A phylogenetic framework for the evolution of female polymorphism in anoles

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Female pattern polymorphisms (FPP) are striking, poorly understood, and a major challenge to evolutionary theory. We examined the evolution of FPP in anoline lizards in a phylogenetic context. Accordingly, we used comparative analyses that traced the evolution of female pattern polymorphism over historical time, and overlaid the historical pattern on the biogeographical distribution of current species. Comparative analyses used a maximum likelihood approach with variable rates of trait evolution. We found that, among almost 180 well-described species, 52 exhibited FPP and most of these occurred on the Central American mainland. Pagel’s $\lambda = 0.644$ indicated not only a moderately strong phylogenetic signal in FPP among 162 species with sound estimates of phylogeny, but also independent evolution. Their common ancestor was not polymorphic (0.003% likelihood of FPP), and there were at least 28 gains or losses of FPP during phylogenetic history. The geographical distribution of FPP indicates that, in the Caribbean islands, it has been present for almost 20 million years, and that parallel evolution of FPP has taken place during that time, including independent evolution on Cuba, Hispaniola, and Puerto Rico. Evidence of parallel evolution of FPP in anoles was fairly strong. © 2011 The Linnean Society of London, Biological Journal of the Linnean Society, 2011, 104, 303–317.


INTRODUCTION

The incidence of multiple morphs within a population (i.e. polymorphism) has inspired hypotheses about its evolution ever since early explorations into evolutionary biology (Darwin, 1859; Darwin, 1871). Variation in morphological characters such as size or colour between males and females (sexual dimorphism) and among males led to sexual selection theory (Darwin, 1871), and both have been thoroughly investigated in a wide variety of organisms (Shine, 1979; Andersson & Iwasa, 1996; Sinervo & Lively, 1996; Houde, 1997; Shuster & Wade, 2003; Pradhan & Van Schaik, 2009). Research on polymorphism among females has concentrated mostly on insects, although it has generally remained understudied. In recent years, the number of attempts to better understand female polymorphism has increased noticeably (Stamps & Gon, 1983; Svensson et al., 2009).

Female polymorphism has been documented mostly for species of Lepidoptera (butterflies) and Odonata (damsel flies and dragonflies) and rarely in vertebrates (Tillyard, 1917; Fisher & Ford, 1929; Richards, 1961; Wickler, 1968; Schoener & Schoener, 1976). Although polymorphism has been described for other species, only a few of these have been subjected to research on its occurrence. Multiple selective pressures may interact to maintain polymorphism that is limited to females (Joron & Mallet, 1998; Sirot et al., 2003). Female colour morphs in damsels flies, for example, are considered to exert alternative techniques to balance predation and male harassment. Despite intensive field studies and molecular
research, especially in Odonata, female polymorphism remains poorly understood (Andres, Sanchez-Guillen & Rivera, 2000; Svensson et al., 2009).

Unexpectedly, most research has focused on single species. Although such contributions are valuable for our understanding of how female polymorphism is maintained, they usually do not address the question of origination. By contrast, macro-evolutionary approaches examine species characteristics in light of their evolutionary history and consider the possibility that current characteristics may have resulted from historical events, rather than as current adaptations (Dobson, 1985). When a character is shared between sister taxa, the most parsimonious explanation is that the trait was retained after origination in their common ancestor. Thus, the trait may have evolved in an ancestral environment, which may differ from the current environment. Conversely, independent evolution of a trait in distantly-related species suggests an adaptive character of the trait if it coincides with occupation of similar environments (Harvey & Pagel, 1991; Larson & Losos, 1996; Schluter, 2000). In this case, the shared character may have evolved from different ancestral states (convergent evolution), or from the same ancestral state (parallel evolution) (Harvey & Pagel, 1991; Zhang & Kumar, 1997). In either case, adaptation can be addressed by relating the shared trait to current environmental variables. Phylogenetic approaches thus provide direction for future research and indicate a possible limitation of population-based studies (Grandcolas & D’Haese, 2003).

Analogous to effects of shared ancestry, geographical distribution can promote or constrain evolutionary change. Wiens et al. (2009) emphasized the importance of a geographical context for a phylogenetic analyses. Geographical isolation is considered to stimulate convergent evolution when the different locations contain similar environments (Simpson, 1953). Furthermore, an environment could become saturated with species sharing a common trait. In this case, geographical isolation could further stimulate parallel evolution through release from this saturated environment into a similar, nonsaturated one, where the same trait can then evolve. The end result is that more species could share a particular adaptation (Wiens et al., 2009). A geographical perspective on a phylogenetic analysis of a recurring trait results in the evolutionary perspective required before further examination of the processes resulting in the evolution and maintenance of a trait.

A study of the phylogenetic context of female polymorphism in damselflies suggested that it was the ancestral state in two genera (Van Gossum & Mattern, 2008). In this case, the reason for origination and for maintenance of the trait each require different explanations and both are important to our understanding of polymorphism. In Papilio swallowtail butterflies, however, female polymorphism is a derived character that evolved repeatedly (Kunte, 2009). Such macro-evolutionary studies require a thoroughly examined group of organisms for which phylogenetic relationships are well known. For female polymorphism, particularly in vertebrates, such lineages have rarely been described. Yet, they could serve as model systems.

Anoles (Squamata: Polychrotidae) are a good model system for female polymorphism because female variation in dorsal patterns is easily observable, and patterns are known to be heritable (Calsbeek, Bonneaud & Smith, 2008). Females generally show two or three variations in mid-dorsal patterns within a population (e.g., Figure 1). Savage (2002) summarized female mid-dorsal patterns into five distinct morphs: mid-dorsal light stripe with or without dark border, diamonds, dark chevrons, and dark X marks. The patterns are already clearly expressed in juveniles and are consistent throughout life. The same patterns are found across species.

Figure 1. Examples of dorsal pattern variations in anoles. The patterns shown are seen in females within a population of Anolis humilis at La Selva Biological Station, Costa Rica. From left to right: mid-dorsal stripe with dark border, blotches, and dark chevrons.
With almost 400 species and recent advances in research of their phylogenetic history, anoles lend themselves well to macro-evolutionary approaches for studying female polymorphism. Anoles comprise an excellent model system for the study of ecology, evolution, and behaviour (Losos, 1992a, 1994; Beuttell & Losos, 1999). The presence of female polymorphism in anoles, however, has received surprisingly little attention, although its presence is commonly known (Fitch, 1975; Stamps & Gon, 1983; Savage, 2002). A relationship between morph and perch use was demonstrated in Anolis sagrei and Anolis polylepis (Schoener & Schoener, 1976; Steffen, 2010). Furthermore, effects of density on variation in immunocompetence and frequency-dependent selection, although not reproductive strategy, may explain female pattern polymorphism in A. sagrei (Calsbeek et al., 2008; Calsbeek, Bonvini & Cox, 2010; Cox & Calsbeek, 2011). Differences between morphs found thus far have focused on mechanisms of maintenance of female polymorphism without considering its evolutionary origin.

Because anoles are a good model for the study of female polymorphism, we examined the evolution of the presence of female dorsal pattern polymorphism (FPP) across species. In particular, we tested whether FPP is a derived character and has evolved independently among anoles. We also incorporated a geographical perspective to investigate whether isolation could have contributed to the current distribution of FPP among species.

**MATERIAL AND METHODS**

**DATA**

Species descriptions were used to determine the presence or absence of pattern polymorphism in females (Lazell, 1972; Fitch, 1975; Rand, Gorman & Rand, 1975; Duellman, 1978; Dixon & Soini, 1986; Ayala & Williams, 1988; Stejneger, 1900; Schwartz & Henderson, 1991; Avila-Pires, 1995; Lee, 1996; Vitt & de la Torre, 1996; Campbell, 1998; Rivero, 1998; Lee, 2000; Stafford & Meyer, 2000; Garrido & Hedges, 2001; Nicholson et al., 2001; Savage, 2002; Duellman, 2005; van Buurt, 2005). This allowed only species-level assessments, so that species were scored positive for female polymorphism, even if some populations lacked this. The presence or absence of dorsal pattern polymorphism was based on the vertebral zone alone. Geographical variation, subspecies variation, and variation as a result of metachromatism (i.e. colour change) were not considered as polymorphism for the purpose of the present study. Data are available in the online supporting information, Appendix S1.

**NOMENCLATURE**

There are almost 400 species of anoles and, despite extensive research on their evolutionary history, some phylogenetic relationships and the related nomenclature remain ambiguous. Recent phylogenies indicate that there are several rather well-established clades within anoles, even though the relationship among some of these major clades remains unclear (Jackman et al., 1999; Poe, 2004; Nicholson et al., 2005), and a more practical nomenclature system eventually may result. Because, in the present study, the use of one genus name for so many species is impractical and many clades are rather stable entities, we refer to monophyletic clades and series within clades (Table 1). We still use Anolis as the genus name to avoid any confusion with future names that are likely to arise.

**PHYLOGENY**

No single phylogeny for all anole species was available. Therefore, we combined recent phylogenies,

<table>
<thead>
<tr>
<th>Clade name</th>
<th>Node number (Poe, 2004)</th>
<th>Series</th>
</tr>
</thead>
<tbody>
<tr>
<td>Norops = Beta anoles</td>
<td>286</td>
<td>Cuba: sagrei series (node: 225)</td>
</tr>
<tr>
<td>(Etheridge, 1960)</td>
<td></td>
<td>Jamaica: grahami series (node: 284)</td>
</tr>
<tr>
<td>Cybotes</td>
<td>293</td>
<td>Northern Lesser Antilles: bimaculatus series</td>
</tr>
<tr>
<td>Ctenonotus</td>
<td>216</td>
<td>Greater Antilles: cristatellus series</td>
</tr>
<tr>
<td>Carolinensis</td>
<td>309</td>
<td></td>
</tr>
<tr>
<td>Chamaeleonorops</td>
<td>197</td>
<td></td>
</tr>
<tr>
<td>Xiphosurus</td>
<td>190</td>
<td></td>
</tr>
<tr>
<td>Equestris</td>
<td>324</td>
<td>Southern Lesser Antilles: roquet series (node: 351)</td>
</tr>
<tr>
<td>Dactyloa</td>
<td>352</td>
<td></td>
</tr>
</tbody>
</table>

Node numbers of the phylogeny of Poe (2004) are included to indicate the specific clade on the tree.

sensu Nicholson et al. (2005), with species added from Poe (2004). The latter phylogeny was also used to resolve remaining polytomies. Species synonyms were checked using the Reptile Database (Uetz et al., 2007). The major differences between the phylogenies we used were the placement of the Cybotes series and placement of some species within the mainland beta anoles. None of the variation between the phylogenies, however, affected our major conclusions.

CHARACTER EVOLUTION AND PHYLOGENETIC SIGNAL
To study character evolution, we applied two different methods: parsimony and maximum likelihood (ML). The benefits and critiques on these techniques were reviewed in detail by Cunningham, Omland & Oakley (1998) and Cunningham (1999). Parsimony reconstruction fails to recognize rapid evolution of a trait, and parsimony is not reliable for unequal rates of evolution between loss and gain of a trait. These issues are largely overcome by ML methods (Schluter et al., 1997). A drawback of ML is its dependence on branch lengths, which may differ depending on which of several standard transformations are applied. These transformations are used when accurate estimates of branch lengths are lacking. Interestingly, ML does not necessarily favour the most parsimonious path of character evolution, although, when the number of character changes is limited, parsimony and ML methods generally result in similar reconstructions (Pagel, 1999).

Because ML approaches (see below) are sensitive to branch length, this analysis was run with equal branch lengths, as well as Grafen’s (1989) arbitrary transformation of branch lengths. The major conclusions, however, remained unaltered, regardless of the branch length transformation applied. Only the results for equal branch lengths are presented because of its slightly more conservative approach and because many studies apply this transformation, including evolutionary studies on anoles (Ord & Martins, 2006; Poe, Goheen & Hulebak, 2007).

Unordered parsimony analysis was performed in MESQUITE (Maddison & Maddison, 2008). This assumes equal rates of forward and backward evolution. ML estimates were obtained with the ‘geiger’ package in R, version 2.8.1 (Harmon et al., 2008). First, we compared an equal-rates (ER) model of evolution, as used in parsimony, with an all-rates-different (ARD) model and found that the ARD model fit the data slightly better \( [-\text{log likelihood}_{\text{ER}} = -87.47; -\text{log likelihood}_{\text{ARD}} = -85.07; P = 0.0286; \text{Akaike information criteria (AIC)}_{\text{ER}} = 177, \text{AIC}_{\text{ARD}} = 174] \). Particularly, forward evolution was found to be approximately two times faster than backward evolution (gain: 0.227 ± 0.05; loss: 0.097 ± 0.02). ML values for the ARD model were plotted onto the phylogenetic tree to visualize the chance of FPP being at every node.

Finally, we tested for phylogenetic signal using Pagel’s lambda (Pagel, 1999). This compares the distribution of a trait among taxa between a star phylogeny \( (\lambda = 0; \text{i.e. all phylogenetic structure removed}) \) and a given phylogenetic structure \( (\lambda = 1; \text{i.e. all branch lengths maintained}) \). Lambda thus varies between zero and one, and a higher value indicates a stronger covariance between the phylogeny and the distribution of the trait. To determine whether lambda is significantly different from zero, a ML ratio test was used in R (Yang, 2006; Harmon et al., 2008).

GEOGRAPHICAL DISTRIBUTION
For the geographical distribution of FPP, all island species were considered, even when phylogenetic relationships were unresolved. Because many mainland species remain poorly known, only the species for which detailed descriptions were available were included for the mainland. To assess geographical distribution of female polymorphism in anoles, we used species distribution maps and presence/absence data of FPP at the species level. This ignores the possible absence of FPP in certain locations of a species’ distribution. To test hypotheses related to the distribution of FPP, a more in-depth study of presence or absence of FPP per population will be required. Species distributions were included in the phylogeny to provide a geographical perspective on the phylogenetic analysis. Some species, however, were not included in any available phylogeny and could only be incorporated for the geographical distribution of FPP.

RESULTS
For 179 species of anoles, a detailed description of dorsal pattern was found. Slightly over 75% were island anoles. Of these species, 52 (approximately 30%) were described as having FPP. The majority of the species with female polymorphism were mainland species, even though island species constituted the larger part in the dataset. Not all species for which colour patterns have been described were included in the phylogenies that we used. Therefore, the number of species available for our phylogenetic analysis was 162.

PHYLOGENETIC SIGNAL
We found a significant phylogenetic signal in the presence of FPP among anoles \( (\text{log likelihood phylogeny} = -81.89; \text{log likelihood unstructured} = -90.61; \)
The lambda value under the ARD model was 0.644. Because lambda varies between zero and one, our value indicates a moderately strong phylogenetic signal.

CHARACTER EVOLUTION

Parsimony analysis

Parsimony analysis indicated that the ancestral state was absence of FPP (Fig. 2E). For the 162 species included, the evolutionary pattern of FPP required a minimum of 28 steps. The entire Carolinensis clade lacked FPP (Fig. 2C). Three other members of this group, which have never appeared in a published phylogenetic tree, lacked FPP. All other clades had at least one species with FPP. Overall, parsimony analysis indicated the independent evolution of FPP across clades. However, FPP was also found in closely-related species, signifying that FPP likely arose in their ancestor. This was the case for island Dactyloa (Fig. 2E; loss of FPP in Anolis bonairensis). In the remaining groups that had multiple species with FPP, including mainland Norops, Cybotes, and the Ctenonotus clades, alternative hypotheses on number of gains versus losses were possible, based on parsimony.

Within the Norops clade, few data were available for species endemic to Mexico, which form the basal radiation for mainland Norops. Therefore, FPP could have arisen in an ancestor of all mainland species or the Norops clade. B, Cybotes and Ctenonotus clades. C, Carolinensis clade. D, Chamaelinorops, Xiphosurus, and Equestris clades. E, Dactyloa clade. Presence of FPP is indicated with grey dots. Pie diagrams from the maximum likelihood analysis are shown for ancestors, with the proportion of black representing the likelihood of FPP being present in this ancestor. Species distributions are given after their name. Jam, Jamaica; Cay, Cayman Islands; GA, Greater Antilles; LA, Lesser Antilles (minus VI); MEX, Mexico; PR, Puerto Rico; NCAM, North Central America; CAM, Central America; SAM, South America; VI, Virgin Islands. The possible number of gains and losses in parsimony analysis is shown as ‘gains : losses’.

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in the ancestor of the mainland species ranging south of Mexico (Fig. 2A). In either case, the trait was lost in Anolis lionotus, Anolis notopholis, Anolis townsendi, Anolis lineatus, and the ancestor of A. uniformis, as well as its sister species, in which a reversal to FPP appeared in Anolis woodi. An alternative scenario described evolution of FPP after the split of the branch leading to A. uniformis. In this case, the ancestor of Anolis nitens and its closely-related species evolved FPP separately from the rest of the mainland species.

In the Cybotes clade, FPP may have developed independently in Anolis whitemani, Anolis armouri, and Anolis cybotes or, alternatively, in an ancestor of these species, with losses in Anolis shrevei and Anolis haetianus (Fig. 2B). Within the cristatellus series of the Ctenonotus clade, the alternatives were evolution of FPP independently in Anolis cristatellus and Anolis ernestwilliamsi, or in the ancestor of these with a reversal in Anolis desechensis (Fig. 2B). All species of the bimaculatus series could have evolved FPP independently, with the exception of the ancestor of Anolis marmoratus and Anolis sabanus. There were three equally parsimonious scenarios with FPP evolving earlier in the clade and subsequent loss of this trait (Fig. 2B).

**ML estimates**

The ML analysis supported the majority of the parsimony analysis (Fig. 2A, B, C, D, E). Importantly, the ancestor of all anoles only had a 0.003% likelihood of FPP. Where the parsimony analysis indicated that FPP and no FPP in an ancestor were equally parsimonious, the ML analysis generally resulted in values near 50% likelihood. Similarly, the presence and absence of FPP in ancestors based on parsimony mostly resulted in high and low ML estimates, respectively. Some of the alternative
scenarios, however, were resolved here and the ancestor of the roquet series had a high ML for FPP, even though parsimony suggested later evolution of FPP.

The ancestor of mainland Norops, with the exclusion of the Mexican radiation, showed 0.936% likelihood for FPP. Therefore, the parsimony scenario of independent evolution of FPP in the clade of A. nitens is less likely. Within the cristatellus series, the scenario for evolution in an ancestor of A. cristatellus and sister species was well supported (ML: 80.1%). Similarly, a 76.0% likelihood for the evolution of FPP in the ancestor of the bimaculatus series supports ancestral evolution of FPP within the series, although the scenario with independent evolution in A. wattsi was better supported (ML: 90.4%). In the Cybotes clade, the best supported scenario was ancestral evolution of FPP (ML: 84.8%). Finally, the ancestor of the roquet series, including A. bonairensis, still had a 69.1% likelihood of FPP.

When excluding A. bonairensis, this likelihood rose to 99.5%, which was consistent with the parsimony result.

GEOGRAPHICAL DISTRIBUTION

The overall geographical extent of FPP encompasses the vast majority of the geographical distribution of the anole radiation. Within this range, FPP is not uniformly distributed among major biogeographical areas (Fig. 3). The trait appears in five of six monophyletic lineages of island anoles, although it is rare on Greater Antillean islands, and the small ancillary islands throughout the Caribbean and Pacific. It is much more common on islands of the Upper and Lower Lesser Antilles and the mainland. For the two major monophyletic lineages of mainland anoles, one (Dactyloa) lacks FPP on the mainland but gains it in the single lineage that invades islands. The other (Norops) has FPP on the main-
land, although loss of FPP has occurred when these lizards invade islands, as seen for example in *A. townsendi* from Cocos Island and *A. lineatus* from Curacao. In at least one case, however, FPP was retained (*A. medemi*, Gorgona). FPP is found on islands as large as Cuba (109 886 km²) and as small as Saba (13 km²). On the smallest islands where FPP was present, FPP did not result from independent evolution, although it did on Grand Cayman (196 km²). Therefore, island size does not appear to constrain the evolution of FPP.

**DISCUSSION**

**PHYLOGENETIC PATTERNS IN THE EVOLUTION OF FPP IN ANOLES**

We investigated whether FPP was a derived character in anoles and if it could have been the result of parallel evolution. Both parsimony and ML methods supported the absence of FPP in the common ancestor of anoles and the consequent occurrence of multiple independent evolutionary events generating FPP across the tree. Within this context, however, we document three independent cases (Norops, *bimaculatus*, and *roquet* groups) in which the derived state of FPP is largely retained by closely-related species, a feature that explains why a phylogenetic signal was found. Nevertheless, we estimate that FPP arose independently at least 15 times, so that phylogenetic relationships alone could not explain the complete distribution pattern of FPP, as indicated by the moderate value of lambda.

Similar to the independent evolution of FPP, we estimate the loss of FPP at least five times across the tree, both for clades of species for which loss of FPP is a synapomorphy and for single species in which loss
of FPP is an autopomorphy. Despite the much slower rate of loss compared to gains, independent losses were seen in both island and mainland clades. Once lost, FPP was not regained, except in *A. woodi*. The possibility of regaining a trait once it has been lost remains controversial (Dollo, 1893; Simpson, 1953; Cunningham, 1999), and our analysis suggests that it is, at best, unusual for FPP within anoles.

Any analysis based on evolutionary relationships among species relies on the accuracy of the available phylogeny and the number of species for which a character of interest is known. Future changes in phylogenetic inference could therefore affect the results reported in the present study. Nevertheless, we expect the main conclusions concerning the evolution of female polymorphism in anoles to be robust for several reasons. First, differences between recent phylogenies did not drastically affect the evolutionary path of female polymorphism, especially in the case of ML estimates. Next, future changes to the hypothesis of evolutionary relationships in anoles are expected to be minor (Nicholson et al., 2005). Last, current descriptions of FPP are sufficiently numerous and sufficiently distributed widely across the phylogenetic tree to make it unlikely that the general patterns of our analysis will be modified by additional descriptions of colour patterns.

Most Caribbean anoles have detailed descriptions of variations in dorsal patterns generated by multiple authors. For the mainland, fewer species have been described as completely. Nevertheless, mainland species of the Norops clade for which colour patterns are known are sufficiently numerous to suggest that our inference of FPP being present in the ancestor of this group is unlikely to be altered by description of additional species. Similarly, colour descriptions of mainland Dactyloa are distributed sufficiently widely across the phylogenetic tree for this group to make it unlikely that future data will reject our conclusion that this group is derived from an ancestor that...
lacked FPP. Thus, evolutionary events that we describe support multiple independent origins of FPP in anoles, suggesting a response to a common environment (Harvey & Pagel, 1991; Larson & Losos, 1996; Schluter, 2000), which is a hypothesis that remains to be tested.

**LOCATION AND TIMING OF THE EVOLUTION OF FEMALE POLYMORPHISM**

The results of the present study show that FPP evolved in ancestors of three clades and divergence estimates for those ancestors provide an estimate for how long FPP has been present in two of those clades. Within the *roquet* group from the southern Lesser Antilles, the deepest split is estimated to be between 15.5 and 17 Mya (Creer et al., 2001). The *bimaculatus* series from the northern Lesser Antilles is estimated to have diverged between 7.9 and 9.7 Mya (Thorpe et al., 2008). Within this clade, the female polymorphic sister species *A. marmoratus* and *A. sabanus* are estimated to have diverged from their common ancestor approximately 1.8–3.6 Mya (Stenson, Thorpe & Malhotra, 2004). These estimates are based on molecular clocks.
and should be approached with caution (Crother & Guyer, 1996; Bromham, 2002; Graur & Martin, 2004). Nonetheless, the estimates indicate that FPP may have been present in Caribbean anoles for almost 20 million years. Continued presence of polymorphism over such a long period of time is an indicator of the presence of stabilizing selection, because random processes or directional selection are expected to result in fixation (Nei & Li, 1975; Futuyma, 1998; Richman, 2000). Additionally, selection for FPP to arise likely originated long ago, when the location of Caribbean islands and habitat characteristics of those island are likely to have been quite different than today (Roughgarden, 1995; Iturralde-Vinent, 2006).

**Geographical isolation and the evolution of female polymorphism**

The results of the present study indicate that once FPP evolves, it is unlikely for this characteristic to disappear. In those cases where this has happened, dispersal appears likely to have been important. To colonize novel areas, survival of a few individuals from dispersal events would suffice. Female polymorphism, on the other hand, probably requires multiple alleles and this variation must be represented in the founder population for polymorphism to be maintained. Consequently, a larger number of individuals would have had to reach the new location to maintain FPP in a colonizing population. Although such a scenario is not impossible, long distance dispersal would likely lead to a small founder population and consequent loss of alleles (Gorman & Kim, 1976; Gorman, Kim & Yang, 1978). This idea is supported by the absence of FPP on Cocos Island and Curaçao, which are two islands that were populated by descendants from mainland Norops in which FPP was found to be common (Williams, 1969).

The wide geographical distribution of anoles should provide abundant opportunities for parallel evolution of FPP. Anoles inhabit almost all islands in the West Indies, most of the Neotropical mainland, and a few islands in the Pacific Ocean. This pattern of geographical isolation is assumed to increase the number of times a trait can evolve independently, if similar environments are encountered in the separate locations (Simpson, 1953; Schluter, 2000; Wiens et al., 2009). Moreover, anoles are known for rapid evolution in response to their environment (Malhotra & Thorpe, 1991; Losos et al., 2006b). Indeed, geographical distribution patterns of anoles have been used to explain repeated evolution of some of their morphological characteristics in response to habitat use and competition (Rand & Williams, 1969; Williams, 1972; Losos, 1992b; Losos et al., 1998, 2006a; Harmon et al., 2005). The phylogenetic and geographical distribution pattern of FPP indicates that similar processes shaped colour patterns of anoles. This isolation yielded multiple relatively recent independent derivations of FPP for species on the Greater Antilles, and three older derivations retained by most descendant taxa within two clades of Lesser Antillean and one clade of mainland anoles.

The evolutionary history of FPP on Cuba, Hispaniola, and Puerto Rico suggests that FPP was absent in the common ancestor of the clades that established on these islands. Generally, FPP evolved here in species that diverged relatively recently compared to the first establishment of each of the clades. The absence of FPP in founder populations could have resulted from loss of allelic variance in the founder population. Our analysis, however, suggests that FPP may not have been present in the source populations for these islands. Although we have no explanation for why FPP should be so rare on these islands, we note that large island size and northerly location of these islands are obvious correlates that might explain a lack of selective pressures generating FPP. Additionally, the rarity of FPP resulting from independent evolution supports the idea of parallel evolution in these lineages.

For mainland Norops and two groups of anoles on the Lesser Antilles, FPP was likely maintained after it arose in an ancestor. All three clades appear to be sufficiently old to have been geographically contiguous during the tectonic activities that developed the Aves Ridge (Roughgarden, 1995; Nicholson et al., 2005). Thus, these three clades might have generated FPP from a common history associated with geographical development of the southern islands. The female polymorphic roquet radiation only occupies the southern islands up to Martinique. The islands from Dominica north to Anguilla are inhabited by the polymorphic bimaculatus series, which are more closely related to Hispaniolan and Puerto Rican species, and reached the Lesser Antilles from the north (Gorman & Atkins, 1969; Williams, 1969; Guyer & Savage, 1986). In both clades, FPP evolved in an early ancestor. Overwater dispersal between islands must have occurred here too, although we hypothesize that a shorter migration distance could have increased the chance for FPP to be maintained. A shorter distance might increase the chance for adults (rather than eggs) to migrate and some variation is considered to survive bottlenecks in anoles because females can store sperm of multiple males (Eales, Thorpe & Malhotra, 2008). A shorter migration distance would also facilitate multiple migration events, which can contribute to maintaining variation (Kolbe et al., 2004, 2007, 2008). To test these ideas, however, historical locations of the islands along with timing of speciation events are required.

Our analyses presented a framework of opportunities and limitations for further study of female polymorphism in anoles. Female polymorphism of dorsal patterns in anoles was found to be partially associated with phylogenetic relationships among species, and further analyses should account for this dependence on evolutionary history. Phylogenetic relationships, however, did not fully explain the current distribution of female polymorphism among anoles; multiple independent evolutionary events occurred in almost every geographically isolated location within the distributional range of anoles. In the Greater Antilles, the evolution of FPP happened relatively recently within each clade that contains female polymorphic species but, on the Lesser Antilles and the mainland, FPP evolved in an early ancestor of modern species. Repeated independent evolution, along with the repeated evolution after founding arrivals in geographically isolated locations, is indicative of an adaptive nature for FPP. If this pattern is indeed the result of convergent and parallel evolution in response to selective pressures, then female polymorphic anoles are expected to share similar environments. Moreover, female polymorphism should disappear in species that evolve in different habitats from their polymorphic relatives, which is a hypothesis that remains to be tested.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Presence of female pattern polymorphism (FPP) for species included in the phylogenetic analysis and geographical distribution.

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