Integrating movement behavior with sexual selection in the lizard *Anolis sagrei.*

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Abstract

Individuals' locations in space and time determine their potential social and reproductive interactions, and thus the extent to which they experience sexual selection. However, movement behavior is rarely considered when quantifying sexual selection. We used an explicitly spatiotemporal Markov chain modelling approach to estimate the number of potential mates of male and female *Anolis sagrei* lizards from their movement behavior, and used genetic paternity assignments to complement and corroborate our model results. Females frequently encountered and mated with multiple males, offering ample opportunity for sexual selection through female choice. Further, sexual selection favored larger spatial extents and larger body sizes in males, though the effect of body size is difficult to disentangle from evidence for last-male precedence. We posit that explicitly spatiotemporal quantifications of space-use behavior could help to reconcile widespread dissonance across studies of mating systems in animals, and will be necessary for quantifying sexual selection in the wild.

Keywords: mating system, territory, territoriality, polygyny, sexual selection, *Anolis sagrei*, anole, encounter rates, movement

Introduction

17

18   Knowing the locations of males and females in both space and time is crucial to predicting

19   mating patterns and quantifying the opportunity for sexual selection (Emlen & Oring 1977; Wade

20   1995; Shuster & Wade 2003). Animals' movement patterns are a likely target of sexual selection

21   because how individuals move across space through time can directly influence the number of

22   potential mates they encounter (Wagner 1998; Kvarnemo & Simmons 2013). But by bringing about

23   such encounters between potential mates as well as between potential competitors, individuals'

24   movement patterns also set the stage for subsequent sexual selection through male-male

25   competition and female choice acting before or after copulation (Jones 2009). Integrating movement

26   behavior as both a target and a facilitator of sexual selection is thus a central challenge for

27   understanding how sexual selection acts in the wild.

28   In particular, individuals' movement patterns constrain the potential for female choice to

29   drive sexual selection. The extent to which female mate choice exerts sexual selection on males in

30   natural populations remains contentious, as do the precise mechanisms by which female mate choice

31   arises and is maintained (reviewed in Jones & Ratterman 2009; Firman *et al.* 2017). Common to all

32   models of female choice, however, is the idea that females have the opportunity to choose among

33   males. But whether and to what extent individual females in fact have such a choice depends in large

34   part on how many males they encounter (Morris 1989; Wagner 1998). Failing to account for how

35   movement behavior facilitates social interactions can therefore lead to a dissonance between

36   experimental studies offering females a choice between males, and field studies documenting mating

37   systems that only rarely allow females to choose among males (Dougherty & Shuker 2015)—if the

38   latter studies are true, then the former are largely irrelevant. Thus incorporating movement behavior

39   is integral to formulating a holistic view of sexual selection.

40   In this paper, we develop an explicitly spatiotemporal approach to estimate the number of

41   potential mates from observations of the movement behavior of male and female *Anolis sagrei*

42   lizards, to understand what mating patterns are possible in the sampled population. In particular, we

43   investigate if females encounter multiple males, which could offer females the possibility of mate

44   choice. We use genetic methods to confirm that females do in fact mate with multiple males, and

45   then characterize sexual selection in this population by examining the predictors of male

46   reproductive success at two levels. First we ask if the number of potential mates encountered by

47   males is associated with either the spatial extent of their movements or their body size. Second, we

48   test three hypotheses to understand which of the males that females encounter end up siring

49   offspring. We first examine if females bear offspring sired by the males they encounter more often

50   (Kokko & Mappes 2012). Then, we ask if males encountered later in the breeding season are more

51   likely to sire offspring than males encountered earlier ("last-male precedence"; Birkhead & Hunter

52   1990). Finally, given widespread sexual selection in animals for larger males (Andersson 1994), as

53   well as pronounced male-biased sexual size dimorphism in *A. sagrei*, we ask if females

54   disproportionately bear offspring sired by larger males. We find evidence that females both

55   encounter and mate with multiple males, and that sexual selection acts on movement behavior,

56   male-female interactions, and body size in male *A. sagrei*, suggesting the possibility for complex

57   polygynandrous reproductive dynamics including both pre- and post-copulatory mate choice.

58

Methods

59   **Methods**

60   *Field sampling and egg collection*

61   *Anolis sagrei* is a low-perching arboreal lizard native to Cuba and the Bahamas that has been

62   established in Florida for nearly a century (Kolbe *et al.* 2004; 2008). It co-occurs with the native,

63   higher-perching *Anolis carolinensis* throughout most of its range in the US, including in our sampled

64   population; however, few interactions between the two species were observed.

65   *Anolis sagrei* lizards were captured, marked, and monitored to estimate their movement

66   patterns in the University Gardens on the University of Florida campus in Gainesville, FL, from

67   March 4, 2015 to May 25, 2015 between 0900 and 1800 hours. The start date of sampling coincided

68   approximately with the increased activity of these lizards after the winter and the beginning of the

69   breeding season; we concluded sampling at about the time at which female *A. sagrei* began laying

70   eggs. We caught almost every lizard within a 7140 m^2 area and marked each captured individual with

71   a unique bead tag (Fisher & Muth 1998), which allowed us to subsequently observe and identify

72   individuals from a distance without disturbing them (in total, 4% of observations were of unmarked

73   individuals). When captured, we measured each individual's snout-vent length (SVL) as a measure of

74   body size, and removed ~2-3 cm of tail tissue for genetic analysis. At each subsequent observation

75   of a lizard, we noted its identity as well as the time and location of the observation. We avoided

76   observing the same individual more frequently than once per hour, allowing ample time for lizards

77   to resume normal behavior if disturbed by us. Approximately once a month, we recaptured and re-

78   measured males to estimate the average growth rate of males in this population.

79   We measured distances between the locations at which lizards were observed to triangulate

80   their relative positions. In areas of continuous vegetation, locations more than 1m apart were

81   considered distinct. We also mapped the location of all trees within the site at which lizards were not

82   observed, to include all trees to which a lizard could potentially have moved in our estimations of

83   their movement patterns.

84   At the end of the observation period, we captured 36 marked females and brought them into

85   captivity. Females were housed singly under established anole husbandry conditions (Sanger *et al.*

86   2008) until mid-November. Each cage contained a pot of soil in which the resident female laid eggs

87   fertilized by sperm stored from her copulations in the field. Eggs were incubated for two to ten

88   days, after which embryos were dissected from them for genetic analysis.

89   *Movement pattern analysis*

90   Analyses were carried out in R v. 3.3.2 (R Core Team 2016). We used a discrete-time Markov

91   chain to model lizards' movements between the mapped locations in the site. We divided daytime

92   hours (0800 to 2000 hours; anoles are diurnal, so we assumed that the lizards did not move at night)

93   over the sampling period (83 days) into 996 hour-long blocks. Observations were assigned to the bin

94   closest to the time of the observation. Transition probabilities (P_{ij}) between locations i and j were

95   modelled as exponentially declining with the distance between the locations (d_{ij}), with rows of the

96   transition matrix then normalized to sum to one (N is the total number of locations):

97
$$P_{ij} = \frac{e^{\lambda d_{ij}}}{\sum_{j=1}^{N} e^{\lambda d_{ij}}}$$
(Equation 1)

98   In other words, lizards were modelled as less likely to move to distant locations than to close

99   locations, with a total probability of 1 of moving from each location to *some* location within the site,

100   including staying at the same location. The value of the exponential decline parameter λ was

101   estimated by maximizing the likelihood of the observed data using the *bbmle* package (Bolker & R

102   Development Core Team 2016); separate models were fit for males and females.

103   The probability that a lizard was at a particular location at a particular hour was inferred using the

104   Markov chain model described above. Methodological details can be found in the Supplementary

105   Information below and data and code can be found at https://github.com/ambikamath/anolismovt

106   but briefly, this probability depended not only on where that lizard was seen previously but also

107   where it was seen next. We thus calculated, for each lizard, a matrix of probabilities that it occupied

108   a particular location at a particular hour, for all locations and hours. Then, we performed element-

109   wise multiplication of pairs of these matrices to calculate the probability of co-occurrence at each

110   one hour-long time bin, for every possible pair of lizards. Encounters were categorized for each pair

111   at each hour ("yes/no") from these probabilities by setting cutoffs based on the co-occurrence

112   probabilities calculated for pairs of lizards observed in the same location within an hour of one

113   another. For each hour, we inferred an encounter between a pair of lizards if their co-occurrence

114   probability was larger than the cutoff.

115   To quantify potential mating opportunities for each individual, we calculated the number of

116   females encountered by each male and the number of males encountered by each female, as revealed

117   by our model. The proportion of females that encounter multiple males and the mean number of

118   males encountered by females reveal the extent to which multiple mating by females is possible in

119   this population.

120   We quantified the spatial extent of an individual's movement by calculating the mean of the

121   distances from each observation of the individual to the centroid of all observations of the

122   individual (mean distance from centroid). Lower mean distance from the centroid indicates smaller

123   spatial extent. We jittered points randomly within a 0.5 m radius along both the X and Y axis of our

124   site before calculating mean distance from the centroid to account for the 1 m resolution at which

125   locations were mapped.

126   We estimated a growth curve for males by fitting a logistic equation to males' SVL measured

127   initially and at recaptures, using nonlinear least squares regression (Schoener & Schoener 1978; see

128   Supplementary Information). We used this logistic growth curve to estimate the SVL of each male

129   on the day of each of his inferred encounters, based on his SVL at the nearest capture, to test for

130   sexual selection on male body size and male avoidance of size-matched males (see below).

131

132   *Parentage analysis*

133   DNA was extracted from the 36 females housed in captivity, all 161 sampled males, and 383

134   offspring using an AutogenPrep 965. Six microsatellite regions were amplified for these individuals

135   (see Table S1 for primer and amplification protocol details; Bardeleben *et al.* 2004; Wordley *et al.*

136   2011), with fragment analysis performed at the DNA Analysis Facility at Yale University. Alleles

137   were scored manually after examining chromatogram peaks in Geneious v10.0.9 (Kearse *et al.* 2012).

138   Parentage analyses were performed in CERVUS v3.0.7 (Kalinowski *et al.* 2007). High

139   proportions of null alleles were estimated at three loci (Table S1); following Le Bas (2001) and

140   Husak *et al.* (2006), we retained these loci in the analysis but typed apparent homozygotes at only

141   one allele, with the other allele coded as missing. All offspring had known mothers, and we provided

142   as candidate sires for each offspring the list of males that its mother was estimated to have

143   encountered, as described above. In the simulation to determine LOD score cutoffs for assignment,

144   we provided a genotyping error rate of 0.01 (based on mother-offspring mismatch across all loci);

145   the proportion of loci typed was 0.81. Simulations were run with 23 candidate sires and the

146   proportion of sires typed set to 0.75, based on the maximum number of males encountered by any

147   female in the population (17 males). These parameters were chosen after running preliminary

148   analyses with simulations in which the proportion of sires typed was set to 0.25, 0.5, or 0.75 and the

149   number of candidate sires set correspondingly to 68, 34, or 23; following Rasmussen *et al.* (2008), we

150   chose the parameter combination with the closest match between the proportion of sires typed and

151   the observed assignment rate. We performed further analyses to test the effects of restricting the

152   number of candidate sires relative to the whole population, and of providing all sampled males as

153   candidate sires for all offspring. Detailed methods and results for these analyses are in the

154   Supplementary Information.

155   *Hypothesis Testing*

156   The number of potential mates encountered and spatial extent (mean distance to the

157   centroid) had right-skewed distributions, and were therefore log-transformed before parametric

158   analyses; SVL was analyzed untransformed. We compared spatial extent between males and females

159   using a t-test weighted by the number of observations per individual, and investigated if variation in

160   males' spatial extent was related to body size, using a linear regression of SVL at first capture vs.

161   mean distance to the centroid, weighted by the number of observations per individual.

162   Next, we examined if the number of females encountered by males varied with the spatial

163   extent of males' movement (mean distance from the centroid) and with mean male body size at their

164   encounters with females, using a multiple linear regression weighted by the number of observations

165   per individual.

166   To assess if males avoided size-matched males, we examined the differences in estimated

167   SVL between pairs of males estimated to encounter one another, and compared these differences to

168   the differences in estimated SVL between randomly chosen pairs of males. For males that were

169   estimated to encounter one another, we used the logistic growth curve to estimate their SVL on the

170   day of the encounter. We initially sampled five random pairs per pair of males estimated to

171   encounter one another, estimated their SVLs on the same day as the corresponding encounter, and

172   eliminated random pairs in which either individual had an estimated SVL less than the minimum

173   observed SVL. We then repeated this random sampling a total of 100 times to assess if the number

174   of male-male encounters among size-matched males (estimated SVL difference of 0-2 mm) was

175   significantly lower than expected by chance.

176   We used a resampling approach to examine (1) if males who sired individual females'

177   offspring encountered the mother significantly more often than males who encountered the same

178   females but did not sire offspring (encounter rate hypothesis), (2) if males who sired individual

179   females' offspring encountered those females later than males who encountered the same females

180   but did not sire offspring (last-male precedence hypothesis) and (3) males who sired individual

181   females' offspring were bigger than males who encountered the same females but did not sire

182   offspring (body size hypothesis).

183   We first calculated the difference between medians of the number of encounters between

184   male-female pairs for sires and non-sires across all offspring. We also calculated, for each male-

185   female pair, the last hour at which the pair encountered one another and maximum SVL estimated

186   for the male across all encounters between the pair as an estimate of male body size, and then

187   calculated the difference between median hour of last encounter and median body size between sires

188   and non-sires. We then recalculated these differences between medians after randomly assigning

189   each offspring a sire from the set of males that encountered the mother of that offspring.

190   Random sire assignments were performed in two ways. To address hypothesis (1), we

191   sampled uniformly from the list of males encountered by each mother. Then, to address hypotheses

192   (2) and (3), we sampled in proportion to the rate at which each male encountered each mother. The

193   former allowed us to test if sires encountered mothers more often than did non-sires, and the latter

194   allowed us to test if later-encountered males and bigger males sired offspring more often than

195   earlier-encountered males and smaller males, after accounting for variation across males in

196   encounter rates. Each resampling was repeated 10000 times.

197

Results

199   A total of 253 individuals (161 males, 92 females) were caught and marked during the

200   sampling period, and were observed a total of 5629 times. The number of observations per

201   individual ranged from one to 128; the median number of observations per individual for males and

202   females was 11 and 15 respectively.
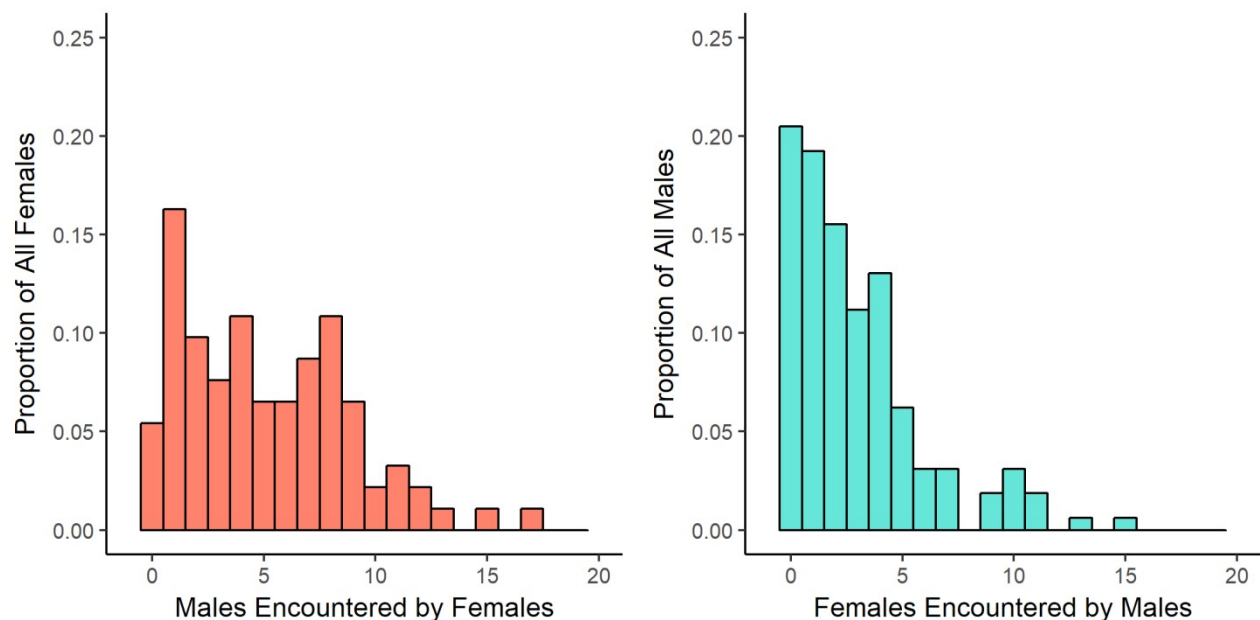
Figure 1. Histograms of the number of males encountered by females (left) and females encountered by males (right).

203   We used a Markov chain to model lizards' movements between locations in the site, where

204   transition probabilities were modelled as exponentially declining with the distance between locations.

205   We estimated λ values of -0.78 and -1.27 for males and females respectively (see Equation 1),

206   indicating that males were more likely than females to move longer distances. Using this Markov

207   chain model to estimate individuals' movement patterns, we calculated that females encountered 5.1

208   ± 3.7 males (mean ± S.D.) and males encountered 2.9 ± 3.0 females; 78% of females and 60% of

209   males encountered multiple individuals of the opposite sex (Figure 1). Males encountered an average

210   of 4.5 ± 3.6 other males.

211   The mean distance from the centroid of all of an individual's locations ranged from 0.2 m to

212   41.3 m for males and from 0.2 m to 20.8 m for females (mean ± standard deviation for males vs.

213   females: 6.8 ± 7.0 m vs. 2.7 ± 3.3 m; $t = 8.1$, $df = 208.7$, $P < 0.001$). This measure of spatial extent

214   was weakly associated with SVL at initial capture for males ($r^2 = 0.04$, $F_{1, 135} = 4.91$, $P = 0.03$).

215   To estimate male body size at their encounters with females using a logistic growth curve, we

216   recaptured 68 males and re-measured their SVLs a total of 94 times, with 32 ± 15 (mean ± SD) days

217   elapsed between measurements. The mean difference in estimated SVL between pairs of males

218   estimated to encounter one another (7.1 ± 4.5 mm) was comparable to the mean difference between

219   randomly chosen pairs of males (7.4 ± 5.7 mm). However, observed size differences were

220   underrepresented in the smallest (0-2 mm) category compared to random pairwise size differences

221   (0.11 vs. 0.18 ± 0.002; $P < 0.01$; Figure 2).
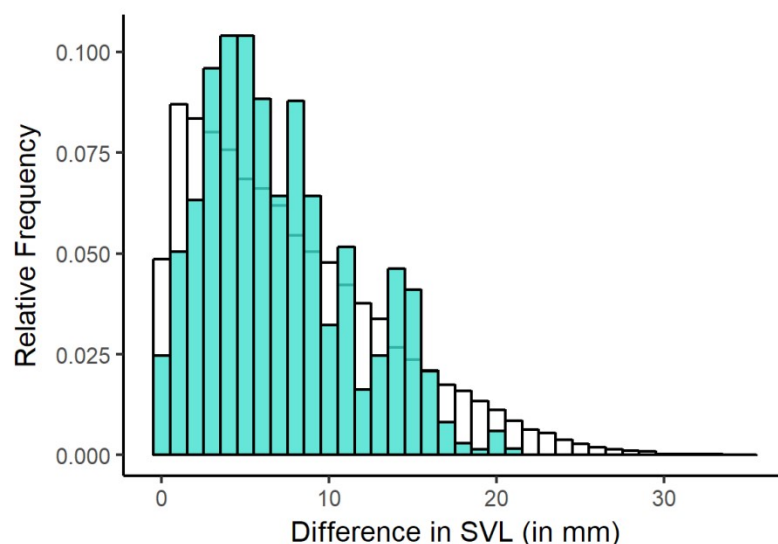
Figure 2. Estimated SVL differences between male pairs estimated to co-occur (blue bars), compared with pairwise SVL differences between randomly chosen pairs of males, with random males' sizes estimated on the same days at the observed co-occurrences (white bars).

222   Males that encountered more females had a greater spatial extent ($r^2 = 0.10$, $F_{1, 113} = 13.0$, P

223   <0.001; Figure 3) and were larger in size on average at their encounters with females ($r^2 = 0.09$, $F_{1, 113}$

224    $= 13.0$, P <0.001; Figure 3); the interaction between spatial extent and SVL was not significant ($r^2 =$

225   0.0, $F_{1, 113} = 0.03$, $P = 0.87$)
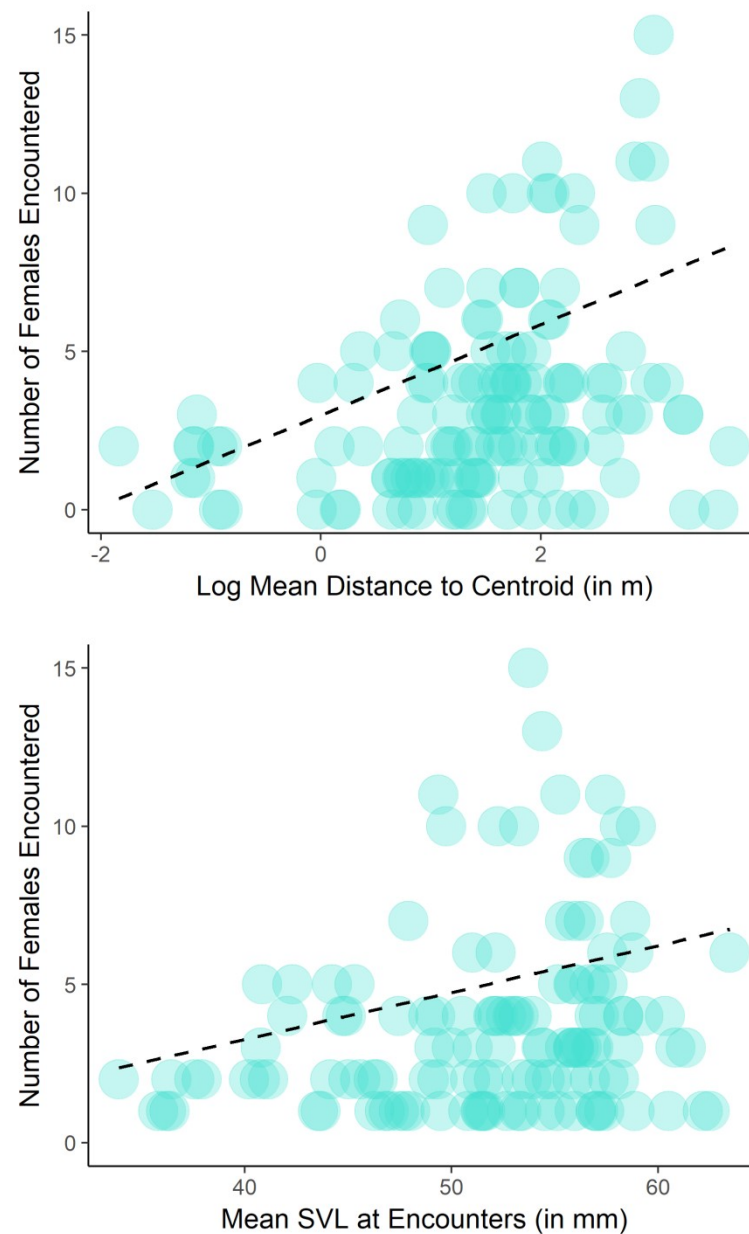
Figure 3. Relationship between the number of females encountered by males and the males' spatial extent

(top; measured as the mean distance to the centroid) and males' mean estimated SVL across encounters

(bottom).
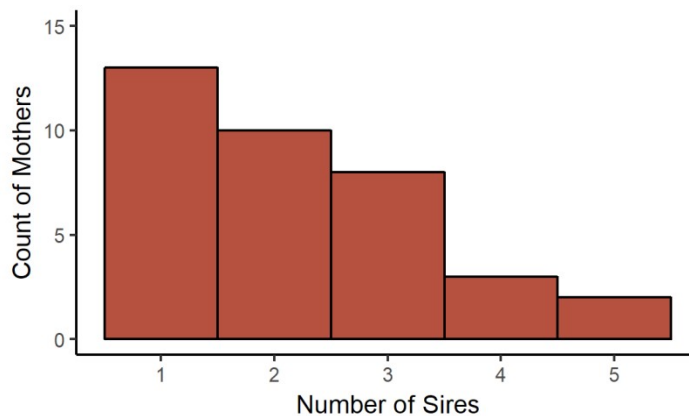
Figure 4. Histogram of the number of sires of females' offspring; 64% of females bore offspring sired by more than one male.

226 Under the parentage analysis in which we set the potential sires for each offspring to be the
227 males estimated to have encountered their mother, paternity was assigned to 84% of all offspring
228 (323 individuals) at an 80% confidence level. We found that 64% of mothers bore offspring sired by
229 more than one male (Figure 4); including offspring with unassigned sires, this proportion rose to
230 81%. Using a resampling approach, we found that sires of offspring encountered mothers
231 significantly more often than did non-sires (median number of encounters between mothers and
232 sires: 40; non-sires: 17; $P < 0.0001$). Accounting for variation across males in how often they
233 encounter mothers, we found that sires encountered females significantly later than non-sires
234 (median of the last hour of encounter for sires: 955; non-sires: 648; $P < 0.0001$) and were
235 significantly bigger than non-sires (median of the maximum male SVL across encounters for male-
236 female pairs, for sires: 58.4 mm; non-sires: 54.2 mm; $P < 0.0001$; Figure 5).
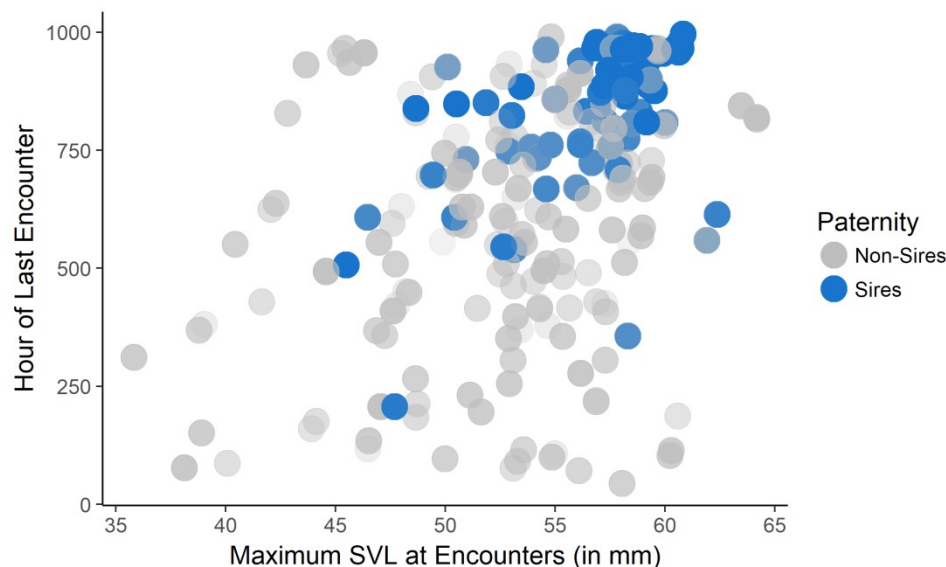
Figure 5. Maximum male snout-vent length (SVL) and the hour of last encounter for male-female pairs, colored by whether or not the male sired any of the female's offspring.

237

238 **Discussion**

239   Understanding the relationship between animals' movement patterns, mating patterns, and
240 reproductive success is essential not only for characterizing the mating system of a population or
241 species but also for determining how movement behavior both facilitates and is shaped by sexual
242 selection. In particular, female mate choice can contribute to sexual selection in natural populations
243 only if individuals' movement patterns give females the opportunity to choose among mates.

244   Developing a spatiotemporal characterization of the movement patterns of a population of
245 *A. sagrei* lizards, we found that a majority of females (78%) encountered multiple males over the first
246 three months of the breeding season. Moreover, a majority of females (64%–81%) bore offspring
247 sired by multiple males, indicating the potential in *A. sagrei* for complex polygynandrous mating
248 patterns.

249   Previous behavioral descriptions of movement patterns and mating systems in *Anolis* lizards
250 have leaned heavily on, and been constrained by, the framework of territoriality (Kamath and Losos
251 2017). These descriptions were often coupled with an implicit expectation that anoles mate strictly
252 polygynously, i.e., males mate with multiple females, but females mate with just the one male in
253 whose territory they reside. Consequently, field studies have often implied that the opportunity for
254 female choice in anoles is limited because it is precluded by territoriality (e.g. Schoener & Schoener
255 1980; Stamps 1983; Jenssen *et al.* 2001; but see Tokarz 1998). However, all the genetic evidence
256 collected so far suggests that female anoles frequently mate with multiple males (Passek 2002;
257 Calsbeek *et al.* 2007; Johnson 2007), indicating that the potential for female mate choice exists in
258 anoles. Concurrently, despite varying evidence as to whether female choice is even possible in
259 natural populations, laboratory studies have offered females the choice between males to assess
260 precopulatory mate preference (Andrews 1985; Lailvaux & Irschick 2006; Flanagan & Bevier 2014)
261 and have mated females with multiple males to assess postcopulatory sexual selection (Calsbeek &
262 Bonneaud 2008; Cox & Calsbeek 2010). Our demonstration that individual *A. sagrei* lizards in a
263 natural population move such that females frequently encounter and mate with multiple males
264 indicates that female anoles definitely have the opportunity to exert post-copulatory mate choice;
265 moreover, depending on the time-scale of mating decisions, females might also exert pre-copulatory
266 mate choice. This implies that lab-based studies of female choice can be biologically relevant, and
267 calls into question the utility of territorial polygyny as a description of these lizards' mating system.

268   That said, territoriality is a multi-faceted concept, pertinent not only to reproductive interactions but

269   also to habitat selection, space use behavior, and social interactions among males (Maher and Lott

270   1995). Our results support long-standing views in some of these facets. We found that males are

271   more likely to move greater distances and had a greater spatial extent than did females, which is

272   consistent with previous estimates of sex differences in territory size (e.g. Schoener & Schoener

273   1982; Jenssen & Nunez 1998), and with evidence for male-biased dispersal in anoles (Johansson *et al.*

274   2008; Calsbeek 2009). But the spatial extent of individuals in this population is orders of magnitude

275   higher than previous estimates of territory size in this and ecologically similar species (e.g. ~3 m^2 for

276   females and ~10 m^2 to ~14 m^2 for males; Rand [1967]; Schoener & Schoener [1982]; Calsbeek &

277   Marnocha [2006]). Although it is always possible that lizards in our site behaved unusually or, more

278   generally, that movement behavior varies across populations and species, the discrepancy may also

279   be due in part to limited spatial and temporal sampling in previous studies leading to underestimates

280   of anole space use. Limited sampling may also partially underlie why female multiple mating has

281   rarely been considered important in past research on anole territoriality—studies with limited spatial

282   or temporal sampling extents will be constrained in what behaviors they can detect (Kamath and

283   Losos 2017). Indeed, subsampling from our dataset shows that if we had limited our spatial or

284   temporal sampling extent to match the median sampling of previous studies, we would have

285   detected a greatly reduced number of male-female pairs whose home ranges overlap with one

286   another (see Supplementary Information). In sum, we posit that while certain tenets of territoriality

287   are well-supported in anoles, previous studies have likely underestimated the complexity of *Anolis*

288   lizards' movement patterns and social interactions by being constrained by a territorial framework.

289   Future studies of movement patterns that explicitly do not depend on a territorial framework,

290   conducted in a diversity of populations and species across a range of habitats and densities, will be

291   necessary to determine if we are correct.

292   Larger males encountered more females and were more likely to sire offspring than smaller

293   males. These results are consistent with conventional wisdom in anoles that larger males achieve

294   higher reproductive success than smaller males (Losos 2009), and, more generally, with evidence

295   from across animals that body size in males predicts reproductive success (Andersson 1994).

296   However, most previous evidence in favor of this hypothesis in anoles is based on the estimation of

297   mating patterns from home range area and overlap within the framework of territoriality (e.g.

298   Schoener & Schoener 1982; Ruby 1984). More recent genetic evidence has been less definite,

299   including no difference or marginal trends towards larger males siring more offspring in the wild

300   (Johnson 2007; Harrison 2014) and in lab experiments (Cox & Calsbeek 2010). In contrast to this

301   equivocal evidence, all evidence from our study points to sexual selection favoring larger body size

302   in males, helping to explain the marked male-biased sexual size dimorphism seen in this species. As a

303   species with largely indeterminate growth, body size in these lizards can be an indicator of age

304   (Schoener & Schoener 1980; Stamps 1993), or the ability to survive and thrive, suggesting an

305   adaptive reason for females to choose to mate with or bear offspring sired by larger males (Cooper

306   & Vitt 1993).

307   Selection on body size is difficult to disentangle from the possibility that large males sire

308   more offspring simply because they have encountered and mated with females more recently than

309   have small males. Last-male precedence is found in many animals (Birkhead & Hunter 1990),

310   including reptiles (e.g. Friesen *et al.* 2014), but previous evidence from laboratory experiments in *A.*

311   *sagrei* suggests instead that the first male to mate with a female is more likely than a later male to sire

312   offspring (Duryea *et al.* 2013). More targeted laboratory experiments could readily separate size

313   effects from mating order effects, lending insight into the mechanisms by which post-copulatory

314   mate choice may act in these animals. But in nature, these two effects may be largely concordant—

315   males mated with later in the mating season are likely to be bigger *simply because* they have grown

316   since earlier in the season.

317   Additionally, sexual selection may act on movement behavior—males with larger spatial

318   extents encountered more females than males with smaller spatial extents. Because male body size

319   and spatial extent were only very weakly correlated, the results do not indicate strong ontogenetic

320   shifts in movement behavior. Thus, it appears that there are multiple ways for males to achieve

321   reproductive success—they can grow large, and they can traverse large areas. Our results are similar

322   to those of Noble *et al.* (2013), who found evidence for independent effects of body size and home

323   range area on reproductive success in male skinks, *Eulamprus quoyii*.

324   However, understanding how the effects of body size, spatial extent, and last-male

325   precedence integrate with the processes of males first encountering females and then siring their

326   offspring is not necessarily straightforward. In particular, it remains unknown, but is unlikely, that a

327   single movement or mating strategy can be adaptive in the face of such social complexity. Instead,

328   animals may make decisions about movement depending on their social and environmental context,

329   as opposed to adopting fixed patterns of space-use. Such context-dependent decision making is

330   often referred to as the maintenance of "alternative mating strategies" (reviewed in Shuster 2010)

331   though this variation need not be strictly discrete (e.g. Shine *et al.* 2005; Noble *et al.* 2013).

332   The correlates of male encounter rates and reproductive success in the sampled population

333   of *A. sagrei* offer some insight into what such context-dependent decision-making could look like.

334   Unless spatial extent is correlated with other phenotypic traits, females have no way of discerning

335   males' spatial extent upon encountering them, suggesting that males' decisions to traverse large

336   distances likely only help them to encounter more potential mates. Thereafter, the number of

337   encounters between male-female pairs is related to siring success, and a male could maximize his

338   reproductive success by attempting to encounter a female repeatedly, though agonistic interactions

339   with other males may prevent such attempts. Moreover, males' siring success also depends on body

340   size. Though, to some extent, a male could evaluate the sizes of his potential rivals through displays

341   and agonistic interactions directed towards males in the vicinity of his potential mates, he has no

342   certain way of deducing the sizes of males that a female has mated with previously if those males

343   have since moved to different locations. Individual-based models that incorporate these various

344   compounding influences on reproductive success could reveal if males can make adaptive context-

345   dependent decisions to move or stay at particular locations based on their phenotype and the social

346   and environmental situations they find themselves in.

347   Discerning if the decision rules used by individuals in a species are consistent across habitats

348   and populations likely represents a promising way of understanding animal mating systems with any

349   generality, and the Markov chain modelling approach presented here could be modified in future

350   studies to incorporate both social and environmental variation influencing these decision rules—

351   transition probabilities between locations could be scaled according to habitat preferences,

352   occupancy of a location by specific individuals, and so on. Finer spatial and temporal scales of

353   location sampling, made possible with the advancement of automated methods of tracking animals

354   in the wild (Kays *et al.* 2015), could also allow for individual-level parameterization of any movement

355   model, potentially improving the accuracy with which encounters are estimated. For example, 26

356   individual offspring (7% of total) were assigned sires not among the males estimated to encounter

357   their mothers (see Supplementary Information)—it is possible that greater temporal resolution of

358   location observations would in fact have detected the movements bringing about these encounters

359   and subsequent matings. At present, however, the size and cost of tracking or receiving devices and

360   the spatial resolution of GPS data limit the range of taxa for which such methods can be employed.

361   Ultimately, even finer scale location sampling will be insufficient for determining which

362   encounters in fact lead to matings—discovering this crucial aspect of animals' behavior will depend

363   on focal animal observations of encounters in natural or naturalistic conditions. For a male, the gap

364   between encountering a female and siring her offspring can include the sequential gauntlets of male-

365   male competition, female mating preferences, and post-copulatory competition and choice—

366   disentangling effects at these various levels will be essential to fully understanding how sexual

367   selection shapes behavior, and will require close observation of animal interactions prior to and

368   including mating.

369   However, movement behavior is a precursor to bringing about any of these interactions, and

370   its quantification is therefore necessary for understanding the shape that sexual selection can take. In

371   this paper, we develop a framework to quantify movement behavior spatiotemporally to estimate

372   encounters between potential mates, and show that it reveals an infrequently-recognized opportunity

373   for female mate choice in *Anolis* lizards, as well as evidence for selection for larger males across

374   multiple levels of sexual selection. We hope that such a framework can help to organize disparate

375   studies that approach sexual selection at different levels in a variety of animal taxa.

376

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390

391 **Supplementary Information**

392 *Modelling lizard locations.*

393 As described in the main text, we modelled lizards' movements between locations using a

394 Markov chain model, where transition probabilities were fitted as exponentially declining with the

395 distance between locations (Equation 1 in main text). If **M** is the transition matrix of the Markov

396 chain model, and an individual lizard was observed at location A_m within hour T_m and then later at

397 location A_n within hour T_n, then we calculated the probability that that individual was found at a

398 particular location (L) within the hour $T \in (T_m, \ldots, T_{n-1})$ as follows:

$$P(L, T|A_m, T_m, A_n, T_n) = \frac{\mathbf{M}^{T-(Tm)+1}[A_m, L] \times \mathbf{M}^{(Tn)-T+1}[L, A_n]}{\sum_{i=1}^{N} \mathbf{M}^{T-(Tm)+1}[A_m, A_i] \times \mathbf{M}^{(Tn)-T+1}[A_i, A_n]}$$

399 N is the total number of locations mapped; in our site, we mapped a total of 318 locations,

400 which included not only locations at which lizards were observed but also trees within the site on

401 which lizards were not observed but to which they might have moved. For the hours preceding the

402 first observation and following the last observation for each individual, lizards were assumed to be

403 equally likely to be anywhere in the site (i.e. the appropriate row or column of the transition matrix

404 in equation 1 was replaced by a unit vector). In sum, after this procedure, we obtained, for each

405 lizard, a vector of probabilities of the lizard being in each of the 318 locations within each hour

406 during the sampling period.

407 *Estimating Encounters*

408 To estimate whether or not a pair of lizards encountered one another, we first performed an

409 element-wise multiplication of the two matrices of the individuals' probabilities of being at each

410 location within each hour, and then summed probabilities across all locations for each hour in the

411 resultant matrix for the pair. Probabilities were summed across locations so that two individuals that

412   may be moderately likely to co-occur at multiple locations could still be estimated as encountering

413   one another.
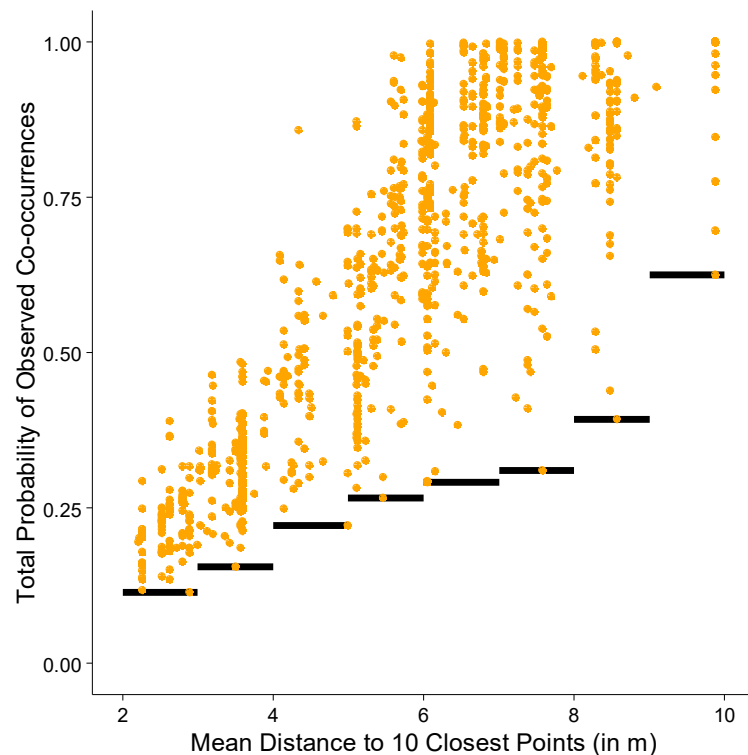
Figure S1 Cutoffs (black horizontal lines) for defining encounters, based on the mean distance from each location to the ten closest locations. Points indicate the sum of probabilities of co-occurrences across all locations, for pairs of individuals at hours where the two were observed at the same location within an hour of one another.

414

415   The calculated probabilities of observed co-occurrences, defined as a pair of lizards observed

416   in the same location within one hour of each other, were used to set the probability cutoff by which

417   we defined whether or not other pairs of lizards encountered one another. These cutoffs depended

418   on location. The 318 locations in this site were not uniformly distributed, with some locations

419   clustered more closely together than others. When the probability of movement declines with

420   distance, as modeled here, it is easier to leave a focal location that is close to other locations than it is

421   to leave a relatively isolated location. Consequently, the estimated probability of remaining at the

422   former location will be lower compared to the probability of leaving the latter location. We therefore

423   set probability cutoffs to vary by the locations at which lizards in the pair were seen, on the basis of

424   the focal locations' proximity to nearby locations First, for the location of each observed co-

425   occurrence, we calculated the mean distance to the ten closest locations to it, and saw that, as

426   expected, the calculated probability of an encounter at that location between two lizards observed to

427   co-occur increased with increasing distance to the ten closest points (Figure S1). We therefore

428   binned locations on the basis of these distances, into 1 m increments. The minimum probability

429   calculated for observed co-occurrences in each bin, denoted by the black horizontal lines in Figure

430   S1, was set as a cutoff for estimating whether or not an encounter took place, for all pairs of lizards

431   for all hours in the sampling period. Of course, using such a distance-based probability cutoff to

432   estimate encounters meant that we needed to assign a distance to all pairs of lizards for all hours. To

433   do so, at each hour we considered the previous and next locations at which the lizards in the pair

434   were observed, and found the minimum of the mean of the ten closest distances for these locations.

435   For defining encounters (as a binary "yes/no" variable) for each pair of lizards at each hour, we

436   assessed if the probability of their encounter at that hour was higher than the appropriate probability

437   cutoff based on the assigned distance.

438   To assess the sensitivity of the number of male-female encounters to the probability cutoff

439   described above, we repeated analyses using the 25% quartile instead of the minimum probability in

440   each bin; a higher cutoff is more stringent, and will recover fewer encounters, but we were curious

441   whether females would still be estimated as encountering multiple males across the sampling period.

442   Not surprisingly, conservatively increasing the probability threshold for defining encounters from

443   the minimum probability of observed co-occurrences to the 25% quartile reduced estimates of the

444   number of potential mates encountered by both females (3.4 ± 3.1) and males (2.0 ± 2.1), but the

445   potential for females to mate with multiple males remained.

446   Because boundary effects of a closed site might artificially increase the number of

447   encounters, we also assessed if the number of male-female encounters was sensitive to treating the

448   site as closed, by repeating the analyses described above with a simulated buffer of 50 locations

449   placed randomly within 20 m around the perimeter of the site to which lizards could move. Adding

450   a simulated buffer of 50 locations within 20 m of the site perimeter and allowing individuals to move

451   to these locations did not alter estimates of the average number of males encountered by females

452   (5.1 ± 3.7) or females encountered by males (2.9 ± 3.0).

453   *Growth Curve for Males*

454   We estimated the growth curve of males in this population by fitting the following logistic

455   equation (with parameters *a* and *r*) to the observed data, using nonlinear least squares regression

456   (Schoener and Schoener 1978):

$$L2 = \frac{aL_1}{L_1 + (a - L_1)e^{rD}}$$

457   where L_1 and L_2 are the SVL of an individual measured at two successive captures, and D is

458   the number of days between the two captures. We used this logistic growth curve model to estimate

459   the SVL of each male on the day of each of his encounters, based on his SVL at the nearest capture.

460   Parameters for the logistic growth curve for male SVL (Equation 3) were estimated to be a = 63.7

461   and r = -0.016. Snout-vent lengths predicted by the model were highly correlated with measured

462   SVLs ($r^2 = 0.92$).

463   *Paternity analysis*

464   Tests for sexual selection were performed on the paternity assignments in which candidate

465   sires for offspring were the list of males their mother was estimated to have encountered (described

466   in main text). However, we ran two further analyses. First, to assess if high paternity assignment

467   rates in the main analysis were a consequence of restricting the number of candidate sires relative to

468   the whole population, we also ran ten replicates of the analysis in which we sampled potential sires

469   randomly from all 161 males, preserving the number of potential sires for each offspring individual

470   and supplying the same group of potential sires for all offspring of a single female. Randomizing the

471   identity but not the number of males encountered by each mother yielded 18% paternity assignment

472   on average (13% to 24%, at an 80% confidence level), suggesting that the four-fold difference in

473   assignment rates was due to identifying potential sires with greater accuracy based on their

474   spatiotemporal movement patterns (assignment rate of 84% in the main analysis).

475   Second, we ran an analysis in which all sampled males were provided as candidate sires for

476   all offspring. Simulation parameters specified for this analysis were 161 candidate sires and 0.96

477   proportion of males typed, based on the proportion of observations in the field that were of marked

478   males. Paternity assignments were concordant for 80% of the individuals that were assigned

479   paternity by both analyses. Of the remaining 39 individuals, the LOD scores for 21 mother-sire pairs

480   differed between analyses by less than 1; these were considered false positives from the second

481   analysis, and the assignments of the first paternity analysis were retained for downstream analysis.

482   For the remaining 18 offspring, with mother-sire pairs where the LOD scores between the two

483   analyses differed by more than 1, we found that results were not altered if we conducted

484 downstream hypothesis testing both including and excluding their paternity assignments from the

485 first analysis.

486   Twenty-six individuals that were assigned paternity only when all males were provided as

487 candidate sires. For these individuals, we calculated the minimum distance between any locations at

488 which the mother and putative sire were observed, to assess the minimum distances that these

489 individuals would have had to move to mate with one another. The minimum distance between

490 locations at which mothers and sires of these 26 offspring were observed (regardless of *when* these

491 lizards were found at those locations) ranged from 0 m to 56 m, with a median of 8.7 m.

492   *Subsampling in Time and Space*

493   To understand the effect of limiting sampling in space or time on male-female home range

494 overlap (i.e. how mating patterns have often been assessed in previous studies of anoles), we asked if

495 a purely spatial predictor— the overlap in minimum convex polygons (MCPs) between pairs of

496 individuals—is affected by subsampling from our dataset to match either the median area (400 m^2)

497 or the median duration of sampling (4 weeks) or both of previous studies (see Table S2 for studies

498 and sample areas and durations included in the calculation of the medians).

499   On average, in the whole dataset, female MCPs overlap with those of 12.8 ± 8.7 males,

500 whereas male MCPs overlap with those of 8.1 ± 6.7 females. In subsamples of a randomly selected

501 area of 400 m^2 (repeated 404 times), we calculated that females overlapped a mean of 5.5 ± 3.1 males

502 and males overlapped a mean of 2.3 ± 1.2 females. In subsamples of a duration of four weeks (for

503 each of a possible 55 start dates), we calculated that females overlapped a mean of 4.5 ± 1.0 males

504 and males overlapped a mean of 3.4 ± 0.8 females. In subsamples with a randomly selected area of

505 400 m^2 and duration of four weeks, we calculated that females overlapped a mean of 2.4 ± 1.9 males

506 and males overlapped a mean of 1.5 ± 1.0 females. Thus, limited sampling in space or time decreases

507 the number of mates inferred from spatial overlap of MCP estimates of home range. That said, at all

508 scales of subsampling, we recovered that females overlap with multiple males, possibly suggesting

509 that our study population may be dissimilar to many of those studied previously, and also hinting

510 that limited sampling in space and time is not the full explanation for why previous studies of *Anolis*

511 territoriality have largely ignored the potential for females to encounter and mate with multiple

512 males (but see Tokarz 1998).

Table S1

Locus	Reference	Primers (5' – 3')	Amplification Conditions*	Null allele frequency (for bolded loci, apparent homozygotes typed at only one allele)	Number of alleles
S70	Bardeleben et al. 2004	GCAAGAGGTAGCCTCAGC GTTATCAGTACGAGGCACTG	TD1	-0.002	18
S77	Bardeleben et al. 2004	GAGTAAAGGTCTGGGTCAGG GCAGTACAAATACCACAGAGC	TD1	-0.006	16
AC8	Wordley et al. 2011	CCCAATAGAGGAAAGGGACC AGAATCACGCCTTCTGCTTT	57.7°C	**0.053**	10
AC19	Wordley et al. 2011	GAAAAGTAGTGGGGCATTGG AGTTTCCCAAGAAAACCCGT	TD1	0.007	16
AC45	Wordley et al. 2011	GCATCACCAGTCCCTTTG GCTTTGGTTGAGTTGTATTGT TTG	57.7°C	**0.11**	6
G11	J. Kolbe (pers. comm.)	GGTGCCACTGGGTATTCTGT CTCAATCCTGCTGTCACCTG	TD2	**0.16**	19

*Amplification conditions:

1. 57.7°C: 95°C for 2', 35 cycles of 94°C for 45s, 57.7°C for 45s, 72°C for 1', 72°C for 10'.

2. TD1: 95°C for 5', 10 touchdown cycles of 95°C for 30s, 55°C – 50°C for 30s, 72°C for 45s, 25 cycles of 95°C for 30s, 50°C for 30s, 72°C for 45s, 72°C for 5'.

3. TD2: 95°C for 5', 10 touchdown cycles of 95°C for 30s, 64°C – 55°C for 30s, 72°C for 45s, 25 cycles of 95°C for 30s, 55°C for 30s, 72°C for 45s, 72°C for 5'.

Table S2. Sampling area and duration of previous studies on *Anolis* home ranges

Note that though the median duration is 3.5 weeks, a more conservative value of 4 weeks was used in the subsampling analysis above.

Study	Sampling Area (in m²)	Sampling Duration (in weeks)
Evans 1938	150000	3
Greenberg and Noble 1944	25	47
Gordon 1956	400	52
Sexton et al. 1963	200	4
Rand 1967	425	5
Jenssen 1970	930	8
Jackson 1973	14000	1
Philibosian 1975	420	0.2
Stamps 1977	9.5	5
	34	13
	47	13
	37	15
Hicks and Trivers 1983	12000	9
Ruby 1984	441	28
Fleishman 1988	169	10
Jenssen and Nunez 1998	36	1
Tokarz 1998	137	5
Pereira et al. 2002	12	1
	70	1
Paterson 2002	400	1
McMann and Paterson 2003	400	1
Calsbeek 2009	1500	2
Johnson et al. 2010	500	3
Nicholson and Richards 2011	14000	52
Bush et al. 2016	875	3
Schoener and Schoener 1982	100	–
Fitch and Henderson 1976	–	1
Fitch and Henderson 1987	–	2
Fobes et al. 1992.	–	1.5
Median	**400**	**3.5**

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