004	0.023 ± 0.002	0.074 to 0.235	-0.008 to 0.065
		Promiscuity ( $\lambda=3$ )	0.15 ± 0.005	0.026 ± 0.002	0.073 to 0.239	-0.003 to 0.055
		Promiscuity ( $\lambda=8$ )	0.283 ± 0.007	0.046 ± 0.003	0.133 to 0.413	0.004 to 0.106
	F500M500	Monogamy	0.005 ± 0.001	0.005 ± 0.001	-0.01 to 0.02	-0.011 to 0.024
		Polygyny	0.006 ± 0.001	0.004 ± 0.001	-0.013 to 0.024	-0.015 to 0.019
		Promiscuity ( $\lambda=3$ )	0.004 ± 0.001	0.004 ± 0.001	-0.014 to 0.026	-0.011 to 0.022
		Promiscuity ( $\lambda=8$ )	0.015 ± 0.001	0.011 ± 0.001	-0.004 to 0.039	-0.011 to 0.034
mtDNA vs. Y Chromosome	F100M100	Monogamy	0.111 ± 0.003	0.096 ± 0.003	0.06 to 0.17	0.051 to 0.152
		Polygyny	0.148 ± 0.004	0.214 ± 0.006	0.079 to 0.246	0.118 to 0.336
		Promiscuity ( $\lambda=3$ )	0.137 ± 0.003	0.087 ± 0.003	0.082 to 0.21	0.032 to 0.16
		Promiscuity ( $\lambda=8$ )	0.255 ± 0.007	0.111 ± 0.004	0.142 to 0.4	0.055 to 0.194
	F100M500	Monogamy	0.113 ± 0.003	0.006 ± 0.001	0.066 to 0.169	-0.02 to 0.028
		Polygyny	0.142 ± 0.004	0.011 ± 0.001	0.074 to 0.235	-0.015 to 0.037
		Promiscuity ( $\lambda=3$ )	0.15 ± 0.005	0.005 ± 0.001	0.073 to 0.239	-0.017 to 0.028
		Promiscuity ( $\lambda=8$ )	0.283 ± 0.007	0.009 ± 0.001	0.133 to 0.413	-0.014 to 0.036
	F500M500	Monogamy	0.005 ± 0.001	0.005 ± 0.001	-0.01 to 0.02	-0.014 to 0.026
		Polygyny	0.006 ± 0.001	0.008 ± 0.001	-0.013 to 0.024	-0.012 to 0.028
		Promiscuity ( $\lambda=3$ )	0.004 ± 0.001	0.005 ± 0.001	-0.014 to 0.026	-0.009 to 0.021
		Promiscuity ( $\lambda=8$ )	0.015 ± 0.001	0.007 ± 0.001	-0.004 to 0.039	-0.014 to 0.023



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0 100 200 300 400 ≥500

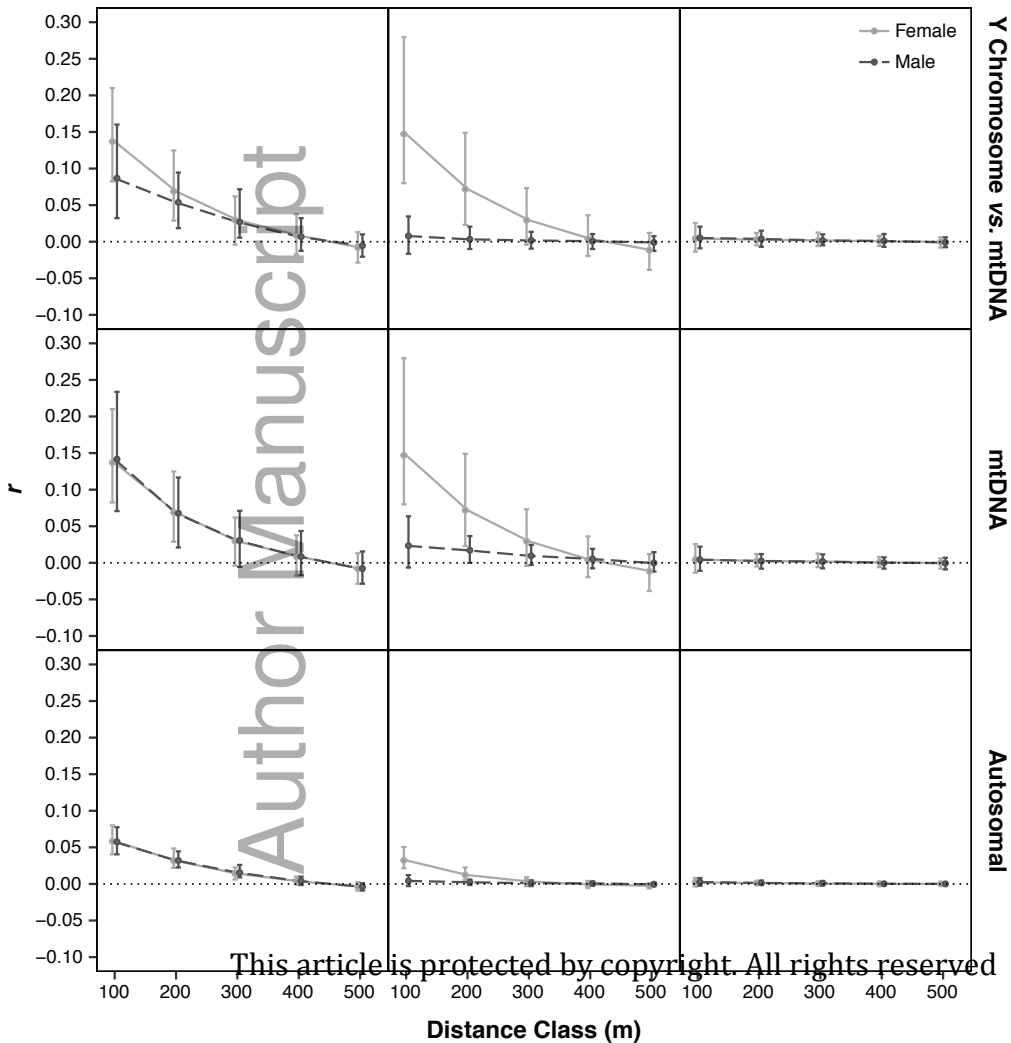
Dispersal Distance (m)



a) F100/M100

mec\_1430/BspI

c) F500/M500



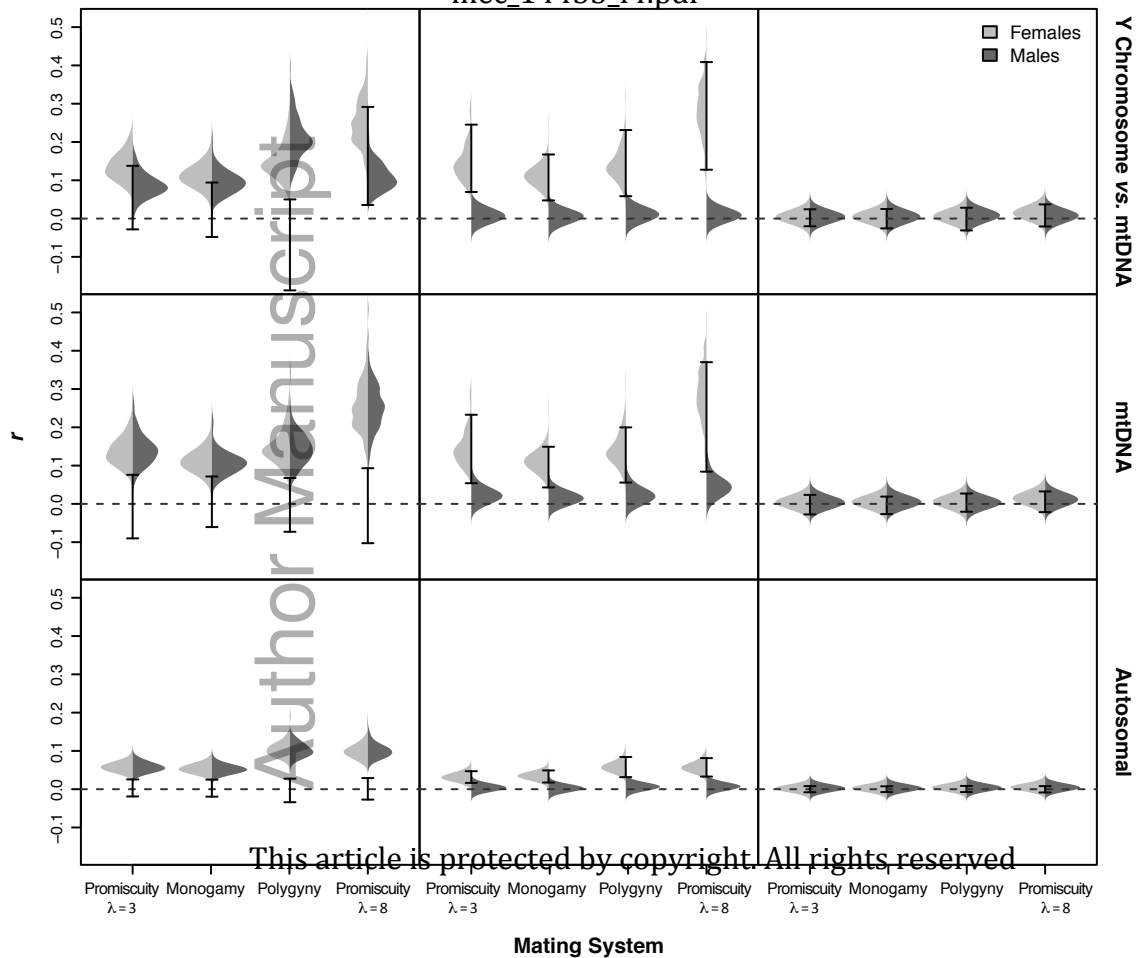
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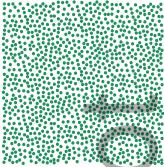
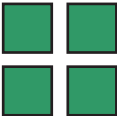
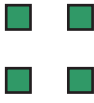
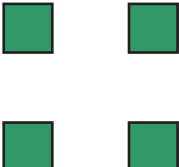
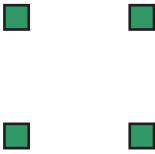
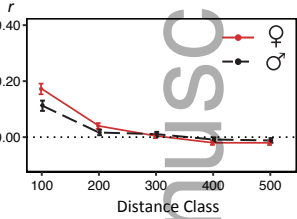
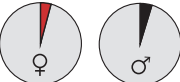



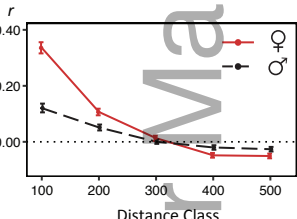




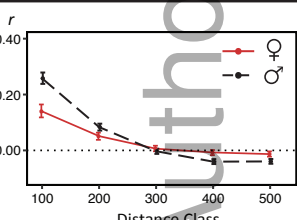




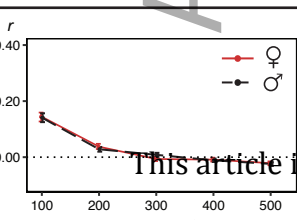





a) F100/M100

b) F100/M500

c) F500/M500



	Fine-scale Among-Individuals	$\Phi_{PT}$ Among-Populations			
Sampling scheme over 5.6 x 5.6 km	 <p>Entire landscape All individuals</p>	 <p>Close populations Spread-out sampling</p>	 <p>Close populations Focused sampling</p>	 <p>Distant populations Spread-out sampling</p>	 <p>Distant populations Focused sampling</p>
Promiscuity ( $\lambda = 3$ )		<p>4.4%    4.9%</p> 	<p>10%    7.4%</p> 	<p>9.8%    7%</p> 	<p>13.5%    8.2%</p> 
Promiscuity ( $\lambda = 8$ )		<p>10%    5.1%</p> 	<p>8.9%    9.7%</p> 	<p>14.8%    8.2%</p> 	<p>25.8%    7.4%</p> 
Polygyny		<p>8.4%    13.8%</p> 	<p>11.2%    20.8%</p> 	<p>6.3%    21.7%</p> 	<p>12.7%    26.4%</p> 
Monogamy		<p>3.7%    3.2%</p> 	<p>6.4%    4.6%</p> 	<p>4%    1.8%</p> 	<p>4.7%    3%</p> 