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ORIGINAL PAPER

Factors leading to the evolution and maintenance of a male ornament in territorial species

Grace K. Charles · Terry J. Ord

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Abstract Male ornamentation is assumed to have evolved primarily from selection by female mate choice. Yet this is only one possible reason for ornament evolution. Ornaments might also be useful in aggressive competition by improving opponent assessment between males, or they might function to enhance signal detection by making males more conspicuous in the environment. We tested both these ideas in territorial *Anolis* lizards in which female choice is either absent or secondary to males competing for territories that overlap female home ranges. Male tail crests only evolved in species in which territory neighbors were distant, consistent with the signal detection hypothesis. Once the tail crest had evolved, however, it seems to have become a signal in itself, with variation in the frequency and size of tail crests within species correlating with variables predicted by the aggressive competition hypothesis. Our study presents an apparent example of a male ornament in which the selection pressure leading to variation among species in ornament expression is different from the selection pressure acting on variation within species. The *Anolis* tail crest is therefore likely to be an exaptation. We caution that conclusions made on the evolution of male ornaments are dependent on the phylogenetic perspective adopted by a study. Studies restricted to single species are useful for identifying selection pressures in contemporary settings (i.e., the current utility of traits), but may lead to erroneous conclusions on the factors that initially lead to the origin of traits.

Keywords Caribbean anoles · Exaptation · Visual signal · Phylogenetic comparative method · Ancestor state reconstruction · Sexual selection · Natural selection

Introduction

Conspicuous ornaments are a prominent feature of many animals. Familiar examples include the elongated tailfin or "sword" in male swordtail fish (Basolo 1990) and the elaborate trains of peacocks (Petrie et al. 1991) and male widow birds (Pryke and Andersson 2002). Such ornaments have been of longstanding interest to researchers because of their putative role in female mate choice (Darwin 1874; Andersson 1994). Males are frequently the most ornamented of the sexes and courtship rituals often function to allow female inspection of male ornaments (e.g., the backward swim of male swordtails—Rosenthal et al. 1996; the train-rattling display of peacocks—Dakin and Montgomerie 2009). Ornamental structures are sometimes so exaggerated in males that movement is impaired, increasing the risk of predation and reducing foraging efficiency (e.g., Park et al. 2001; Basolo and Alcaraz 2003). These costs, in addition to the energetic requirements of developing a large ornament in the first place, result in a trait that can provide valuable clues to a male's condition. Hence, female mate choice is assumed to be responsible for the evolution of most conspicuous ornaments in males

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G. K. Charles
Museum of Comparative Zoology and the Department of Organismic and Evolutionary Biology, Harvard University,
Cambridge, MA, USA

T. J. Ord (✉)
Evolution and Ecology Research Centre and the School of Biological, Earth and Environmental Sciences,
University of New South Wales,
Kensington, NSW, Australia
e-mail: t.ord@unsw.edu.au

(Darwin 1874; Andersson 1994). However, whenever males compete directly amongst themselves for access to females, any cue that conveys information on a rival's condition will also be useful in assessing potential fighting ability. The obvious example here is the assessment of weapon size (e.g., horns, antlers), but it is also reasonable to expect the assessment of non-weapon-based ornaments (Rohwer 1982). Alternatively, elaborate morphological structures may have little to do with the assessment of mates or rivals and instead function as "amplifiers" of an otherwise separate display or to facilitate the detection of a displaying individual in a visually difficult environment. Wolf spiders have large black tufts of hair on their front legs that enhance the visual impact of a leg waving display (Hebets and Uetz 2000). Female common frogs have been suggested to visually locate a calling male by the reflection of moonlight off his inflated white throat pouch (Sztatecsny et al. 2010). In both cases, the ornament is not being evaluated directly, but functions to direct the attention of the receiver towards another characteristic or the signaller more generally. Just how frequently elaborate ornaments evolve in males as a consequence of aggressive competition or to enhance signal detection rather than via female mate choice is uncertain.

While the adaptive advantage or function of some trait in a population might be revealed through observation or experimentation, the factors leading to that trait's initial evolution could have been quite different (Prum 1994). For example, a morphological structure might have originated to enhance the localization of a displaying male but was subsequently co-opted as a signal in itself because its expression was (or became) condition dependent. Such a trait is known as an exaptation (Gould and Vrba 1982): a trait that initially evolved in response to one selection pressure but was later co-opted to serve a different purpose in response to a new selection pressure. Proving exaptation or that a co-option of trait function has occurred is difficult. Possible examples in sexual signaling might include the origin of the sword in male swordtails or the conspicuous orange coloration of male guppies (see also Garcia and Ramirez 2005). Both ornaments have generally been confirmed to have originated because they exploit a sensory bias in females (e.g., a preference for large size in swordtails (Rosenthal and Evans 1998) and orange-colored food items (Rodd et al. 2002) and the detection of male suitors in murky aquatic environments in guppies (Endler 1987)), yet both ornaments have also been shown to be used by females to discriminate among males based on condition (e.g., long swords are energetically costly for swimming (Basolo and Alcaraz 2003); bright male coloration reflects the quality of a male's diet (Grether 2000)). Each trait initially evolved to exploit a sensory bias in females but became direct targets of selection as assessable signals in their own right. An important implication here is that the selection pressure leading to variation among species in the expression of a trait (e.g., signaler detection or the presence of a sensory bias) might differ from the type of selection acting on variation among individuals within a population (e.g., sexual selection).

We had two goals in our study. The first was to investigate whether aggressive competition or signal detection might account for the evolution of a conspicuous tail crest in male territorial lizards. The second goal was to determine whether the likely selection pressure that led to the origin of the tail crest was the same or different from the selection pressure that acts on variation among males in the size of tail crests within populations. Female mate choice in *Anolis* lizards has not been convincingly shown in any species so far studied (e.g., reviewed in Tokarz 1995; see also Tokarz 1998). Instead, female *Anolis* lizards seem to settle in areas based on resource availability (food and refugees; Stamps 1973; Paterson 1999). Males subsequently attempt to monopolize access to females by establishing exclusive territories that overlap female home ranges (Stamps 1983). To defend and advertise territory ownership, male *Anolis* perform elaborate body movements or headbob displays that can include tail arching. Displays are frequently accompanied by the extension of a large throat fan or dewlap. The function of the *Anolis* dewlap is still poorly understood, but data suggests multiple functions from species recognition (Leal and Fleishman 2002), enhancing the detection of headbob displays in visually difficult environments (Ord and Stamps 2008; Ord et al. 2010, 2011), and opponent assessment (Vanhooydonck et al. 2005). In addition to the dewlap, adult males of several *Anolis* species also possess a prominent tail crest, the size of which varies considerably among males within those species. To our knowledge, no study has investigated the evolution or function of the tail crest.

While deciphering the historical origins of the dewlap is complicated because of its almost ubiquitous presence throughout the *Anolis* genus, this is not the case for the tail crest. Among the approximately 150 *Anolis* species found throughout the Caribbean, the possession of a prominent tail crest in male lizards is rare. However, several examples of species with tail crests are clustered in a monophyletic clade that radiated on and around the island of Puerto Rico. We have detailed information on the ecology and behavior of most species in this clade. The group therefore provides an excellent opportunity to investigate the origin and maintenance of a male ornament in a system centered on male territoriality. We began our study by exhaustively surveying all species within the clade for the presence of a tail crest and reconstructed its evolutionary history. We then tested two non-mutually exclusive hypotheses for the evolution of male ornamentation, the "detection" hypothesis and the "competition" hypothesis. The detection hypothesis infers that a tail crest facilitates advertising territory ownership by increasing the conspicuousness of a displaying male. That is, the tail crest exaggerates the apparent size of the lizard in the environment and, in turn, the size of the stimulus moving across the retina of receivers as the male displays. Species living in poorly lit habitats or habitats in which territorial neighbors are distant should therefore be more likely to possess prominent tail crests compared to species living in bright habitats or where neighbors are nearby. The competition hypothesis, on the other hand, infers a direct competitor advantage to having a large tail crest, either because large size generally appears more threatening to rivals or because a large crest expressly conveys reliable information on condition and potential fighting ability. It assumes that tail crests are costly: only males in good condition can incur the energetic and developmental costs associated with possessing a prominent tail crest. Here, species in which competition for territories is high, either because there are few females or because male population density is high, should be species possessing tail crests. Within populations, the competition hypothesis also predicts that males with territories overlapping the most females will also be males possessing the largest tail crests. To test this latter prediction, we examined two populations of a single species in which the tail crest was especially common. We tested whether variation among males in the size of the tail crest correlated with the number of females residing in a male's territory, and whether this relationship was dependent on the intensity of competition for territories within that population.

Methods

Ancestor state reconstructions

We mapped the evolutionary history of tail crests in 15 taxa belonging to the monophyletic Puerto Rican radiation to examine the likelihood that crests evolved several times independently or once in a common ancestor within the group. The presence of tail crests was determined by stills taken from an extensive video library of Puerto Rican *Anolis* species (Ord et al. 2007, 2010, 2011) and the inspection of preserved specimens in the collections of the Museum of Comparative Zoology at Harvard University. Tail crest presence was defined as a noticeable crest on top of all or part of the tail. Stills extracted from video were high-quality close-ups of adult male territory holders in which the male filled most of the visual field of the image and was side-on to the video recorder. If a male possessed a tail crest, it would have been clearly visible in stills. Videos were of unmarked free-living adult males. To ensure that males were not inadvertently re-sampled, recording sessions were conducted systematically such that areas were visited only once and consecutive recordings were made well out of visual range of one another (see Ord et al. (2007) and Ord and Stamps (2008) for details). Between 13 (*Anolis poncensis*) and 76 individuals for 10 taxa were examined from the video library, while between 1 (*Anolis ernestwilliamsi*) and 20 specimens for the remaining 5 taxa where examined from the museum collections. We then used the phylogeny of Nicholson et al. (2005; presented with branch lengths in Losos (2009)) to map ancestor states using the maximum likelihood algorithm in the program Mesquite ver 2.71 (Maddison and Maddison 2009). In cases where two populations were surveyed for a given species (*Anolis cristatellus* and *Anolis gundlachi*), we set branch lengths based on the minimum expected divergence between physically isolated populations (see Jackman et al. 2002 and Ord et al. 2010). We chose to treat populations as separate taxa to be consistent with phylogenetic regressions (see next section). In any respect, reconstructions based on single data points for each species recovered equivalent node assignments (analyses not reported).

Phylogenetic regression analyses

For hypothesis testing we focused on ten taxa for which we had detailed ecological data. Populations were treated as separate taxa in these analyses because variation between populations existed in both the expression of tail crests and the variables predicted to influence crest evolution. Crest presence in males was determined from video stills as described in the previous section. The sample size of males surveyed for each species is also given in the previous section. All habitat and demographic data used in our analyses were collected immediately following each observation and are outlined below.

The detection hypothesis predicted that, among species, the proportion of males possessing a noticeable tail crest would be negatively correlated with habitat light and positively correlated with receiver distance. Habitat light was measured using a LI-250A handheld light meter with a LI-190SA Quantum Sensor at the site of first display using the procedure outlined in Ord (2008). Briefly, the sensor was position at the site the focal lizard was first observed to perform a territorial advertisement display. The sensor was positioned horizontal to the ground and two measurements of light were taken corresponding to where the left and right eye of the lizard had been. The average of these two measures was taken. Data were measured as μmol m^{-2} s^{1} and were log-transformed before being averaged again over all males surveyed for a given species. Receiver distance was measured as the average distance to all male territorial neighbors seen over the 20–30 min observation period and that were within line of sight of the focal lizard to a distance of 20 m (see also Ord and Stamps 2008; adult male *Anolis* lizards are quite small, ranging from 5 to 10 cm in snout-to-vent length and occupy territories 3–5 m in radius (Ord et al. 2010; see also Fleishman 1992)). Measurements were taken with a tape measure anchored at the site of first display of the focal lizard. The average distance to territorial neighbors for each male subject was then averaged again across all males surveyed for a given species. There was no correlation between habitat light or any other habitat measure (environmental motion, habitat clutter; e.g., see Ord et al. 2011), and estimates of neighbor distance (data not reported). While some territorial neighbors might have been missed during our surveys, our sampling protocol was consistent for all lizards and should consequently provide a reliable, relative measure of neighbor distance among males within and between species.

The competition hypothesis predicted that, among species, the proportion of males possessing a tail crest would be positively correlated to the density of males competing for territories in a population and the ratio of males to females within a population. That is, competition for territories should be high whenever there are more males than females in a population (a male-biased sex ratio). However, competition for territories can also be expected to increase if the environment becomes saturated with competitors (high male density) with no change to a population's sex ratio. Hence, both male density and sex ratio were used to test the competition hypothesis. Male density was estimated as the total number of territorial neighbors observed for a male over the 20–30 min observation period, averaged over all males surveyed for the species or population. Sex ratio was estimated as the average density of male neighbors divided by the average number of females residing within male territories for a given species or population (female number was determined by noting all females observed over the observation period that were within 5 m of a male's site of first display, a distance that would correspond to the maximum likely radius of a male's territory).

Although the two hypotheses are not mutually exclusive, we chose to maximize our statistical power by testing each hypothesis separately rather than attempt to include all variables in a large multivariate analysis. We implemented the phylogenetic generalized least squares regression analysis in COMPARE 4.6b (Martins 2004) based on the phylogeny used for ancestor reconstructions (see previous section). The level of phylogenetic signal or inertia in data is summarized by the parameter α, with large values of α consistent with little or no phylogenetic signal in data (15.50+; e.g., traits are free to potentially evolve adaptively), while small values of α are consistent with the presence of a strong phylogenetic effect (0.00; e.g., traits are limited in the extent they can respond to selection; see Revell et al. (2008) for an important cautionary note on the biological interpretation of estimates of phylogenetic signal). Statistically significant relationships were determined by slope estimates in which 95% confidence intervals (CIs) did not overlap zero.

Population analyses within species

The competition hypothesis further predicts that, within populations, the number of females residing in a male's territory should be correlated to the size of the territorial owner's tail crest. To test this, we focused on two populations of *A. gundlachi*, a species that was estimated to have the highest prevalence of tail crests of all the species we surveyed. These populations were located in the shade forest near the town of Ciales in the northwestern region of Puerto Rico, and in the montane forest surrounding the El Verde Field Station on the eastern portion of the island. The populations were separated by 65 km (as the crow flies) and were considered to be physically, and consequently reproductively, isolated from one another.

Images of 18 males from the Ciales population and 16 males from the El Verde population were extracted from video records (see the previous section "Ancestor state reconstructions" for details). Sample size was dependent on finding images in which the male was side-on to the camcorder and his tail free of visual obstructions. A single observer (GKC) measured precisely the area of the tail crest and the snout-to-vent length in pixels using ImageJ ver 1.42q (W. Rasband 1997–2009, NIH). These data were then converted into mm using a calibration value that controlled for the distance and magnification of the camcorder at the time of recording (see Ord et al. 2007). This calibration value was calculated by measuring an object of known size (a ping pong ball) positioned in frame and at the exact site that the lizard was video recorded (whenever a lizard shifted perches its new position was noted down and an inconspicuous flag used to mark the position of the camcorder). The tail of anole lizards is autonomous and is typically dropped during a perceived predator attack as a means of distracting the predator while the lizard attempts an escape. Although the tail grows back, whether a tail has been regenerated could affect our estimate of crest size because regenerated tails do not include a crest. To account for this, any indication that a tail may have been regenerated was noted (e.g., evidence of missing proportions of the tail or a clear line of discoloration indicating regrowth on the tail itself).

We used a linear regression model implemented in R ver 2.8.1 (R Development Core Team) that included tail crest area as the dependent variable and the number of females within a male's territory as the main predictor variable. Tail regeneration history (scored as "0" if tail appeared not to be regenerated and "1" if there was evidence that the tail had been lost and subsequently regrown) and snout-to-vent length were included as covariates. Each population was tested separately.

Situations in which multiple comparisons were performed *p* values were evaluated against a false discovery rate threshold (Benjamini and Hochberg 1995) computed based on the number of comparisons performed and an initial a *p* value of 0.05.

Results

History of tail crest evolution

There was some evidence for two independent origins of the tail crest—once in the six-species clade that includes *A. cristatellus* and once in *A. gundlachi* (likelihood probabilities around 45% at corresponding nodes; Fig. 1b). However, we can refine this reconstruction further using our knowledge of the natural and evolutionary history of the species in question. We suggest instead that the tail crest evolved only once in the common ancestor of *A. cristatellus* and *A. gundlachi*, and was subsequently lost in *A. poncensis* (Fig. 1b). We feel this is a more realistic scenario because *A. poncensis* is one of the rare *Anolis* species in which the conspicuous dewlap has also been greatly reduced (Fig. 1a), suggesting selection against (or the absence of selection for) conspicuous ornamentation in this species (*A. poncensis* are found perched out in the open on shrubs among the sand dunes behind Bahia de la Ballena on south-western Puerto Rico and are extremely wary, although males are aggressive and defend territories with elaborate push-up displays; Ord et al. 2010).

Predictors of tail crest evolution

The distance of territorial neighbors was positively correlated with the proportion of tail crests exhibited by males within taxa in a phylogenetic regression, supporting the detection hypothesis (Table 1). Figure 2 clarifies this relationship as a threshold: taxa with territorial neighbors at average distances greater than 5 m had males with a tail crest, while taxa with territorial neighbors within an average distance of 5 m or less lacked a tail crest altogether. This threshold was confirmed in a phylogenetic ANOVA in which the proportion of males with crests was examined as a function of neighbor distance coded as "0," if neighbors were within 5 m, or "1" if neighbors were typically farther than 5 m ($N=10$, $r^2=0.44$, $\alpha=6.63$; β (95% CI)=0.49 (0.09–0.89)). Nevertheless, for those taxa with neighbors farther than 5 m, it was clear that neighbor distance could not account for variation in the number of males within taxa that had tail crests (Fig. 2), nor was this likely explained by variation among those taxa in habitat light (Fig. 2; Table 1).

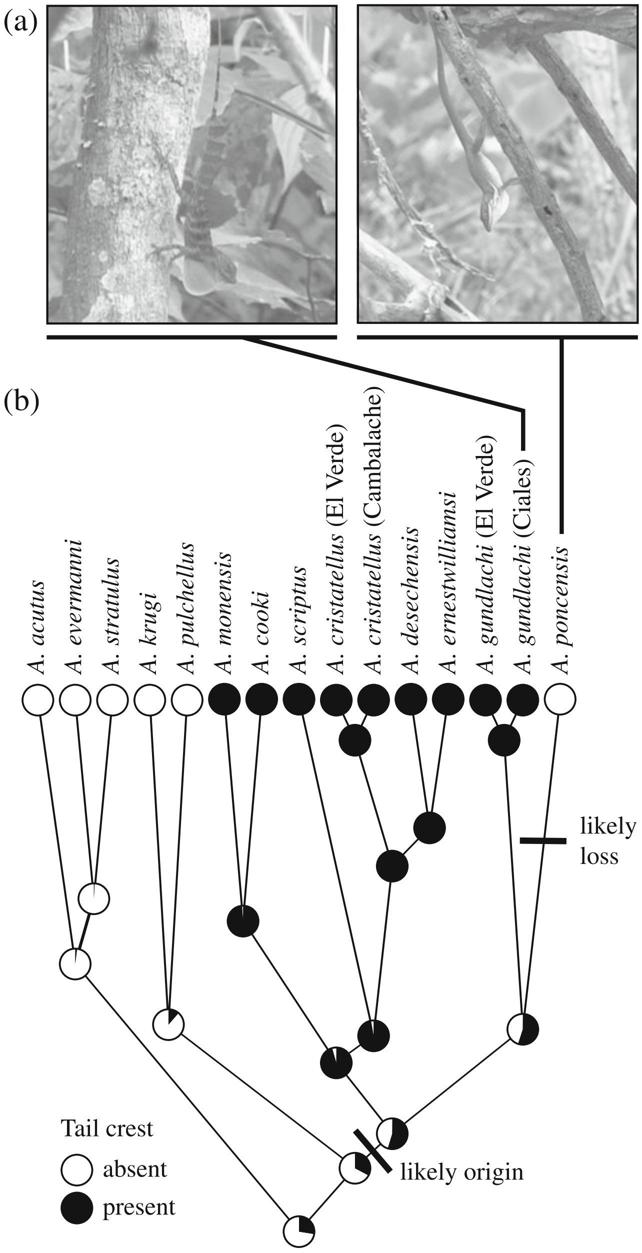


Fig. 1 Tail crest evolution in male *Anolis* lizards. Representative stills **a** extracted from digital video show an adult male *A. gundlachi* from Ciales in mid-display and with a prominent tail crest (*left*) and an adult male *A. poncensis* in mid-display without a tail crest (*right*). Ancestor state reconstruction **b** of male tail crest evolution in the Puerto Rican island radiation of territorial *Anolis* lizards. Reconstructions were computed using maximum likelihood with the proportion of filled circles at phylogenetic nodes corresponding to the probability of tail crests being present in an ancestor. The point at which the crest most likely evolved and an instance where it was most likely lost are indicated. See text for details

Table 1 The proportion of territorial males possessing a tail crest among Puerto Rican *Anolis* species, as predicted by variables affecting signal detection and the intensity of sexual selection

Variable	β (lower CI, upper CI)
Detection hypothesis	
N=10 taxa, r^2=0.56, α=3.11	
Intercept	−0.45 (−1.19, 0.29)
Habitat light	−0.14 (−0.41, 0.13)
Receiver distance	0.19 (0.05, 0.33)[a]
Competition hypothesis	
N=10 taxa, r^2=0.27, α=15.50+	
Intercept	0.13 (−0.48, 0.74)
Male density	0.38 (−0.09, 0.85)
Sex ratio	−0.03 (−0.71, 0.11)
Crested taxa only	
N=5 taxa, r^2=0.67, α=15.50+	
Intercept	−0.60 (−1.58, 0.38)
Sex ratio	1.11 (0.22, 1.99)[a]

Results are from phylogenetic generalized least squares regressions

[a] 95% confidence intervals that do not overlap zero

Male density and sex ratio did not correlate with the proportion of tail crests in a phylogenetic regression (Table 1). However, sex ratio did explain a significant amount of variation (67%) among taxa that did have a tail crest (Fig. 3; that is, in taxa with neighbors at distances greater than 5 m; Fig. 2).

Tail crest size in *A. gundlachi*

The number of females within a male's territory was positively correlated with the size of a male's tail crest within the Ciales population (Table 2; Fig. 4a), but not the El Verde population (Table 2; Fig. 4b). In general, a Ciales male with two or more females residing in his territory had a tail crest twice as large as the crest of a male with one or no females in his territory (see Fig. 4a), and this was consistent with the competition hypothesis. The lack of a similar relationship in the El Verde population was at first puzzling. However, Fig. 2 infers a potential difference in the competitive environment between the two populations: *A. gundlachi* at Ciales had the highest male density of any population or species we surveyed (virtually double that of other taxa studied). On closer examination we found significant differences between *A. gundlachi* at Ciales compared to El Verde in both the density of male neighbors (95% CIs, Ciales: 1.78–2.95; El Verde: 0.90–1.52) and the variance among males in the number of females within a male's territory (V, Ciales: 1.99; El Verde: 0.85), both of which are consistent with the notion that competition for territories was greater for males in the Ciales population than in the El Verde population. It follows from the competition hypothesis that a greater effect of tail crest size should be detected in the Ciales population than the El Verde population, which is exactly what we found (Ciales, t=2.39; El Verde, t=0.11; Table 2).

Discussion

Our results are consistent with the notion that the tail crest is an exaptation. It appears the crest first originated in male *Anolis* lizards to enhance the conspicuousness of a displaying male to distant territorial neighbors (the detection hypothesis). Once it evolved, the crest seems to have been

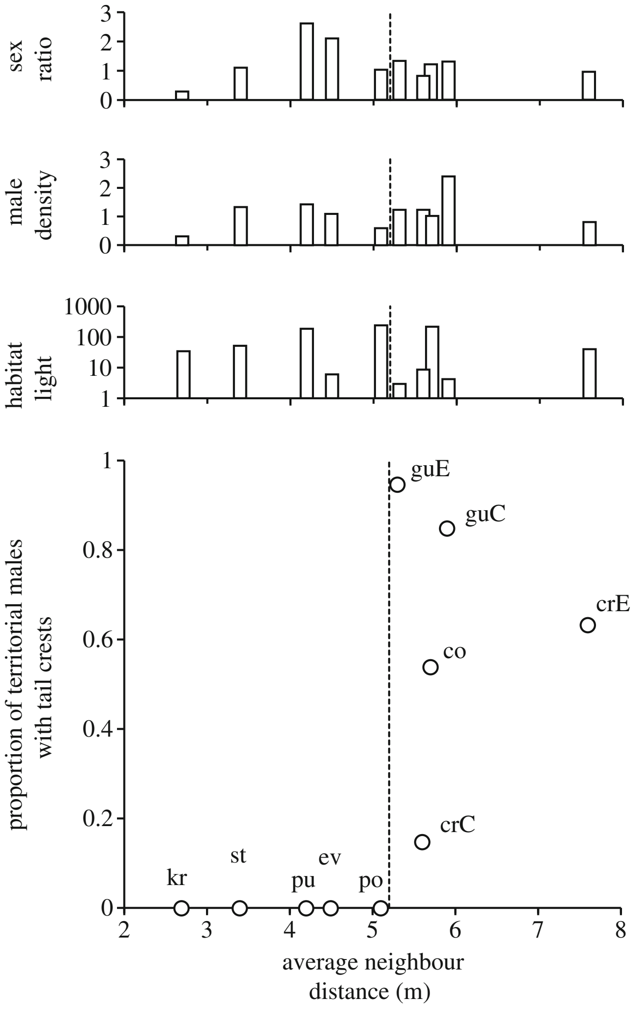


Fig. 2 *Anolis* species in which territorial neighbors were at distances greater than 5.2 m were those species in which males possess prominent tail crests. Also shown for reference are habitat light (measured as μmol m^{-2} s^{1}), male neighbor density, and sex ratio estimates for each species. Species codes are as follows: kr, *A. krugi*; st, *A. stratulus*; pu, *A. pulchellus*; guE, *A. gundlachi* (El Verde); guC, *A. gundlachi* (Ciales); co, *A. cooki*; crC, *A. cristatellus* (Cambalache); crE, *A. cristatellus* (El Verde)

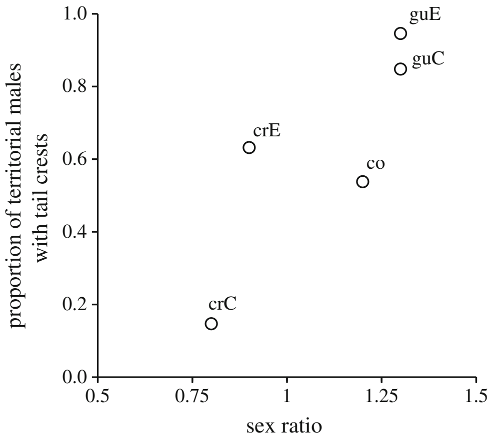


Fig. 3 Of those *Anolis* species with a tail crest, the frequency of males possessing a prominent crest was predicted by the male-biased sex ratio of a population. See Fig. 2 for definitions of species codes

co-opted as a signal in its own right, for example as a means of opponent assessment among competing territorial males. This led to its increasing prevalence in species in which males competed intensely for territories (the competition hypothesis). Within at least one population, males with large tail crests were also those males able to defend a territory that encompassed many females, which should in turn lead to higher reproductive success for these males and a subsequent selective advantage for large crests. Future work is needed to confirm that a displaying male with a large tail crest viewed at a distance (5 m or greater) is significantly more conspicuous than a displaying male without a tail crest, and that a large crest is indeed perceived as more intimidating to rivals than a small tail crest (e.g., both could be tested using robot playback experiments; Ord and Stamps 2008, 2009). In any respect, our study does show that a male ornament has evolved in a group of territorial species via processes that need not include female mate choice, and that different selection pressures can promote variation in ornament expression at different phylogenetic scales. Indeed, one of the most interesting patterns we documented was at the clade level, where a threshold effect for neighbor distance was apparent.

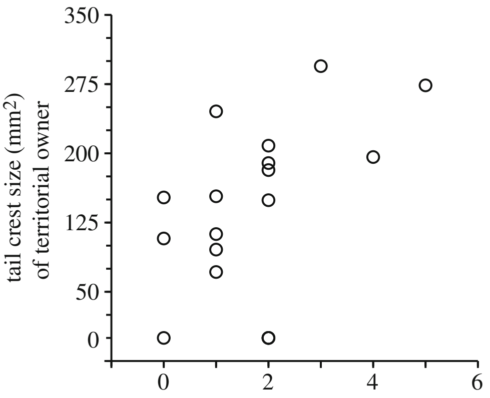
Table 2 Tail crest size in territorial males of *A. gundlachi* as a function of the number of females within a resident male's territory

Variable	*B*	*t*	*P*
Ciales population			
r^2=0.67, $F_{3,10}$=6.63, P=0.010[a]			
Intercept	−123.10	−0.57	0.584
Females within territory	27.28	2.39	0.038[a]
Tail regeneration history	−63.69	−2.37	0.039[a]
Snout-to-vent length	4.98	1.15	0.275
El Verde population			
r^2=0.28, $F_{3,9}$=1.16, P=0.378			
Intercept	−61.44	−0.47	0.650
Females within territory	3.11	0.11	0.917
Tail regeneration history	−24.15	−0.46	0.654
Snout-to-vent length	3.42	1.78	0.109

Two populations were examined: Ciales and El Verde. Regeneration following tail loss and male body size were included as covariates Note: tail regeneration history was scored as 0 if tail did not appear to be regenerated and 1 if clearly regrown following tail loss

[a] Statistically significant once false discovery rate (FDR) is controlled for based on two multiple regression analyses

(a) *A. gundlachi* (Ciales)



(b) *A. gundlachi* (El Verde)

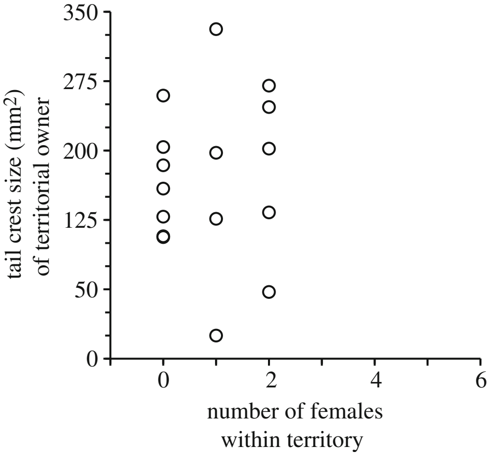


Fig. 4 The relationship between the number of females residing in a male lizard's territory and the size of his tail crest in two populations of *A. gundlachi*, which are as follows: **a** Ciales and **b** El Verde

It should be noted that those species above the neighbor distance threshold, and all species possessing a tail crest in the Puerto Rican radiation more generally (Fig. 1), are species belonging to the same ecomorph category. The Caribbean *Anolis* lizards are a classic example of convergent evolution in which a similar set of ecomorphs have evolved independently on each of the four islands of the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico;

reviewed in Losos 2009). Each ecomorph is named based on where in the environment species are typically found and there are three ecomorph types within the clade that we focused on: grass bush (*Anolis krugi*, *Anolis pulchellus*, and *A. poncensis*), trunk-crown (*Anolis acutus*, *Anolis evermanni*, and *Anolis stratulus*), and trunk-ground (all others). There is an obvious association between tail crests and the trunk-ground ecomorph (Fig. 1), which draws into question whether crest evolution was in fact driven by neighbor distance or some other aspect shared among species of this ecomorph (the trunk-ground ecomorph is named because species are found primarily on tree trunks and to some extent on the ground). Based on several lines of reasoning, we believe this association with the trunk-ground ecomorph is coincidental. First, the environments of the trunk-grounds that we were able to study in detail were generally open: *A. gundlachi* and *A. cristatellus* were found defending territories in forests at perch heights above the understory, while *Anolis cooki* maintained territories centered on coconut trees among the sand dunes of Bahia de la Ballena where there was little or no understory. The distribution of defended trees for populations of these species meant that territorial neighbors were necessarily quite distant from one another. That is, it is not the ecomorph per se but the open environments more specifically that resulted in greater neighbor distances for these species. Second, there are two trunk-ground ecomorphs on Jamaica, *Anolis lineatopus* and *Anolis sagrei* (an invasive from Cuba), and both lack a tail crest and both have average neighbor distances below the 5 m threshold (4.2 and 4.5 m, respectively; Ord et al. 2011). Third, according to observations from field biologists that have worked extensively on *Anolis* trunk-grounds on Hispaniola, all lack tail crests (indeed, no species on Hispaniola seems to have a tail crest except an introduced population of *A. cristatellus* in the southeast; D.L. Mahler, personal communication; neighbor distances for Hispaniola species are unknown). Fourth, there are several *Anolis* species that are not trunk-ground ecomorphs but do possess a tail crest (on Puerto Rico: *Anolis cuvieri*, a crown-giant ecomorph; in the Lesser Antilles: *Anolis ferreus* and *Anolis leachii*, no particular ecomorph; neighbor distances for *Anolis curvieri* are likely greater than 5 m (T.J. Ord, personal observation); no information on neighbor distances are available species in the Lesser Antilles).

Finally, while there are several trunk-ground species on Cuba that possess prominent tail crests, the association with ecomorph is incomplete. Of the 13 trunk-ground species on Cuba (Losos 2009), our survey of the literature (Rodríguez Schettino 1999) and specimens in the MCZ collections found 7 trunk-ground species in which the tail crest was clearly present in males (*Anolis imias*, *Anolis rubribarbus*, *Anolis jubar*, *Anolis homolechis*, *Anolis mestrei*, *Anolis guafe*, and *Anolis confusus*), two species in which the crest was absent in males (*Anolis sagrei* and *Anolis bremeri*) and two species in which males may have a tail crest, but it is greatly reduced (*Anolis ahli* and *Anolis allogus*; no records were available for the two remaining species *Anolis delafuentei* and *Anolis birama*). Furthermore, inspection of the phylogenetic relationships among the Cuban trunk-grounds (Losos 2009) shows that those species possessing a tail crest are not monophyletic, indicating either multiple origins or multiple losses of the crest within the trunk-ground group. As far as we are aware, no other Cuban anole outside of these trunk-ground species possess a tail crest. Taken together, while it is possible that there is something about species belonging to the trunk-ground ecomorph that might predispose trunk-ground clades to evolve a tail crest, the mechanism prompting crest evolution seems to be selection for enhanced signal detection when receivers are distant (Fig. 2), and tail crests subsequently proliferate further within species following selection for improved opponent assessment (Figs 3 and 4). We anticipate that future study of other territorial lizards outside of *Anolis* that exhibit tail crests and lack ecomorphs, most notably the Old World agamid lizards (e.g., Ord and Stuart-Fox 2006), will corroborate that crest evolution is specific to the type of the social environment in which lizards defend territories.

While female mate choice is clearly an important factor generating the evolution of elaborate male ornaments (Andersson 1994), it is by no means the only selection pressure leading to ornament evolution. Furthermore, studies seeking to elucidate the origins of any phenotypic trait need to consider that the factors leading to a trait's evolution and variation among species might be different to or at least augmented by other factors that maintain the selective advantage of a trait within populations. Had we only focused on variation in crest size among males within a single population, we would have missed the richer story behind the variation in crest expression among species. Indeed, an exciting outcome of our study was the discovery that the *Anolis* tail crest seems to be an excellent example of an exaptation (Gould and Vrba 1982). This finding could have only been possible by integrating studies over different phylogenetic scales (comparative analysis combined with detail within species study).

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