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COMMENTARY

Polygynandrous anoles and the myth of the passive female

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Abstract

Kamath and Losos (Kamath A, Losos J (2017) Behav Ecol Sociobiol 71:89) appropriately pointed out that researchers studying *Anolis* lizards have persisted for years in erroneously assuming that females only mate with the territorial male with whom they share space. However, Bush and Simberloff (Bush JM, Simberloff D (2018) Behav Ecol Sociobiol, in press) correctly suggested that this error did not arise because male anoles are not territorial. Instead, I suggest that, as was the case for other vertebrate taxa, researchers studying *Anolis* mating systems implicitly assumed that females could be viewed as "resources" defended by males, and that each female passively mated with the male who won the territory that overlapped her home range. This assumption was maintained in spite of behavioral observations indicating that female anoles might have access to sperm from males other than the current territory owner, until it was explicitly refuted by genetic data indicating that some females mate with more than one male. However, we still don't know the extent to which male anoles increase their paternity by defending territories that overlap with female ranges, or the extent to which female anoles increase their control over the paternity of their hatchlings by actively mating with or utilizing the sperm of different males.

Keywords Mating systems · Lizards · Territoriality · Female choice

I think that Bush and Simberloff (2018) "got it right". The literature on *Anolis* territoriality over the years has been perfectly consistent, in terms of both definitions and observations, with the literature on territoriality in other vertebrate and invertebrate taxa. However, Kamath and Losos (2017) were also correct in pointing out that researchers studying anoles erred in assuming that female anoles only use the sperm of the territory owner whose territory boundaries currently overlap each female's home range or territory. I would argue that this erroneous assumption did not persist because anoles are not territorial, but because anoles are not strictly polygynous.

The assumption that females living within a male's territorial boundaries only used sperm from that male was by no means unique to anoles. In the late twentieth century, this assumption was widely held by researchers studying many vertebrate taxa, including small rodents whose spacing patterns are similar to those of anoles (e.g., Ostfeld 1990). In turn, this assumption was based on earlier suggestions that females could be viewed as "resources," to be fought over and defended by males, after which each female would simply accept the male who won the male-male competition as her mate (Emlen and Oring 1977). However, the advent of paternity testing, which demonstrated extra-pair copulations in female birds and mammals, encouraged behavioral ecologists to more closely examine the assumption that females in territorial species passively mate with the male with whom they share space (Stamps 1997). The result was a shift of focus from the male defense of space to female reproductive behavior, physiology, and morphology.

These studies revealed that females were far more active in selecting the sperm used to father their offspring than anyone previously suspected. Examples included observations of female birds surreptitiously sneaking across territory boundaries to mate with neighbors other than their putative mate (Double and Cockburn 2000; Smith 1988), and studies of post-copulatory (or "cryptic") mate choice, which occurs when females store and use sperm from long-ago matings, or use sperm from preferred males after mating with more than one male (Eberhard 1996).

What is interesting to me is that it took so long for the insights from the general literature on mate choice to be

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noticed by researchers studying *Anolis* mating systems. Perhaps this was because it was only recently that anyone thought to conduct the paternity analyses in anoles that forced researchers studying other taxa to reexamine their assumptions about who mates with whom. Or perhaps it is because it is more difficult to assign maternity to *Anolis* eggs, which are buried one at a time in scattered locations, than it is to assign maternity to avian eggs or mammalian neonates. Even so, it is not as if field workers lacked evidence that female anoles might have access to more than one mate. Females often share space with two courting, sperm-producing males (a territory owner and a subordinate male) (e.g. Trivers 1976; Stamps 1977), and mark-recapture studies indicated that large adult males without fixed territories (floaters) might be common in some populations. In addition, female anoles have been observed mating with both floaters and subordinates (Trivers 1976). There is also evidence that at least some female anoles are able to store sperm for extended periods of time (Calsbeek et al. 2007). This is relevant because as Bush and Simberloff (2018) noted, male owners do not necessarily retain ownership of the same territory for months to years. Instead, territory takeovers and rapid replacements of dead or defeated territorial males by new owners have been observed over the course of a breeding season in many *Anolis* populations and species. Indeed, in one study in which 75% of the females copulated with more than one male, virtually all of the multiple matings occurred when the female mated with the new male who had usurped the territory from its previous owner (Tokarz 1998).

What has not changed over the years is 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. We don't yet have the data required to test this assumption. 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. This would tell us whether the proportion of a female's hatchlings fathered by the territory owner(s) who overlapped her home range or territory was higher than one would expect, if that female had mated at random with any of the adult males she encountered during that breeding season. Such studies would encourage a more-nuanced view of *Anolis* mating systems, which considers the tactics (including territorial defense) that males use to increase their probability of fathering offspring by the females they prefer, and conversely, the tactics female use to increase their probability of producing offspring by the males they prefer.

Compliance with ethical standards

Conflict of interest The author declares that she has no conflict of interest.

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