



# Reconsidering territoriality is necessary for understanding *Anolis* mating systems

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## Abstract

In a paper titled *The erratic and contingent progression of research on territoriality: a case study* (Kamath and Losos 2017, Behav Ecol Sociobiol 71:89), we sought to understand the inconsistency between behavioral and genetic descriptions of *Anolis* lizards' mating system. We argued 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,” and demonstrated such a research trajectory in *Anolis* lizards. In their responses to our historical review, Bush and Simberloff (2018, Behav Ecol Sociobiol in press) and Stamps (2018, Behav Ecol Sociobiol in press) criticize the definition of territoriality we employed and de-emphasize the link between conceptions of territoriality and descriptions of mating systems in *Anolis*. Here, we respond by reiterating how our understandings of territoriality and of mating systems in *Anolis* and other animals have long been intertwined. Moreover, we argue that our definition of territoriality is precisely well suited to investigating mismatches between behavioral and genetic descriptions of mating systems.

**Keywords** Territorial · Polygyny · Anole · Mating system

In Kamath and Losos (2017), we focused on understanding the mismatch between the expectation that *Anolis* lizards are primarily polygynous and the reality of genetic data showing extensive polygynandry. This expectation of a polygynous mating system is based on behavioral conceptions of *Anolis* territoriality. Concepts of territoriality and mating systems have built upon and informed each other for decades, including in the literature on *Anolis* lizards (Hinde 1956; Rand 1967a, b; Orians 1969; Emlen and Oring 1977; Ruby 1984; Jenssen and Nunez 1998). Indeed, prior to the advent of molecular methods for determining parentage and individuals' reproductive success, mating patterns were inferred almost solely on the basis of animals' space-use behavior. These

inferences were fundamental to behavioral ecologists' understanding of mating systems. We thus sought an explanation for the observed mismatch between behavioral and genetic descriptions of *Anolis* mating systems in the literature on these lizards' movement patterns and social interactions, i.e., in the literature on anole territoriality.

In their response to our paper, Bush and Simberloff (2018) suggest that our “rejection of territoriality is based on [Kamath and Losos's (2017)] particular definition of territoriality, which differs from the behavioral definition used in the majority of anole studies.” They propose instead the definition of a territorial animal as one that “defends some part of its home range from rivals,” followed by a description of defensive behaviors as “displays...or escalated aggressive displays.” Thus defined, territoriality is only obliquely pertinent to mating systems, because such a description is insufficient for making direct predictions about mating patterns. Nevertheless, it is incontrovertible that descriptions of animals as territorial have long been used as a basis for making inferences about their mating systems, specifically for inferring polygyny, as we detailed for anoles in our paper. We are thus confused by Bush and Simberloff's (2018) statement that “rather than challenging the anole mating system literature, [Kamath and Losos's

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(2017)] review specifically targets the territorial literature, spending much of its space criticizing papers that do not address mating patterns”—the territorial literature and mating system literature in anoles and many other animal taxa are inextricably linked to one another.

We argued in Kamath and Losos (2017) that the very first studies of anole territoriality conducted in the 1930s, though certainly path-breaking at the time, were simply not very robust foundations on which to build an understanding of *Anolis* mating systems, because of either the type or the amount of data collected. Some decades later, Rand's (1967a, b) excellent work on *Anolis lineatopus*<sup>1</sup> firmly established that anoles can be territorial in the sense that many males were aggressive toward each other, remained in particular areas for some amount of time, and tended to exclude comparably sized males from these areas. Concurrently, the idea that such behavior had evolved to facilitate polygynous mating systems was becoming widespread (Hinde 1956, Orians 1969, Emlen and Oring 1977), and starting with Rand (1967a, b), anole researchers began concluding, on the basis of observations of some aggression, some site fidelity, and some exclusivity, that anoles conform to the polygyny paradigm. However, these conclusions were made without considering that to infer a polygynous mating system from territoriality, it is *necessary* for territoriality to be defined to include both strict site fidelity and exclusivity relative to all reproductively active males. In other words, the definition of territoriality we employed in Kamath and Losos (2017) was justified in the context of critiquing how and why dozens of papers following Rand (1967a, b) inferred a link between territoriality and polygyny in anoles, because it is the *only* definition of territoriality that necessarily implies polygyny. As we discussed in Kamath and Losos (2017), the degree to which a population departs from this strict definition of territoriality will determine the degree to which that population can depart from a polygynous mating system, and if these departures were only occasional in anoles, then polygynandry would be a rare exception as opposed to a frequent occurrence (Passek 2002; Calsbeek et al. 2007; Johnson 2007; Kamath and Losos 2018).

The framework of territoriality is not necessary to imbue decades of behavioral ecology research in *Anolis* lizards with value, and we disagree with Bush and Simberloff (2018) that “the complexity revealed by these studies further illustrates the importance and usefulness of the territorial framework in

this genus.” As we showed in Kamath and Losos (2017), the framework of territoriality has constrained results and interpretations of anole behavior in ways that have de-emphasized, and likely biased against the discovery of, the full complexity of these animals' behavior. That said, every study we critiqued in Kamath and Losos (2017) includes data on these animals' space-use behavior and social interactions that remain valuable outside of the overarching interpretive structure imposed by territoriality. It remains a mammoth task to determine precisely how this vast body of work can best be unified without leaning on conceptions of territoriality, but it is indisputable that previous research on anole behavior can and should inform our research going forward. Nevertheless, we stand by our assessment that territoriality is not the best framework within which to interpret data on *Anolis* space-use behavior and social interactions, and continue to caution against the imprecise and uncritical description of animals as territorial, particularly in the context of their mating systems.

In her critique of Kamath and Losos (2017), Stamps (2018) focuses on the persistent assumption that anoles are polygynous even in the face of behavioral and genetic evidence of their polygynandry. We agree with Stamps' (2018) description of decades of research on *Anolis*, namely the statement that “we don't yet have the data required to test [the] assumption” that “territorial males defend large territories during the breeding season in order to increase their chances of fathering the hatchlings of females who live within those territories.” Specifically, we agree completely that any fitness advantages conferred by putatively territorial behavior remain hypotheses in need of testing in anoles, rather than established fact. Moreover, we also agree with Stamps' (2018) suggestion that “instead of simply estimating the proportion of females in a population who mated with more than one male, it would be more useful to have detailed behavioral and spatial data for both sexes, in conjunction with paternity data.” Indeed, in Kamath and Losos (2018), we executed precisely such a study, quantifying male and female space use, estimating encounters between individuals, and using genetics to determine which of the encountered males actually went on to sire particular females' offspring, thereby quantifying sexual selection in the sampled population of *Anolis sagrei* in a manner that did not rely at all on territoriality. We found that the movement patterns of lizards in the sampled population were dynamic and variable across individuals and across the sampling period, resulting in a majority of females both encountering and mating with multiple males. Further, we found evidence for sexual selection on male body size, the spatial extent of male movements, and the extent and timing of male-female interactions. We look forward to further studies on *A. sagrei* and other anoles that test the generality of the patterns that we reported.

Going forward, we can test the utility of interpretive frameworks such as territoriality in particular taxa such as *Anolis* by

<sup>1</sup> As an aside, we note that Bush and Simberloff (2018) mentioned that we spent nearly a page discussing Rand's (1967a, b) papers. The reason we did so is that Rand's work—still among the best studies of lizard social behavior ever conducted—was groundbreaking, well ahead of its time, and foundational to the study of anole mating systems, and thus demanded in-depth engagement. His 10-month-long study is longer than almost all studies conducted in the past half-century and is a model for future work. We do not agree with all of the conclusions that Rand came to, but the fact that those conclusions are being discussed in such detail more than half a century after their publication is testament, we believe, to his lasting legacy.

comparing predictions made about these animals' behavior from within and without such frameworks. Exposing such frameworks to rigorous testing will not only serve to further our understanding of particular animals' biology but also help us zero in on the conceptual abstractions that are most useful for making sense of the natural world. Though it has long been assumed, it remains unproven—and we remain unconvinced—that territoriality is a useful conceptual abstraction for understanding the social and reproductive biology of *Anolis* lizards.

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

### References

- Bush JM, Simberloff D (2018) A case for anole territoriality. Behav Ecol Sociobiol, in press
- Calsbeek R, Bonneaud C, Prabhu S, Manoukis N, Smith TB (2007) Multiple paternity and sperm storage lead to increased genetic diversity in *Anolis* lizards. Evol Ecol Res 9:495–503
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223
- Hinde RA (1956) The biological significance of the territories of birds. Ibis 98:340–369
- Jenssen TA, Nunez SC (1998) Spatial and breeding relationships of the lizard, *Anolis carolinensis*: evidence of intrasexual selection. Behaviour 135:981–1003
- Johnson MA (2007) Behavioral ecology of Caribbean *Anolis* lizards: a comparative approach. Dissertation. In: Washington University
- Kamath A, Losos JB (2017) The erratic and contingent progression of research on territoriality: a case study. Behav Ecol Sociobiol 71:89
- Kamath A, Losos JB (2018) Estimating encounter rates as the first step of sexual selection in the lizard *Anolis sagrei*. Proc R Soc B 286: 20172244
- Orians GH (1969) On the evolution of mating systems in birds and mammals. Am Nat 103:583–603
- Passek KM (2002) Extra-pair paternity within the female-defense polygyny of the lizard, *Anolis carolinensis*: evidence of alternative mating strategies. Dissertation, Virginia Polytechnic Institute
- Rand AS (1967a) Ecology and social organization in the iguanid lizard *Anolis lineatopus*. Proc U S Natl Mus 122:1–79
- Rand AS (1967b) Lizard ecology: a symposium. In: Milstead WW (ed) The adaptive significance of territoriality in iguanid lizards. University of Missouri Press, Columbia, pp 106–115
- Ruby DE (1984) Male breeding success and differential access to females in *Anolis carolinensis*. Herpetologica 40:272–280
- Stamps (2018) Polygynandrous anoles and the myth of the passive female. Behav Ecol Sociobiol in press