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Thoughts on the ecology and evolution of anoles; insights from 5 years of meandering strolls

“When an observer is fortunate enough to see and record behavior significant in the natural history of a species, his observations should be published. The advocates of biometrical methods need to recognize that some types of behavior are not readily quantified because they are so rarely observed. Even a single observation may constitute a valuable contribution, and may be a break-through in understanding the species’ ecology. There are many kinds of anecdotes, and the fact that some are trivial is a poor excuse for condemning all narrative statements or accounts in scientific writing.”

Fitch, H.S. 1987. The sin of anecdotal writing. *Herpetological Review* 18 (4): 68

While conducting my dissertation research in Miami I found myself in a situation not afforded to all graduate students, especially those that choose to study tropical lizards; I was able to live and walk among a rich and diverse community of my study organisms every day. This fortune wasn’t frivolous – I found myself indirectly familiarizing myself with anole behaviors, subconsciously tracking activity times, and catching the occasional glimpse of a bizarre interaction, which all added towards my education of anole biology. Any student entering the world of anoles, in whichever of the countless sub-disciplines this remarkable model system now spans, would benefit from this same opportunity. I echo Michele Johnson’s thoughts in her contribution to this *Newsletter* that it is still vitally important to better understand anole behavior. Those of you that are the head of your own research labs – encourage your students to spend some time on field trips watching lizards under no obligations or pressure to complete a project or collect data. And, as a call to you students, regardless of your research interests – sit and watch lizards. Learn to take informal field notes and record observations of behavior, ecology, physiological, or morphology, especially those that appear atypical, however seemingly small and uninteresting! *Anole Annals* provides a wonderful outlet for sharing these insights with the research community, as does the *Natural History Notes* section of journals such as *Herpetological Review*.

On that note, here I present some ideas, perspectives, and hypotheses that have crossed my mind over the past few years from some of my wanderings through south Florida – many of which I have little (or no) actual data to support them, but have been the subject of my musings nonetheless.

Character displacement in the crown and the evolution of frugivory

The tree canopies of the Greater Antillean islands are broadly inhabited by three classes of anole ecomorph; Trunk-Crowns, Crown-Giants, and Twigs. Twigs are fairly obscure and unique in their perch use, morphology, and behavior compared to other ecomorphs, and so it is the two former classes that I will focus these thoughts on. Trunk-Crown and Crown-Giant species often appear to overlap in perch use and activity patterns³¹, however there is a very obvious axis through which these ecomorphs differ dramatically; body size. Here I will present a



Fig 1. A freshly noosed adult knight anole exhibiting the gaping behavior typical for this species upon capture. However, this time the gape comes with a present; a freshly ingested palm fruit. (Fairchild Gardens, Miami FL)

hypothesis outlining how this difference in body size between the two ecomorphs may have originally been driven by partitioning in the size of prey items, which was then reinforced by the prey items which fell within the respective size classes as divergence ensued.

Over the past few years, I have become increasingly interested in the dietary relationships of anoles, leading to several research projects with trophic ecologist Sean Giery. Originally, we had two primary questions of interest; (i) do replicated patterns of ecomorph community organization (e.g. in perch use) extend to diet, and (ii) how does diet vary within species and between populations (Sean has written at length on this in his contribution to this *Newsletter*).

³¹ Of course, this could just be an artifact of it being difficult to study canopy anoles, nevertheless lots of independently collected data generally point towards this being true.



Fig 2. Knight anoles do definitely eat other anoles, but do they do it any more frequently than other species? Here I found a young *A. equestris* ingesting an adult bark anole (*A. distichus*). This was during an attempted mark-recapture project where I had managed to find and mark an astounding...6 bark anoles in my study plot; this lizard had eaten 17% of my bark anole population in one go.

Fairchild Gardens in south Miami were fruit³³. We were a little stumped. On delving into the

When we first started discussing these topics, Sean surprised me with one of his early findings of anole diets. In a study of an anole community in North Miami, FL (Florida International University, Biscayne Bay Campus; Giery et al. 2013), one of the main items which Sean found in the stomachs of Cuban knight anoles (*A. equestris*) – a large and established crown-giant ecomorph in Florida – was various types of fruit. In fact, Sean found that 50% of all items found in the stomachs of 24 (!) individual *A. equestris* was fruit (Fig 1).

This wasn't what I had naturally expected. From my readings of the classic anole literature, I was under the assumption that the trophic ecology of crown-giants was to be quite different. Various authors have written about the predator-prey relationship between crown-giants and all other ecomorphs, some even suggesting a role for it in the evolution of the ecomorph community structure. And, in *A. equestris* at least, they certainly do eat other anoles. In Miami, we have been keeping track of each time we observe an *A. equestris* chowing down on an unlucky anole³² (Fig 2). So, perhaps Sean's findings were idiosyncratic to that study site and not representative of the general ecology of crown-giants? So, we set about sampling knight anoles from other communities. To our surprise, we found exactly the same result. Similar to Sean's findings in north Miami, we discovered that ~60% of all stomach items in 10 adult *A. equestris* from

³² No surprises here – they eat all of them; *A. sagrei* (multiple pers. obs.), *A. cristatellus* (Ljustina & Stroud 2016), *A. distichus* (Stroud 2013), and even several instances of cannibalism (pers. obs. – Winter Beckles also posted a series of great photos on *Anole Annals* of a cannibalism event he observed in south Miami). Thawley et al. (2017) also observed *A. equestris* eating a house gecko (*Hemidactylus* sp.), while Dalrymple et al. (1980, and references therein) report on them feasting on nestling birds and tree frogs.

³³ The majority of the fruit from Giery et al. (2013) were from fig trees (*Ficus* sp.); conversely, we found the Fairchild population to eat a lot of palm fruits (*Roystonea* sp., among others). This

literature, we were surprised to find more of the same; Brach (1976) recorded fruit comprising ~50% of stomach items, while Dalrymple (1980³⁴) observed ~30% (both studies were also from Miami populations).

Our immediate questions pointed towards the ecological importance of this behavior; if *A. equestris* are eating lots of fruits, is it possible that they have a role as seed dispersers? Kirsten Nicholson's excellent work at the nearby campus of the University of Miami (Nicholson & Richards 011³⁵) provided us with data on home range size to think this could be a possibility. Nicholson & Richards (2011) discovered that *A. equestris* have average home ranges of ~0.06ha, which would provide ample distance for an ingested seed to move far enough away from a parent tree to avoid parent-offspring competition (i.e. a radius of approx. 14m from a given tree, improving the density/distance dependent mortality relationship as predicted by the Janzen-Connell hypothesis). However, this was all still hypothetical – although we had found lots of fruits in the stomachs of knight anoles, we hadn't yet established if those seeds, once passed, are viable. And so we set about testing this hypothesis.

After collecting several knight anoles, we patiently sat and waited for stomach contents to be passed and discover if seeds were among them. After a few unsuccessful individuals, we managed to retrieve our first seeds passed from a wild caught and naturally foraging knight anole. After examination, these turned out to be from the fruit of the royal palm (*Roystonea regia*), which we frequently found knight anoles in Fairchild Gardens inhabiting. We duly took the seeds, planted them, and waited (again, patiently) to see if they would germinate, neither of us really believing that anoles might actually disperse the seeds of...palm trees. Yet, they sprouted! Who knew crown-giants might play a role as seed dispersers? And of palm trees! To our knowledge, this provided the first empirical evidence supporting the hypothesis of any *Anolis* acting as viable seed dispersers³⁶ - you can read more about this study in Giery et al. (2017). However, our discovery of widespread and consistent frugivory of *A. equestris* throughout Florida lead me to think about how this might have driven the evolution of large body size in crown-giants.

Fruits are generally large (especially from the perspective of most anoles) and often have a small surface-volume ratio. Therefore, a large intestinal tract is generally needed to consistently digest them (King 1996), as well as to actually pass the seeds themselves. Similarly,

is probably driven by the composition of the trees at each site, but it's variability also suggests that it is a widespread and flexible component of the ecology of *A. equestris*.

³⁴ Coincidentally, this study was also conducted at Fairchild Gardens, nearly 40 years before ours.

³⁵ Data were first presented in the *Anolis* Newsletter V (p. 95-98).

³⁶ Although frugivory has been recorded in many species and certainly isn't limited to crown-giants (see Herrel et al. 2004 for a much more comprehensive review and discussion).

Table 1. Diet of coexisting Crown-Giant (*A. equestris*) and Trunk-Crown (*A. carolinensis*) anoles; data collected from Fairchild Tropical Botanic Gardens, Miami FL. Values represent proportion of prey items.

Ave. size (mm ³)	Prey item (Taxa)	Crown-Giant <i>A. equestris</i>	Trunk-Crown <i>A. carolinensis</i>
3143.400	Gastropoda: <i>Snails</i>	0.40	-
1202.320	<i>Fruit</i>	0.33	0.03
426.506	Lepidoptera: <i>Adult</i>	0.07	0.06
167.422	Lepidoptera: <i>Caterpillar</i>	0.07	0.13
139.995	Homoptera: <i>True bugs</i>	-	0.07
48.939	Hymenoptera: <i>Bees and Wasps</i>	0.07	0.11
21.480	Diptera: <i>Flies</i>	-	0.14
14.130	Squamata: <i>Lizards</i>	0.07	-
3.022	Coleoptera: <i>Beetles</i>	-	0.04
2.201	Hymenoptera: <i>Ants</i>	-	0.14
1.143	Psocoptera: <i>Bark lice</i>	-	0.07
1.042	Arachnida: <i>Spiders</i>	-	0.14
0.461	Thysanoptera: <i>Thrips</i>	-	0.03
0.196	Arachnida: <i>Pseudoscorpions</i>	-	0.01
0.003	Arachnida: <i>Mites</i>	-	0.01
Ave. size prey item (mm ³)		1416.17	42.69

anoles – those which are to be eaten by another hungry anole, that is – are comparatively larger than most arthropod prey and so presumably a larger body size (of the predator) would benefit both ingestion and digestion. Perhaps size differences between trunk-crown and crown-giant anoles were first driven by small divergences in prey size, with the prey items which fell into those classes accelerating divergence in body size. Our dietary analysis of trunk-crown anoles in Florida (*A. carolinensis*) revealed that they generally consume prey items 33x smaller than crown-giants (*A. equestris*), and of a completely different composition (see Table 1 below). As larger bodies better process and digest large prey items, perhaps initial divergence in the diet of crown anoles could have driven character displacement in body size, accelerated by an increasing capacity for frugivory (and, to a lesser extent, predation³⁷) in crown-giants. Although

³⁷ I choose to highlight frugivory rather than predation because I think this is the most likely *driver*. Nearly all other anoles will also eat other anoles (both conspecifics and heterospecifics), and so that trait is often present across species and ecomorphs. In our studies we have noticed that the consumption of entire fruits, however, is largely constrained to the crown-giants – although other species will forage on fruit, I have most often seen them taking bites from fruit flesh, rather than attempting to consume it whole (seed included).

whether (and how) this occurred depends on the perspective of the ancestral phenotype of Greater Antillean *Anolis*. In other words, if the ancestor was similar to a crown-giant, then perhaps frugivory is a conserved trait, with trunk-crown anoles instead diverging to exploit a niche of smaller prey items (most evidence points to this not being the case).

So what happens when two crown-giants co-occur? I have no idea – as I mentioned before, I find canopy anoles tough to study well³⁸. But for anyone interested in tackling the question, All America Park in South Miami may provide the opportunity. Here two crown-giants exist in very close proximity; *A. equestris* and the Jamaican crown-giant *A. garmani* (Fig 3), although the population size of the latter is small and sensitive to periodic collecting by members of the pet trade.



Fig 3. Habitat overlap of two Crown-Giants, the Cuban knight anole (*A. equestris*) and the Jamaican giant anole (*A. garmani*), in South Miami, FL. These two species have probably been sympatric at this site for ~40 years, but their coexistence and interactions have not yet received much research attention. (Photo: March 2014)

³⁸ For this same reason, I think it is also difficult to get at the behavioral and ecological mechanisms underlying coexistence in trunk-crowns, especially those newly coexisting pairs which provide particularly exciting opportunities, for example *A. carolinensis*, *A. chlorocyanus*, and *A. allisoni* in Florida.

On diel activity patterns and interspecific interactions

The hallmark of most ecological studies of anoles since the development of the ecomorph model revolves around perch use. Population level patterns in this aspect of anole ecology can be linked to population level patterns in morphology, providing insights into our populations are adapted to different environments (i.e. under the form-function relationship). However, how consistent is perch use within a population? How does habitat use change throughout the day?

As anole communities appear to be largely structured by partitioning of perches, variation in perch use could have profound impacts on how interspecific interactions are understood within a community. For example, although direct behavioral interactions are fairly rare between sympatric *A. sagrei* and *A. distichus* in Miami, FL³⁹ (*A. sagrei* perch low, while *A. distichus* generally perch higher), there are periods within the day where perch use is highly overlapping (Fig 4; shaded area) versus highly divergent.

The common view that these two species only marginally interact – population level patterns of mean perch use is often consistently significantly different, and they also generally eat different things⁴⁰ – could just be a factor of when sampling took place. If perch data from Fig 4 were collected from 1100-1300h (grey shading) instead of 1300-1500h, for example, perhaps conclusions would be very different. The extent to which perch use is fluid vs. static throughout a day is unclear (at all scales – individuals, populations, and species), and deserves more research attention.

The evolution of the nocturnal niche: who is better adapted?

Anoles and geckos have both come to exploit one of the many new anthropogenic niches which exist in human settlements; the night light niche⁴¹. The illuminating presence of lights at night in urban areas provides the opportunity for lizards to extend activity periods, particularly for foraging (Fig 5). Many ecological, physiological, and evolutionary questions immediately jump out: Are night light foragers exposed to a whole new community of prey species? Are the same individuals active during both the day *and* night? If so, do lizards get tired? Or, are there individuals who are nocturnal specialists? What are the consequences of anole-gecko interactions? Are night light foragers *adapting* to this new niche?

³⁹ I base this on not having seen it very often – I more frequently observe *A. sagrei* in confrontations with *A. cristatellus* (both Trunk-Ground anoles), while *A. distichus* (Trunk) and *A. carolinensis* (Trunk-Crown) seem to have a particular penchant for annoying each other. Of course, this isn't saying it doesn't happen.

⁴⁰ In Miami, we have found that *A. distichus* eat primarily ants as they stream up and down tree trunks and branches (as in other diet studies of *A. distichus*; e.g. Schoener 1968) while *A. sagrei* is much more of a broad generalist of various leaf-litter invertebrates.

⁴¹ Often now referred to as the 'ALAN' niche ("Artificial Light At Night"); Jason Kolbe's lab (and driven by Chris Thawley's recent postdoctoral work) are providing a comprehensive assessment of the impact of ALAN on anoles, but several researchers have been interested by this quirky behavior (e.g. see Henderson & Powell 2001 and Perry et al. 2008, among others).

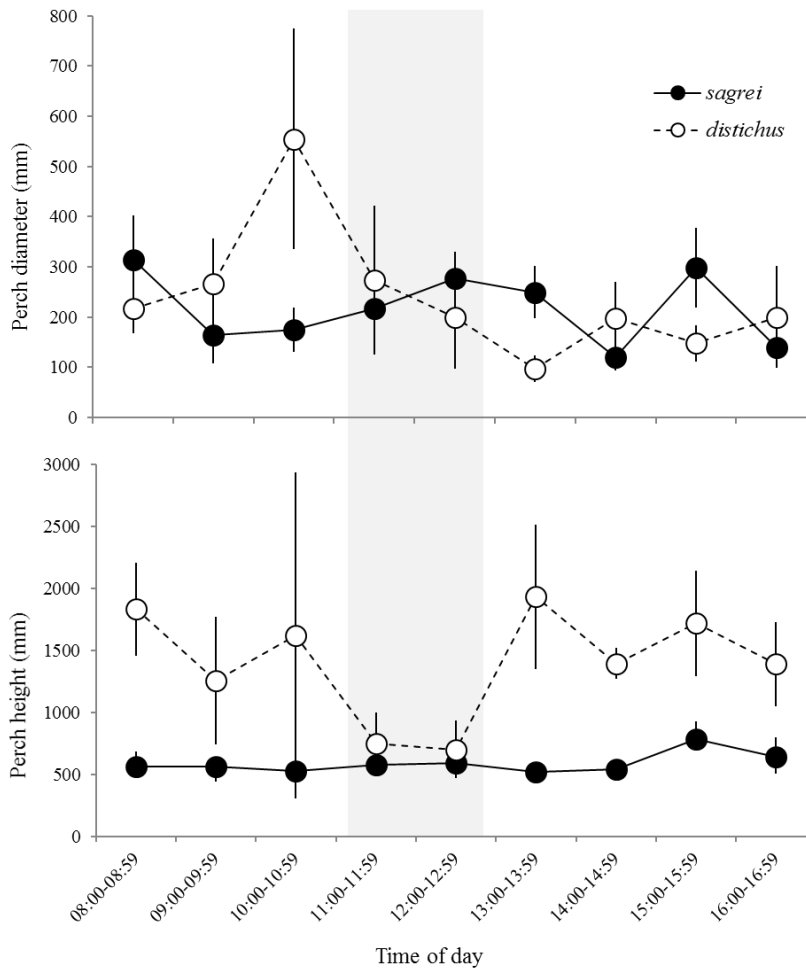


Fig 4. Perch use of Cuban brown anoles (*A. sagrei*; Trunk-Ground ecomorph) and Hispaniolan bark anoles (*A. distichus*; Trunk ecomorph) throughout a continuous sampling session. These data are from only 1 day...because after I finished I promised myself that I would never do this type of sampling ever again (it didn't help that I had the bright idea to do this during a typical 100F Summer day in Miami FL). Error bars indicate ± 1 S.E.

I will offer an alternative question: who is already better adapted? Anoles are diurnal, geckos are nocturnal. Subsequently, one would presume, each has developed visual apparatus best suited to their respective periods of highest activity⁴²; during the day and during the night. These two time periods are at polar ends of the light spectrum.

So when anoles and geckos collect at lights during the night, who is best suited to take advantage of the ensuing barrage of flies, moths, and other inverts? The species which can best observe insects arriving from outside the spotlight, but may be subsequently blinded by the light

⁴² Anoles can be seen in the crepuscular period and occasionally at night, but it's not a general trend. Much like geckos may be seen basking during the day, but it isn't when they are most active.



Fig 5. A [diurnal] knight anole (*A. equestris*) shares a light at night with [nocturnal] house geckos (*Hemidactylus mabouia*). Photo taken at Fairchild Gardens, Miami, FL (from Stroud & Giery 2013).

while scuttling in to forage (nocturnal geckos), or the species which can see less efficiently when outside the light but at an advantage inside (diurnal anoles). Whether there is partitioning within this niche, for example in foraging times or prey items, is also so far unclear. Lots of research opportunities for future anole biologists in the Anthropocene!

Hawaii might offer a comparative test – there, geckos which are adapted to diurnality (aptly named day geckos [*Phelsuma* sp.]) can also be commonly observed gathering and foraging under lights at night (Seifan et al. 2010), often alongside nocturnal geckos (most commonly also *Hemidactylus* sp.). American green anoles (*A.*

carolinensis) and Cuban brown anoles (*A. sagrei*) are also present and relatively widespread on Hawaii, with some scattered records of *A. equestris*. Communities of coexisting *Phelsuma* and *Anolis* also exist in the Florida Keys, so another possibility for a study site may also be found there.

Don't dismiss territoriality yet! Seasonal shifts as an adaptive strategy?

As many of you may have been aware, the world of anole mating systems has recently exploded! Anoles have long been thought to display typical mating behaviors and strategies associated with polygyny. In its simplest and strictest terms, the classic model posits that males defend spatial territories to ensure exclusive access to mating opportunities of females within them. Male-male aggressive interactions, which can be casually observed throughout the anole reproductive season, are often used as support for this claim of resource defense (whether that resource be space, females, or both). However, it has long been recognized that multiple males can share space, so a strict notion of male spatial segregation appears unlikely. Since the advent of molecular analyses allowing for the identification of parentage, evidence for multiple paternity throughout 'polygynous' and 'territorial' animals has been growing (Uller & Olsson 2008), including in anoles (Calsbeek et al. 2007). So, if multiple paternity is common, what does that mean for the mating systems that underlie this pattern? Assumedly they are not then strictly polygynous? So why are anoles aggressive? What roles do females have in anole mating

systems? Do females choose males? Do males choose females? The nature of territoriality in anoles – and whether it exists at all – is currently a hot topic in anole biology.

Recently, from an extensive and detailed study of a population of brown anoles (*A. sagrei*) in northern Florida, Ambika Kamath presented evidence linking patterns of space use to reproduction (Kamath & Losos 2018a). Specifically, Ambika noted that during the course of a breeding season females frequently encountered and mated with multiple males, which had a substantial influence on the paternity of their offspring (up to 81% of mothers bore offspring sired by >1 male; Kamath & Losos 2018a). Ambika's thesis was that the concept of anoles operating in a traditional model of polygynous territoriality needed a rethink (Kamath & Losos 2017), which led to a healthy discussion in the literature (Bush & Simberloff 2018 and Stamps, 2018 both wrote comments on the debate, including a reciprocal response from Kamath & Losos 2018b), as well as many hearty conversations among the non-peer-reviewed world of anole biologists. I encourage everyone to read these papers.

Here, I will suggest an alternative hypothesis in this debate. And I must be clear that this represents nothing more than an untested hypothesis for those studying mating systems – I have no data to support it, these thoughts simply stemming from casually observing lizards throughout the course of a year and therefore spanning both reproductive and non-reproductive seasons. Specifically, I propose that territoriality may be fluid within the breeding season, and that shifts through time from classically polygynous behaviors associated with territoriality, such as mate guarding and defending of space⁴³, to a relaxation of these behaviors and increased dispersal, may be a viable adaptive strategy that can be evolutionarily stable⁴⁴.

I find the maintenance of strictly polygynous territories in anoles unlikely on two counts; (i) it's incredibly costly to maintain a territory (here I use territory to mean the defense of a spatial area with exclusive access to the females that fall within it), and (ii) not all anoles have the same phenotype (i.e. lizards have different personalities⁴⁵). It is important here to note that

⁴³ Although these are two different things with different underlying predictions. If they occur at the same time then it's reliant on an underlying assumption that females don't move, which in itself may or may not be correct. If not, then one may not happen due to the other (i.e. if females move and mate guarding occurs then spatial defense must not, and vice versa).

⁴⁴ This is similar to the point made by Bush & Simberloff (2018) that the definition of territoriality doesn't explicitly include details about the time period for which a territory may be maintained.

⁴⁵ I recognize this is loaded and controversial to some, but I do not see it that way at all. Also, I think that this is true of both sexes alike, not just males. Although I won't talk about this too much here, the extent to which inter-individual variation (i.e. personalities) in social and sexual behavior influence mating strategies deserves more attention. This ties in with the idea of 'territory-holders' vs. 'sub-ordinates' vs. 'floaters' as different male phenotypes, although

most lizards, even those that fall within the tropics, often exhibit temporal cycles of reproduction within a given year. While the structure or duration of these cycles may not always be consistent among species (or even among populations of the same species), for the sake of this perspective I will treat anole reproduction with a simple unimodal model of activity which I am most familiar with observing in south Florida; lizards begin courting in the Spring, copulate in the late Spring through to early Fall, and cease reproductive activities through the Winter. This is consistent with the reproductive behavior I have observed, as well as being supported by temporal patterns of egg production (see Josh Hall's contribution in this newsletter about our ongoing research on this topic).



Fig 6. An adult male Puerto Rican crested anole (*A. cristatellus*) perches close to a female in early Spring as the breeding season commences. Photo taken on 14th Feb 2017.

Could a mating system exist whereby males change mating strategies as the breeding season progresses? In this scenario, males may be classically territorial in the early stages of the breeding season, in other words demonstrate behaviors consistent with being philopatric, spatially defensive, and with high levels of mate guarding, but this then decreases as the season continues. Whether these three behaviors occur independently or in concert is unclear but testable. In this system, males which establish a 'territory' at the start of the season would therefore guarantee sole access to a female or group of females. In turn, this would mean that those males are highly likely to sire the first series of clutches from those females (especially if it represents their first reproductive season), and, by virtue of sperm storage, may also sire future clutches even if/when females mate with other males. In this

way, if a male has already guaranteed exclusive mating with one (or a small number) of females, then at some stage – perhaps at the onset of egg-laying – it would be beneficial for the male to relax costly behaviors associated with territoriality and attempt to mate with other females in the population. In this way, male anoles may switch from a conservative (high territoriality) to a diversified (high promiscuity) tactic of bet hedging in mating.

This hypothesis comes with a couple of caveats, some I'm sure that I have missed. Firstly, this model assumes that females don't move. Although female anoles do often have significantly smaller home ranges than males, it's unclear if this is a fair assumption. I know

whether these represent distinct behavioral categories or are more likely points along a behavioral continuum remains unclear.

from my own research that the longest surviving females in my survival study on a population of brown anoles are those which are highly philopatric (the ones which don't survive might also be, so the relationship isn't clear just by that observation alone). Secondly, this also assumes that females will copulate with whichever males they share space; the concept of the 'passive' female. Again, this is unclear and deserves more attention. Thirdly, it would be important to determine the difference in time between when anoles start exhibiting copulatory behavior and when egg laying starts (and how consistent this is between populations). It is possible to test all of these caveats in a well-designed study.

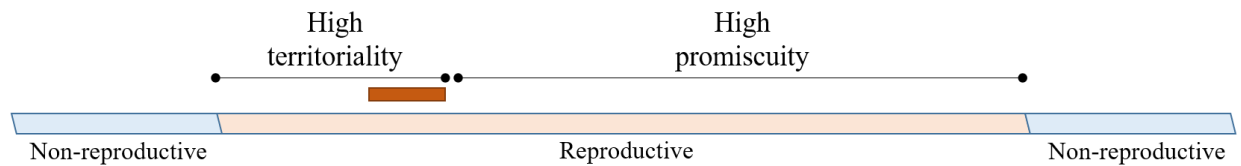


Fig 7. An alternate perspective on the social cycle of reproduction in anoles. If females are collected in the period during (or immediately after) the short dark orange section, representing when egg laying starts in the population, would the ensuing clutches be more likely the result of fertilization from a single male compared to collection at the end of the reproductive season? In other words, is mating with multiple males consistent throughout the entire reproductive season or is there a temporal pattern from one to many?

These ideas stem from casually noticing that early on in the commencement of the breeding season (here I'll call it the 'courtship phase') mature males can nearly always be found within a very short distance of a mature female, although copulations generally don't yet occur (e.g. Fig 6). I have noticed this for *A. sagrei* and *A. cristatellus* (both Trunk-Ground) and *A. equestris* (Crown-Giant). This behavior dissipates as the breeding season continues. Perhaps this happens for two reasons; (i) as I previously mentioned, maintaining exclusive breeding rights to a female (or females) becomes increasingly more difficult and time consuming (i.e. more costly), and (ii) males which may have been immature at the start of the season develop rapidly through the Summer, bringing with it an increase in male-male sexual competition as the reproductive season progresses. In this model, territoriality may play an important role in anole mating systems and in explaining selection for agonistic behaviors, but the temporally static nature of territoriality should not be one of the assumptions.

Lastly, and kind of related but also kind of not, what is the significance of female aggression? Anyone that has sat and watched anoles for extended periods of time will note that while male-male interactions can be dramatic and showy, females can be equally as quick to aggressively confront a conspecific (I have witnessed females attacking both other females and

adult males!). Ellee Cook's current doctoral research is tackling this topic and promises to provide novel insights into female aggression and associated interactions.

My real impetus for writing this piece on territoriality and mating systems isn't to contribute anything of particular substance, but instead to keep the conversation going among anole researchers. This is an exceptionally exciting phase of research into the social and sexual lives of anoles, and one which I hope continues! The accessibility of newer and more advanced technology aimed at mapping fine-scale movement of individuals could provide an interesting opportunity in this field.

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