

The erratic and contingent progression of research on territoriality: a case study.

Ambika Kamath^{1,2} and Jonathan Losos¹

1. Department of Organismic and Evolutionary Biology and the Museum of Comparative Zoology,
Harvard University, 26 Oxford Street, Cambridge, MA, 02138, USA.

2. ambikamath@gmail.com, 617-384-8437

ABSTRACT

Our understanding of animal mating systems has changed dramatically with the advent of molecular methods to determine individuals' reproductive success. But why are older behavioral descriptions and newer genetic descriptions of mating systems often seemingly inconsistent? We argue that a potentially important reason for such inconsistencies is a research trajectory rooted in early studies that were equivocal and overreaching, followed by studies that accepted earlier conclusions at face value and assumed, rather than tested, key ideas about animal mating systems. We illustrate our argument using *Anolis* lizards, whose social behavior has been studied for nearly a century. A dominant view emerging from this behavioral research was that anoles display strict territorial polygyny, where females mate with just the one male in whose territory they reside. However, all genetic evidence suggests that females frequently mate with multiple males. We trace this mismatch to early studies that concluded that anoles are territorial based on limited data. Subsequent research assumed territoriality implicitly or explicitly, resulting in studies that were unlikely to uncover or consider important any evidence of anoles' departures from strict territorial polygyny. . Thus, descriptions of anole behavior were largely led away from predicting a pattern of female multiple mating. We end by considering the broader implications of such erratic trajectories for the study of animal mating systems, and posit that precise definitions, renewed attention to natural history, and explicitly questioning assumptions made while collecting behavioral observations will allow us to move towards a fuller understanding of animal mating systems.

1 INTRODUCTION

2 Variation among species in social and reproductive organization has long been of interest to
3 naturalists and evolutionary biologists. Why are some species monogamous, others polygynous, and
4 yet others polyandrous? Why do some species exhibit a wide variety of different reproductive and
5 social behaviors? Understanding the selective pressures driving such variation requires quantifying
6 the extent to which different behaviors lead to reproductive success. For decades, behavioral
7 ecologists could not quantify reproductive success directly, and used proxies such as the number of
8 observed mates or offspring produced (Emlen and Oring 1977; Klug 2011). Inferring reproductive
9 success from such proxies involved making assumptions about species' biology. For example, using
10 the number of mates as a proxy for male fitness meant assuming that females do not vary in
11 fecundity, and using the number of eggs in the nest of a breeding pair as a proxy for the male's
12 fitness meant assuming that the female does not engage in extra pair copulations or that occasional
13 extra pair mates are unlikely to sire offspring.

14 However, in the last three decades, the advent of molecular means of assessing parentage has
15 allowed direct and precise measurements of reproductive fitness, enabling novel insight into the
16 complex landscapes of sexual selection acting both before and after copulation (e.g. Coltman et al.
17 2002; Birkhead 2010; Fisher and Hoekstra 2010). In many cases, these molecular measures have
18 demonstrated that what we thought we knew about reproductive success was mistaken (e.g. Avise et
19 al. 2002; Griffith et al. 2002; Uller and Olsson 2008; Boomsma et al. 2009). Specifically, biologists
20 have discovered that the assumptions linking behavioral proxies to reproductive success were often
21 not met. For example, females can vary in fecundity (Clutton-Brock 2009), mate outside of observed
22 social bonds (Griffith et al. 2002), and can store sperm, allowing for post-copulatory female mate
23 choice (reviewed in Orr and Brennan 2015). In such cases, the reason for the mismatch between
24 behavioral and genetic descriptions of mating systems is that, despite intensive field studies,
25 researchers were yet to observe important components of a population's mating system.

26 However, in this paper, we argue that mismatches between behavioral and genetic descriptions of
27 mating systems can arise not only from undiscovered biology but also from the erratic and
28 contingent progression of scientific research. In such a progression, poorly-supported conclusions
29 from the earliest studies are inadvertently reified by later researchers, who, without examining the
30 evidence for earlier conclusions, assume rather than test key ideas. Breaking away from such a

31 progression of research is not inevitable, because it requires reinvestigating ideas believed to be true.
32 Consequently, relatively unsupported corpora of knowledge about species' social behaviors and
33 mating systems may remain undiagnosed.

34 We illustrate our argument using *Anolis* lizards, a model system for evolutionary ecology in which
35 social behavior and mating systems have been studied for nearly a century (reviewed in Losos 2009).
36 These decades of behavioral research yielded the near-unanimous conclusion that anoles are
37 territorial and polygynous. In a chapter reviewing behavioral descriptions of *Anolis* mating systems,
38 Losos (2009) concluded that "as a rule, male anoles are highly territorial." Elsewhere, some of the
39 best studied species in this genus have been described, based on behavioral observations, as
40 matching "the paradigm of a territorial polygynous species" (Schoener and Schoener 1982). Stan
41 Rand, in what remains one of the best studies of anole social behavior in the wild (Rand 1967a),
42 described their mating system thus:

43 "...the lizards live together more or less permanently and the females usually mate with a
44 single male (the male with the one or more females that have home ranges within his)."

45 Judy Stamps, who spent her whole career studying anole territoriality, summarized their mating
46 system as follows (Stamps 1995):

47 "During the breeding season, male anoles defend territories that enclose the home ranges of
48 adult females, and defend these mating territories against conspecific males. Although DNA
49 paternity studies are not yet available for anoles, males probably father most of the
50 hatchlings produced by the females within their territory."

51 Tokarz (1998), describing the prevailing views from behavioral data on anole mating systems, said
52 that it is "generally believed that in territorial species of lizards, females that reside within a given
53 male's territory would have relatively few opportunities to mate with more than one male."

54 Together, these quotes help to delineate the prevailing view of anole spatial and social organization
55 based on behavioral data. Under this view, which we describe as "strict territorial polygyny" and
56 illustrate in Figure 1, males have the potential to mate with one or more females within their
57 territory, but females mate with only the one male in whose territory they are contained. If these
58 territories are maintained for the duration of the breeding season or longer, as suggested by Rand
59 (1967a), then all of a female's offspring are expected to be sired by a single male.

Territorial Polygyny in Anolis Lizards

60 However, all the genetic evidence collected subsequently indicated that females' offspring are
61 frequently sired by multiple males, and therefore that the prediction about strict territorial polygyny
62 in *Anolis* lizards was not met (reviewed below; Passek 2002; Calsbeek et al. 2007; Johnson 2007;
63 Harrison 2014). Quite to the contrary, female multiple mating is common in anoles, calling into
64 question the behavioral descriptions predicting that female anoles will mate with just one male.

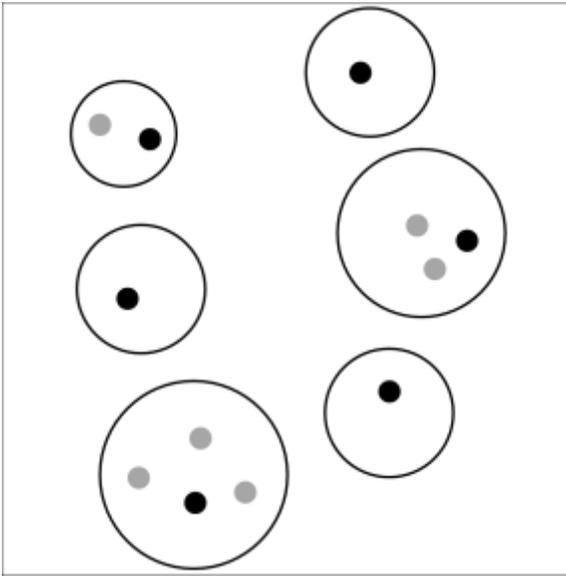


Figure 1. A pictorial representation of strict territorial polygyny. i.e. males (black) may mate with multiple females (grey) within their territories (black circles), but females mate with just the one male in whose territory they are contained. If this spatial organization is maintained for the duration of the breeding season, then all of a female's offspring will be sired by just one male.

65 At the heart of this discrepancy between behavioral predictions and genetic data on female mating
66 patterns is the concept of territoriality. Though territoriality is central to the behavioral descriptions
67 of mating systems in many animals (Emlen and Oring 1977; Fitzpatrick and Wellington 1982; Lott
68 1984), the term itself is fraught with inconsistency and imprecision across different studies. Most
69 often, the term "territorial" is used to describe individuals that defend an exclusive area in a fixed
70 spatial location (Tinbergen 1957; Martins 1994; Maher and Lott 1995), indicating that the definition
71 of territoriality incorporates two features: site fidelity (the tendency of an individual to remain in or
72 return to a fixed spatial location) and exclusivity (the tendency of an individual to exclude other
73 individuals, particularly conspecifics of the same sex, from the area they occupy). Under the strictest
74 interpretation of territoriality in *Anolis* (Figure 1), females mate with just one male; however, more
75 relaxed interpretations of territoriality incorporating some variation in site fidelity, exclusivity, or
76 both, can be consistent with female multiple mating. Imprecise and changing interpretations of
77 territoriality across studies of anole social behavior may therefore have played an important role in
78 producing the mismatch between behavioral and genetic descriptions of their mating system.

79 In this paper, we trace the evidence for the idea that anoles are territorial, and that this idea of
80 territoriality led to the expectation of polygynous mating patterns. To this end, we examine nearly a
81 century of research on *Anolis* mating systems (see the Appendix for a list of papers considered). Our
82 goal is to discern *how* we came to expect that female anoles mate with just one male when in fact
83 they frequently mate with multiple males. Specifically, we examine if this research was somehow set
84 on a path towards reifying a particular conception of territoriality that is inconsistent with
85 widespread female multiple mating, leading to the erroneous expectation that anoles show strict
86 territorial polygyny (Figure 1). Throughout, we highlight whether the definitions and interpretations
87 of territoriality employed by different researchers include site fidelity, exclusivity, or both, and pay
88 attention to whether variation in site fidelity and exclusivity that could have explained female
89 multiple mating remained undetected or was otherwise ignored.

90 We show that current ideas about anole social structure originated in studies whose scope and
91 content is not commensurate with the weight they currently bear. These equivocal demonstrations
92 of territorial behavior in early studies were seemingly taken at face value by later researchers, whose
93 research included implicit and explicit assumptions about the existence of territoriality.
94 Consequently, the design of later studies was often such that these studies were unable to detect
95 variation in site fidelity and exclusivity. Moreover, even when later researchers found evidence for
96 departures from strict territorial polygyny, this evidence was often deemphasized or ignored during
97 data analysis and in the discussion of results. Given that mismatches between behavioral and genetic
98 descriptions of mating systems are taxonomically widespread, our historical investigation reveals
99 concerns that are likely not unique to *Anolis*. We conclude by considering the broader consequences
100 of our case study for future research on animal mating systems.

101 **THE EARLIEST STUDIES OF ANOLE SOCIAL INTERACTIONS**

102 The first study of lizard mating systems—Noble and Bradley (1933)—combined a review of existing
103 natural history literature with laboratory observations on a taxonomically wide variety of lizard
104 species. Both the lizards' survival (“less than a year” for five species of *Anolis*, which typically live for
105 at least a year even in the wild; Losos 2009) and their behavior indicated that the conditions under
106 which these lizards were housed were likely stressful. Nearly half of all instances of copulatory
107 behavior observed in *Anolis* by Noble and Bradley (1933) was between males. While this behavior
108 was recognized as unusual, it was nonetheless interpreted as supporting territoriality—because

109 lizards frequently engage in male-male copulations only in the lab, in nature these male-male
110 copulations must be prevented by *something*.

111 This “something” was concluded to be the maintenance of exclusive territories, as evidenced by
112 males’ propensity for aggression toward one another. Noble and Bradley (1933) remarked that
113 “males tend to fight, and would, no doubt, tend to mark out territories for themselves.” Later, they
114 said, about lizards in general, that “the only mechanism which is present to prevent males from
115 copulating with other males as frequently as with females is that males when meeting each other
116 during the breeding season tend to fight. The result is that males tend to occupy discrete territories,
117 which are difficult to recognize in the laboratory but which have been described in the field.” The
118 field studies of *Anolis* behavior referenced by Noble and Bradley (1933) only describe male-male
119 aggression, and not site fidelity by either males or females. Thus, the existence of territoriality in
120 anoles was first concluded on the basis of male-male aggression.

121 Evans (1936 a, b, c) also concluded from laboratory experiments that male and female *Anolis* lizards
122 maintain territories. Evans (1936 a, c) detailed a weight-based social hierarchy among male *Anolis*
123 *carolinensis* based on their aggressive interactions, which were described as the “urge to hold
124 territory.” Again, conclusions were extrapolated from cages, in which animals were kept at high
125 densities, to the field. For example, Evans (1936c) suggested, without reference to field data, that
126 “the behavior of caged male *Anolis* is probably a modification of the behavior in the field. Under
127 natural conditions when a strange male approached a particular territory which is in possession of
128 another, a fight results...the beaten male retreats, leaving the victor in possession of the territory.”

129 Evans’ (1938a) subsequent field study was the first systematic research on anole territorial behavior
130 in nature. Watching a population of *Anolis sagrei* for about a month, Evans (1938a) concluded that
131 “*Anolis sagrei* exhibits a strong urge to select and defend a definite circumscribed territory.” Though
132 this conclusion was largely based on observations of male-male aggression, Evans (1938a) also said
133 that “proof that the species is territorial is given by the fact that the same individual has been
134 observed many times on consecutive days upon a particular territory.” This dual approach indicates
135 that Evans (1938a) included site fidelity as well as exclusivity in his conception of territoriality.
136 Fortuitously, Evans (1938a) included transcriptions of all field notes taken during this study, which
137 reveal that he concluded site fidelity based on a mean of three distinct observations per lizard.
138 Though his systematic field-based approach was certainly path-breaking for its time, three

139 observations made within a short period relative to the full breeding season (*A. sagrei* breed for at
140 least six months; Tokarz et al. 1998) cannot be considered sufficient to demonstrate persistent site
141 fidelity.

142 Critique from Evans (1938a, b) prompted Greenberg and Noble (1944) to modify the conditions
143 under which observations were conducted in the lab—they housed and observed *A. carolinensis*
144 lizards in larger cages and greenhouses, up to 5 m × 5 m. But these larger arenas may still have been
145 too small to assess if the multiple males they contained each maintained exclusive areas and showed
146 site fidelity. The authors mentioned that “an active adult male usually succeeded in dominating the
147 entire cage,” which implies that males in these cages did not maintain exclusive areas, potentially an
148 artefact of a small arena size. The conditions in the cage were nonetheless described as “near-normal
149 competitive conditions.”

150 Oliver’s (1948) methods for observing *A. sagrei* in the Bahamas were similar to Evans’ (1938a)—17
151 lizards in an area approximately 4 × 20 m were “marked and casually observed for a period of
152 slightly less than one month.” And though Oliver (1948) “planned to present elsewhere at a later
153 date a detailed account of the individual and social activity of this species,” to the best of our
154 knowledge, no such account was published. Oliver (1948) summarized his results as showing that
155 “definite territories are maintained and defended by both sexes.” However, the territories he
156 described were not exclusive, because “within the area occupied by each large male there was a
157 smaller male,” and it is not clear if these smaller males were reproductively active or not. His
158 conception of territoriality in anoles was therefore potentially consistent with female multiple
159 mating.

160 Approximately contemporaneous natural history studies described anoles as territorial based on far
161 less evidence. For example, Thompson (1954) observed a single male *A. carolinensis* displaying at a
162 “jar containing about a dozen swifts (*Sceloporus undulatus*) that I had collected the day before,” as well
163 as at a skink, and concluded that “during the entire performance it seemed that the anolis [sic] might
164 have been trying to hold or establish a territory.” In sum, these early studies of anole social behavior
165 all readily described these lizards as territorial, despite presenting limited data that was insufficient to
166 demonstrate site fidelity and did not always demonstrate exclusivity.

167

168 THE FIRM ESTABLISHMENT OF TERRITORIAL POLYGYNY

169 In the decades that followed these early studies, territoriality remained a frequently used description
170 for anole space use behavior and social interactions; the next watershed moments in this research
171 trajectory came when descriptions of *Anolis* mating systems grew to explicitly include a polygynous
172 mating system.

173 In what remains one of the most detailed studies of *Anolis* territoriality, A. Stanley Rand spent
174 almost a year observing the movement patterns and social interactions of *Anolis lineatopus* in Jamaica.
175 This yielded a paper in which Rand (1967a) fully expressed the tension between adhering to a
176 territorial framework on one hand, and observing variation in site fidelity and exclusivity on the
177 other. Nonetheless, Rand (1967a, b) proposed a tight link between territoriality and polygyny based
178 on the idea that males maintain exclusive mating access to females.

179 At least part of Rand's (1967a) conception of territoriality was derived from earlier research on
180 anoles. For example, he cited Evans (1938a) in describing the pattern of "a male with a home range
181 shared by one or several females that are his mates" in *A. sagrei*. He also suggested that *A. lineatopus*
182 and *A. sagrei* have similar social behavior based on Oliver's (1948) description of the latter as
183 territorial. But Rand (1967a) demonstrated the complications of fitting messy field data into this
184 territorial framework.

185 These complications are best captured by Rand's (1967a) descriptions of these lizards' site fidelity.
186 First, he stated that "an *A. lineatopus* seldom travels far and most of the area it visits is visible to it
187 from its usual perch." But following this he describes how, in calculating the area over which an
188 individual lizard is active, he "omitted the occasional visits that certain *A. lineatopus* made to perches
189 well outside of the area where they were usually seen." Thus departures from site fidelity that may
190 have been reproductively important were excluded while attempting to establish site fidelity.

191 A similar dissonance was also evident when Rand (1967a) first stated that "the activity range of an
192 adult *A. lineatopus* seems relatively permanent and certainly shows no seasonal variation" but then
193 described data that may have suggested otherwise. Documenting the locations of 16 adult males in
194 one of his field sites, he noted that these males were seen multiple times while sampling in
195 September and October but only seven of these—less than half—were still present in the site five
196 months later. Rand (1967a) acknowledged that "of those nine which had not been seen in March,

197 two were dead, but it is possible that the other seven had shifted their areas outside of the study
198 plot.” In other words, Rand (1967a) considered that almost half of the adult males in this site may
199 have shown seasonal departures from site fidelity, but nevertheless concluded that these lizards
200 remain in fixed locations permanently.

201 Rand’s (1967a) thoughts on exclusivity were complex, illustrated by his statement that “individual
202 aggression may be expressed as either of two types: dominance hierarchies and territoriality... The
203 behavior of *A. lineatopus* can not be assigned to either of these categories because it has important
204 aspects of each of them.” He went on to explain that while “every *A. lineatopus* holds a territory,
205 defending it against neighbors of the same size... each is a member of a straight line dominance
206 hierarchy that consists of all those anoles of different sizes whose home ranges overlap its own
207 home range.” Because large as well as small males were observed mating, such a spatial organization
208 appears inconsistent with the idea that males maintain exclusive mating access to the females within
209 their territory.

210 Despite these dissonances and complexities, Rand (1967a) unequivocally linked territoriality to
211 polygyny, by proposing that male territoriality is adaptive in *Anolis* because it allows males to
212 maintain exclusive mating access to females:

213 “I think the general occurrence of aggressive behavior and the spacing out it produces in all
214 sizes of *A. lineatopus* can be explained by... ecological advantages... but the greater
215 aggressiveness of the adult males requires additional explanation. I think the explanation lies
216 in a function of territory discussed at length by Tinbergen (1957), which demonstrates the
217 selective advantage that is conferred on an adult male if he can insure himself exclusive
218 mating rights to certain females by keeping other males away from them. If he can do this
219 for a single female, he insures that he will father at least some offspring, and the more
220 females he can keep isolated, the more offspring he will have and the greater his
221 contribution to the gene pool of the next generation. This being true, there must be a strong
222 selection pressure for any mechanism that will insure a male exclusive mating rights to one
223 or more females. The aggressive behavior of adult male *A. lineatopus* that keeps other males
224 out of the area in which females are permanently living is just such a mechanism.”

225 In a second paper based on these data, Rand (1967b) continued to make the case that *A. lineatopus*
226 exemplifies territorial polygyny, with a more explicit examination of the adaptive significance of

227 territorial behavior in lizards. He concluded that while all individuals defend territories for access to
228 food, males also defend access to mates, thereby reinforcing the link between territoriality and
229 polygyny in *Anolis*. This idea that males maintain exclusive mating access to females was almost
230 certainly a sign of the times. Hinde (1956), in his introduction to an issue of *Ibis* devoted to
231 territoriality in birds, proposed a hypothesis similar to the one espoused by Rand (1967a, b): “Any
232 behaviour of the male which helps to prevent his mate being fertilized by another male is likely to
233 carry a great selective advantage.” This notion of the “monopolizability” of females, or of the
234 resources to which females are attracted, became the foundation of how behavioral ecologists
235 understand the evolution of animal mating systems (Orians 1969; Emlen and Oring, 1977). In
236 anoles, it was quite possibly the basis of the expectation of strict territorial polygyny, which rests on
237 the assumption that males maintain exclusive mating access to the females in their territory (Figure
238 1).

239 Though research on anole mating systems grew rapidly after 1967 (discussed below), the next major
240 step towards firmly establishing the link between territoriality and polygyny came 17 years later.
241 Ruby (1984) examined male breeding success in *A. carolinensis* in the context of space use, motivated
242 by the assessment that “mating systems of reptiles are poorly known...and formative factors remain
243 undetermined.” Sampling for over five months for each of two consecutive years, including daily
244 observations for three months each breeding season (though over only a 460 m² area), Ruby (1984)
245 discovered ways in which these lizards’ behavior did not conform to the expectations of territorial
246 polygyny that were laid out by Rand (1967a, b). For example, he noted that “only 17 of the 68 (25%)
247 males remained 12 weeks or longer during a single breeding season of 20 weeks,” potentially
248 indicating variation among males in site fidelity. Moreover, he found that “female [territories]
249 overlapped more than one male in about 25% of the receptive periods [two week intervals in the
250 breeding season]” and in calculating the number of potential mates of males, each “female was
251 assigned to all overlapping males.”

252 These observations and analytic choices indicate that Ruby (1984) uncovered the potential for
253 females to mate with multiple males, and thus documented a mating system in which males do not
254 maintain exclusive mating access to individual females. Ruby (1984) even considered the possibility
255 that sperm storage is an adaptation for female mate choice in these lizards. Nonetheless, at the very
256 outset of the paper, Ruby (1984) proposed that mating systems in lizards range from monogamy to
257 polygyny and described territoriality as “one means of gaining exclusive mating access to females.”

258 Later in the paper, he stated that “because the *Anolis* breeding system appears to be resource defense
259 polygyny (Emlen and Oring 1977), territoriality is favored as a means of restricting access to mates.”
260 It is possible that Ruby’s (1984) data led him to soften his stand from expecting males to maintain
261 “exclusive” mating access to expecting “restrict[ed]” mating access; nonetheless, Ruby (1984) was
262 subsequently frequently cited as supporting the idea that anoles are territorial and polygynous
263 without explicitly acknowledging this potential for female multiple mating (e.g. Qualls and Jaeger
264 1991; Stamps 1995; Lovern 2000; Jenssen et al. 2000, 2005).

265 **THE CONSEQUENCES OF LIMITED SAMPLING**

266 Research on anole behavior blossomed between Rand (1967a, b) and Ruby (1984). However,
267 because by this point the consensus seemed to be that anoles are territorial, this research was not
268 often designed to explicitly test if these lizards behave territorially, i.e. to show that they exhibit site
269 fidelity and exclusivity. . Specifically, territoriality was an almost foregone conclusion in studies with
270 a limited spatial and temporal extent of sampling. In other words, the design of many of these
271 studies was such that they were unlikely to uncover evidence that individual anoles vary in site
272 fidelity or exclusivity, and therefore were unlikely to point to the possibility that females often mate
273 with multiple males

274 If the sampling period of a study of social behavior is not long enough, then relatively infrequent but
275 reproductively consequential departures from either male-male exclusivity or site fidelity may not be
276 detected often enough that they are considered signal and not noise. For site fidelity, this includes
277 not only occasional forays away from and returns to a fixed territory, but also shifts in territory
278 location that may take place only a few times per breeding season—neither would be detected by
279 studies with short durations. An extreme example of a constrained sampling period can be seen in
280 Philibosian’s (1975) study of *Anolis acutus* and *Anolis cristatellus*, in which he stated that “often an
281 observation period of one day was sufficient to record enough positions and enough encounters
282 involving the residents on a tree to make reasonably accurate territory descriptions.” As researchers
283 became more certain that anoles are territorial, they became comfortable making more extreme
284 assumptions. For example, in estimating the number of neighbors of individual *A. sagrei*, Calsbeek
285 (2009) estimated the center of a lizard’s territory as simply the first location at which that lizard was
286 observed.

287 Moreover, if a study of social behavior does not sample over a large enough area and a sampled
288 individual disappears from the study site, researchers cannot know if the individual has died or
289 simply moved. Thus, studies with limited sampling areas will be most likely to sample only those
290 individuals who stay in the same place. For example, Trivers (1976), studying the Jamaican *Anolis*
291 *garmani*, “attempted to map male territories by concentrating on a small portion of the study area.”
292 He stated that “males are sighted too infrequently to measure territory size the usual way; that is, to
293 construct a volume fitting such sightings.” These infrequent sightings could conceivably be due to
294 the low chance of re-spotting individuals with low site fidelity. But Trivers (1976) continued by
295 saying that “fortunately males 105 mm and larger show a strong tendency to occupy
296 trees...Typically, during a given visit, a large male will be sighted between five and ten times in a
297 large tree.” Thus, Trivers (1976) limited his sampling for estimating territory size to a small area
298 known to be occupied by individuals with high site fidelity.

299 The combination of spatially and temporally restricted sampling can be seen in work by Jenssen and
300 colleagues (e.g., Jenssen et al. 1995; Jenssen and Nunez 1998), who documented the behavior of a
301 population of *A. carolinensis* along the Augusta Canal in Georgia. This population inhabited a thin
302 strip of vegetation (three to six meters wide), which comprised clumps of trees observable from an
303 elevated walkway, and the activity of lizards in each clump of trees was watched for only eight days,
304 out of a months-long breeding season. Nonetheless, these data were interpreted to conclude that
305 “males are polygynous, defend closely monitored and stable territories, and devoted large blocks of
306 time and energy on territory maintenance” (Jenssen et al. 1995). With time, statements of territorial
307 polygyny thought to be supported by these data became even stronger, such as this statement from
308 Jenssen et al. (2000): “the *A. carolinensis* mating system is driven by the outcome of intermale
309 territorial aggression. Winners achieve and maintain direct mating access to varying numbers of
310 females...because females are relatively sedentary and clustered in small contiguous home ranges.”

311 **FOUR FATES OF DOCUMENTED DEPARTURES FROM TERRITORIALITY**

312 Evidence for variation in territorial behavior, namely the extent of site fidelity and exclusivity, was
313 implicitly and explicitly excluded through much of the later literature on *Anolis* social behavior. This
314 exclusion took on at least four different forms. The first and second forms correspond to what is
315 known as the “primary simplification” of scientific research, whereby the construction of facts is
316 influenced by scientists’ decisions on how to present the data in a paper (Dewsbury 1998).

317 In the first form, already seen in Rand (1967a), departures from territoriality were removed at the
318 time of analysis. For example, Trivers (1976) quantified male *A. garmani* territory sizes based on the
319 size of trees that individuals occupied, and “a tree was assigned to a male if he was seen three or
320 more times in it without any other adult male being seen therein.” However, “if, as happened several
321 times, a large tree was also known to be occupied by a small adult male (85 mm – 104 mm), both
322 males were excluded from the data, since too few data were available to partition the tree between
323 them.” Thus, even though male *A. garmani* as small as 87 mm in size were observed copulating with
324 females, their departures from male-male exclusivity were explicitly excluded when considering these
325 lizards’ territoriality. Similar choices were also made in considerations of site fidelity. For example,
326 Schoener (1981) argued that in calculating home range areas based on location data, “the inclusion
327 of the outermost observations...may still be undesirable” because “the utilization may resemble a
328 more compact distribution if outliers were disregarded.” As a result, the home ranges of four anole
329 species in the Bahamas were calculated without including the “10% of points farthest from the
330 geometric center” (Schoener and Schoener 1982). While this analytic choice is certainly justifiable for
331 calculating the centers of individuals’ activity, it compromises the ability to predict mating patterns
332 from space use behavior, unless one is certain that individuals do not mate when at the 10% of
333 points farthest from the geometric center.

334 A second fate of observed departures from territoriality, as seen in Ruby (1984), involved
335 quantifying them but omitting them from interpretation. For instance, Schoener and Schoener
336 (1980) describe *Anolis sagrei* as exemplifying the “paradigm of a territorial, polygynous species” even
337 though between 3% and 28% of males in six populations remained within their study sites for less
338 than a week, potentially indicating frequent deviations from site fidelity. An implicit justification for
339 ignoring this often substantial proportion of males from a description of the lizards’ mating system
340 is that these “floating” males do not mate with females. Though this is a reasonable and testable
341 hypothesis, *assuming* that non-territorial males do not reproduce simply because they are not
342 territorial is unjustified. In another example, Fleishman (1988) categorized adult male *Anolis auratus*
343 as either territorial or non-territorial, based on their display behavior and levels of aggression. Even
344 though non-territorial males were observed copulating with females within the territories of
345 territorial males, Fleishman (1988) stated that “territories of *Anolis* males are primarily for exclusive
346 access to mates.”

347 In a third, distinct fate, research that explicitly documented departures from territoriality stayed
348 unpublished and was therefore relatively uninfluential. Consider two abstracts submitted to the
349 annual meeting of the Society for Integrative and Comparative Biology. Both studies (Alworth 1986;
350 Webster and Greenberg 1988) examined *A. carolinensis* behavior in enclosures. While Webster and
351 Greenberg (1988) found that “the average site fidelity was 52%,” Alworth (1986) concluded that
352 “territoriality in these lizards [should] be regarded as a highly flexible behavioral tactic adaptive only
353 in specific contexts” and that “the broad characterization of a genus or species as territorial is
354 misleading.” However, to the best of our knowledge, neither of these studies was published.

355 Finally, in the fourth fate, deviations from territorial polygyny in *Anolis* were documented and
356 acknowledged fully, but the species’ social behavior was described as an exception to the rule. For
357 example, *Anolis valencienni* was described by Hicks and Trivers (1983) as displaying “many features
358 atypical of other *Anolis*,” including the lack of territorial behavior by either males or females.
359 Consequently, “because many adults of both sexes encounter each other daily, there are unusual
360 opportunities for female choice...over a period of six weeks, a female may copulate with five or more
361 males.” This “unusual” opportunity for female multiple mating was hypothesized to be due to *A.*
362 *valencienni*’s tendency to forage more actively than other anoles. We are not suggesting that *A.*
363 *valencienni* does not differ in its behavior from other anoles; in fact, its behavior *must* be different
364 enough that even researchers working within the paradigm of territorial polygyny recognized it as
365 exceptional. But because *A. valencienni* was positioned as exceptional, its behavior was never cause to
366 question or re-evaluate the behavior of other anole species.

367 **TWO EXCEPTIONS**

368 In seven decades of research on anoles, two studies explicitly described these lizards’ social behavior
369 as being consistent with female multiple mating. The first—Gordon (1956)—remained relatively
370 uninfluential, but the second—Tokarz (1998)—began the process of reconciling behavioral
371 observations with subsequent genetic studies that in fact detected evidence for female multiple
372 mating.

373 In his dissertation, Gordon (1956) aimed “to analyze, biodemographically, two local populations” of
374 *A. carolinensis*. The work comprised primarily of nocturnal censuses in two 20 m × 20 m plots every
375 two weeks for over a year, with all captured individuals marked permanently. Gordon’s (1956) data
376 revealed the potential for departures from site fidelity: 73% of 1024 marked lizards were observed

377 just once within the study site, and only 8% of all lizards, and 13% of adults, were observed three or
378 more times. Though some of the disappearances were undoubtedly due to predation and others
379 must have resulted from the failure to detect individuals again, the data are also consistent with
380 many individuals in this population exhibiting low site fidelity. Gordon (1956) later questioned
381 anoles' site fidelity when describing lengthy disappearances of individual lizards from the study site
382 and frequent long distant movements. He also wrote the following:

383 "The individual female may copulate with more than one male per season. The social group
384 is maintained by the activity of the dominant male, and sexual bonds between the male and
385 his females are loosely formed. Females tend to wander more than males and ample
386 opportunity is present for a female to be attracted to, and take up residence in, another
387 male's territory. In cases of territorial hierarchy, the dominant male and his subordinates may
388 share the same group of females."

389 Though it certainly had the potential to do so, Gordon's (1956) thesis did not end up provoking a
390 shift in how behavioral ecologists think about anole mating systems. For example, three influential
391 papers on *Anolis* territorial behavior (Schoener and Schoener 1982; Ruby 1984; Jenssen et al. 1995)
392 cite Gordon (1956) but do not refer to his conclusion that female anoles may readily mate with
393 multiple males.

394 Over four decades later, behavioral observations by Tokarz (1998) demonstrated even more clearly
395 that female *A. sagrei* have the opportunity to mate with multiple males. He explicitly questioned the
396 idea that males maintain exclusive mating access to females in their territories, saying that "few
397 studies have attempted to record the mating pattern of individual females in nature as a means of
398 evaluating the potential for female mate choice and sperm competition." Tokarz's (1998) data
399 revealed that "most females (75%) had more than one mating partner, and this was due almost
400 entirely to females mating with new males that successfully supplanted previous males from their
401 territories." A decade later, curiously, Tokarz (2008) minimized his own previous findings, saying
402 that "male territories in *A. sagrei* appear to be relatively stable at least during the midsummer portion
403 of the breeding season (Evans, 1938[a]), although instances of males being supplanted from their
404 territories by other males have been observed (Tokarz, 1998)."

405 It is tempting to conclude that Tokarz's (1998) results solve the problem of the mismatch between
406 behavioral and genetic descriptions of anoles' mating system. And to an extent, they do, but his

407 documentation of turnover in male territory occupancy is only one of many different ways in which
408 departures from strict territorial polygyny (Figure 1) could facilitate female multiple mating. Other
409 ways, such as multiple reproductive males occupying overlapping areas, had been documented in
410 anoles by previous researchers, but their potential relevance to female multiple mating was
411 downplayed. Yet other ways, such as the existence of reproductive males or females who wander
412 non-territorially, are unlikely to be detected in studies with small sampling areas or durations. This
413 includes Tokarz (1998), who watched 16 individuals occupying a single tree that was 2 m in
414 diameter, for just over a month. That said, even Tokarz (1998) observed “six instances in which
415 males...entered an adjoining male’s territory and courted females there.”

416 These different possible routes to multiple female mating have different implications for anoles’
417 reproductive dynamics and sexual selection. Multiple mating resulting from male territorial turnover
418 may lead to serial polygyny, in which at any one time, a territorial male is the exclusive mate of
419 females residing within his territory. Alternatively, the other routes lead to situations in which at any
420 given time, females may be able to mate with several males, allowing for female mate choice. While
421 the serial territorial polygyny that Tokarz (1998) observed may certainly be a male adaptation for
422 achieving high reproductive success, we cannot know from existing behavioral data if it is the only
423 reproductive strategy, or even the dominant reproductive strategy, adopted by male anoles.

424 **THE AGE OF GENETICS**

425 The use of genetic tools uncovered female multiple mating in three species of anoles—*A. carolinensis*,
426 *A. sagrei*, and *A. cristatellus*. Each of these studies (one paper published in a peer reviewed journal, as
427 well as three theses that, at present, are unpublished) discussed the implications of their findings for
428 territoriality to different extents.

429 Passek (2002) examined the possibility for sperm choice or competition in *A. carolinensis* using a
430 combination of behavioral and genetic approaches. She invoked variation in site fidelity and
431 exclusivity when saying that “while males defend territories that contain multiple female home
432 ranges (Jenssen et al. 1995), the potential exists for extra-pair paternity due to temporary invasion by
433 “floater” males or female home ranges being overlapped by more than one male (Ruby 1984).”
434 Though Passek’s (2002) description suggests only occasional departures from territoriality, her
435 genetic data showed that 48% of offspring were sired by males other than the one identified as the

436 territory owner, including 21% sired by smaller males within the same territory and 15% sired by
437 neighboring males. The paternity of the remaining 12% of offspring could not be determined.

438 In her conclusion, Passek (2002) expressed skepticism that anyone had accurately measured “the
439 frequency of territorial exchanges resulting from territory takeovers.” She also spoke strongly against
440 laboratory studies that formed the basis of research on *Anolis* social behavior. As she put it, “we
441 cannot remove an animal from its environment and expect to be able to correctly interpret its
442 behavior nor should we make the mistake of failing to question theories constructed solely based on
443 laboratory-derived observations. These mistakes have been made for many years with *A. carolinensis*.”

444 Johnson (2007) mapped *A. cristatellus* space use behavior over a three week period, and found that
445 females’ “territories overlapped an average of 3.3 males.” Genetic data confirmed this potential for
446 females to mate multiply, showing that “52% of females laid eggs sired by multiple males.”
447 Moreover, variation in site fidelity also played a role in facilitating female multiple mating, because
448 “26% of offspring were sired by males whose territories did not overlap that of the mother.”
449 Johnson (2007) concluded that “these results may be explained by a combination of a male
450 dominance hierarchy...and female mate choice,” mating strategies and interactions that are
451 inconsistent with strict territorial polygyny (Figure 1).

452 In the only published evidence for multiple mating by female anoles, Calsbeek et al. (2007) found
453 that “more than 80% of field-caught *A. sagrei* females that produced two or more progeny had
454 mated with multiple males [making] *A. sagrei* one of the most promiscuous amniote vertebrates
455 studied to date.” However, this paper did not tackle the implications of its results for territoriality.

456 Finally, the most direct evidence for departures from territoriality influencing anole mating systems
457 again combined behavioral observations with genetic data (Harrison 2014). Studying *A. carolinensis*,
458 Harrison (2014) assumed site fidelity in her behavioral sampling by mapping the home ranges of
459 lizards after observing individual’s spatial locations for 30-minute focal observations (it is not clear
460 how many focal observations were conducted for each individual; Harrison (2014) does mention
461 that “behavioral observations were conducted at irregular intervals, making it difficult to determine
462 whether males shifted their territories during the study period”). However, her genetic data revealed
463 that spatial proximity, as determined by the focal observations, did not predict mating between pairs
464 of males and females. In fact, the mean distance between mating pairs was 33 ± 22 m, over five times
465 the mean estimated territory diameter in that population. This indicates that individual lizards *must*

466 *have* moved between when they mated and when they were observed. In the face of this evidence,
467 Harrison (2014) continued to invoke a territorial paradigm to understand anole social behavior, at
468 least initially: “males and females from opposite sides of the study site mated relatively
469 frequently...often traversing distances over 60 m. For this to occur, either the male or female (or
470 both) left its territory at some point, or they mated before establishing territories and used stored
471 sperm.” Later, however, she proposed a number of hypotheses for male movement behavior,
472 including the existence of an alternative non-territorial, wandering male strategy adopted by adult
473 males, and temporal variation in individual site fidelity within a single breeding season, that definitely
474 break out of the mold of territoriality.

475 **BROADER IMPLICATIONS FOR ANIMAL MATING SYSTEMS**

476 This century-long trajectory of research on *Anolis* mating systems exemplifies several larger issues
477 that could plague the study of animal mating systems more generally. However, it is challenging to
478 establish that the problems we identify here are generally applicable, because discerning their
479 applicability to a particular taxon demands a close familiarity with the full body of literature on that
480 taxon’s biology, as well as familiarity with the organism’s biology itself. In this final section, we
481 identify the main driving forces that led to the incomplete and possibly incorrect descriptions of
482 *Anolis* social behavior, culminating in the erroneous prediction that each female’s offspring will be
483 sired by the single male in whose territory she resides. We hope this discussion will prompt
484 researchers who are intimately familiar with other organisms’ biology to consider the basis of what
485 we “know” to be true about those organisms’ social behavior.

486 The history of research on *Anolis* mating systems demonstrates multiple ways in which the erratic
487 and contingent progress of research may have prevented researchers from fully describing the
488 behaviors that facilitate female multiple mating in these lizards. The central problem was described
489 well by Stamps (1994), although she was discussing specific aspects of territoriality not covered in
490 this review:

491 “Current ideas about the behavior of territorial animals are based on a series of
492 assumptions...in some cases these assumptions have not been adequately tested. By virtue
493 of repetition, untested assumptions have a tendency to solidify into “quasi-facts.””

494 Such repetition certainly characterized the earliest studies of *Anolis* social behavior, where studies
495 repeatedly concluded that anoles are territorial based on often flimsy evidence. It is not clear
496 whether the authors of these earliest studies considered the implications of these lizards' space use
497 and movement patterns for their mating system. It is possible that territoriality was so readily
498 assumed and concluded in these early studies *precisely because*, under the strictest interpretation,
499 territoriality is incompatible with female multiple mating. Charles Darwin, in his seminal text on
500 sexual selection, expressed the prevailing view at the time that females are generally "coy," "passive,"
501 and "less eager" to mate than are males (Darwin 1871). This view was eventually translated into the
502 assumption that variance in female reproductive success is lower than variance in male reproductive
503 success (discussed in Hrdy 1986; Dewsbury 2005; Tang-Martinez and Ryder 2005; Tang-Martinez
504 2016). Moreover, many biologists at the time believed that females of most species were unlikely to
505 possess the cognitive ability to make choices about which males to mate with, and ignored evidence
506 to the contrary (reviewed in Milam 2010). Invoking a mating system such as territorial polygyny,
507 which under the strictest interpretation leaves females unable to choose between males and implies
508 high variance in male reproductive success, thus may have been a sign of the times.

509 However, Greenberg and Noble (1944) conducted experiments explicitly to test whether females
510 chose mates on the basis of males' dewlaps, asking if females preferred to mate with males with
511 intact or manipulated dewlaps. They found no effect of dewlap manipulation on mating success, but
512 by asking the question, these authors revealed that they considered female mate choice possible in
513 anoles, and thus considered that females have the opportunity to mate with multiple males. In
514 contrast, later researchers studying anole territorial behavior frequently maintained that female mate
515 choice was unlikely because it is precluded by territoriality. For example, Schoener and Schoener
516 (1980) suggested that "adult females seem quite sedentary in [*A. sagrei*], and the opportunity for
517 female choice would seem correspondingly limited," and Stamps (1983), in a review of lizard
518 territoriality and polygyny, said the following:

519 "In most insectivores, female choice of mating partner is probably fairly limited. Since
520 females do not leave their home ranges in order to mate, prospective male partners must
521 have home ranges overlapping that of the female. A female with a home range on the border
522 between 2 male home ranges might be able to choose between them, but this option is
523 restricted in territorial species by the males' tendencies to arrange their territories to
524 completely enclose female home ranges."

525 Thus, though researchers all the way from Noble and Bradley (1933) to Stamps (1983) and beyond
526 described anoles as territorial, the predictions for mating patterns derived from that behavioral
527 description, such as whether females have the opportunity to choose mates, could be inconsistent
528 with one another.

529 That the term “territoriality” as interpreted by different researchers could be compatible with
530 fundamentally different expectations for patterns of mating and sexual selection highlights the fact
531 that very few studies define territoriality explicitly (Maher and Lott 1995). Different authors’
532 conceptions of territoriality include different degrees of variation in both site fidelity and exclusivity,
533 and therefore lead to different expectations for female multiple mating. This fuzziness in the
534 definition of territoriality also raises the following question—at what point might we conclude that
535 territoriality is too imprecise a term to be useful as a predictor of a species’ mating patterns?
536 Departures from male-male exclusivity have been observed in anoles (e.g. Rand 1967a; Trivers 1976;
537 Fleishman 1988), but these examples were still considered to be within the fold of territoriality
538 because “exclusivity” was qualified or limited to mean that males only exclude size-matched
539 individuals. These qualifications were made even though males in smaller size categories were
540 observed to mate with females. Similarly, a lack of clarity about the meaning of site fidelity
541 permeates research on territorial behavior—does “site fidelity” mean staying in the same place,
542 leaving but always returning to the same place, or attempting (but possibly failing) to stay in or
543 return to the same place? How long does an individual have to stay in a certain place to be
544 considered site faithful? Almost all possible answers to these questions have, at some point in the
545 last century, been implicitly or explicitly accepted as consistent with territorial behavior, even though
546 each answer can lead to very different expectations for mating patterns.

547 Once territoriality became established as a description of anoles’ mating system, the design and
548 interpretation of subsequent studies of these lizards’ social behavior made it difficult to detect
549 variation among individuals in site fidelity or exclusivity, variation that could easily be reproductively
550 consequential. Which individuals were studied, the extent of sampling area and duration, the data
551 that were analyzed versus excluded, and the extent to which inconsistent findings were
552 deemphasized—each of these scientific decisions involved choices that would determine whether
553 the study could actually test the precepts of territoriality or whether it simply assumed them. For the
554 most part, the choices made were such that territoriality remained untested. . However, these studies
555 were written and interpreted as if the idea that anoles are territorial had been tested, and each thus

556 seemed to provide independent confirmation of this description of their spatial and social
557 organization. In fact, even though these studies were conducted by different researchers on different
558 populations and species of anoles, they were conceptually non-independent, unintentionally leading
559 the earliest studies to “assume a stature that their original authors never intended” (Stamps 1994).

560 It is this problem—adhering to a conceptual paradigm while designing studies that are consequently
561 unlikely to uncover or take seriously the evidence that would allow you to escape that paradigm—
562 that we believe is the most important problem revealed by our review. This problem cannot be
563 solved simply by collecting more data; reaching a solution additionally requires that we explicitly
564 identify and question the assumptions made when designing research (Gowaty 2003). But framing
565 the challenge thus also makes the solution clear—we should continue collecting observations of
566 animals’ behavior in a manner that is as free as possible from existing conceptual frameworks, even
567 in taxa whose biology we think we know well. In other words, the solution calls for renewed and
568 continued attention to organisms’ natural history (Greene 2005; Tewkesbury et al. 2014). As Greene
569 (2005), who defined natural history as “descriptive ecology and ethology,” put it, “discoveries of new
570 organisms and new facts about organisms often reset the research cycles of hypothesis testing and
571 theory refinement that underlie good progressive science.”

572 The call for a close relationship between natural history observations and the advance of research in
573 animal mating systems is far from new. We conclude with a remarkably apt excerpt from a 1958
574 letter to the editor of *Ibis* from John T. Emlen, following an issue about territoriality in birds (Hinde
575 1956):

576 “There is a growing tendency among ornithologists to blindly and devotedly follow what is
577 becoming a fixed or conventional concept of territory. Instead of describing their
578 observations directly, authors often seem to go out of their way to fit them into the
579 “accepted” pattern through the “approved” terms and phrases.”

580 Emlen (1958) continued:

581 “My concern in this letter is with the tyranny of words and with the dangers inherent in
582 patterned thinking. The fascination of catch phrases and the reverence with which they
583 come to be held are major, though subtle, obstructions to free and accurate thinking.
584 Conventionalized phrasing, furthermore, often leads to conventionalized thinking, the very

585 antithesis of free investigation and the arch-enemy of scientific progress. A neat, substantive
586 definition of territory has the fascination of finality, but in a virile science dead ends must be
587 avoided, not sought; it has the fascination of authority, but basically we recognize that the
588 study of natural phenomena must not be subordinated to the study of intellectual creations.”

589 The accurate quantification by genetic means of individuals’ reproductive success in natural
590 populations is valuable not just because such data help to render more complete descriptions of
591 animals’ social and reproductive behaviors. These data also let us identify taxa in which the erratic
592 and contingent progression of scientific research may have led behavioral ecologists towards
593 erroneous conclusions about animals’ mating systems. But the genetic data alone do not shed light
594 on the question of how we come to believe such conclusions. We contend that taxon-specific
595 historical investigations into this question allow us to escape the confines of “conventionalized
596 phrasing” and “conventionalized thinking,” and are an important step towards designing studies that
597 will let us understand animal social behavior in its full complexity.

598

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737 Appendix

738 A list of all the papers examined in our historical investigation of territorial polygyny in *Anolis*
739 lizards, in alphabetical order. We searched for papers on Web of Science using keywords “*Anolis*” or
740 “*Norops*” and “territor*”. From the results, we selected papers that were directly relevant to *Anolis*
741 territoriality, in that the authors studied male-male aggression or site fidelity, including mapping
742 home ranges, or based their study or discussion of *Anolis* social or reproductive behavior on prior
743 conclusions of territoriality. We also followed relevant citations from within the sampled papers,
744 yielding a set of 106 papers that spanned over nine decades and included field- and lab-based
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