Evolution of Female Polymorphism in a Neotropical Radiation of Lizards

by

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Abstract

Color pattern polymorphism – the occurrence of multiple color patterns within populations – has provided excellent opportunities for the study of evolution. Recently, a renewed interest in polymorphism was sparked by the realization that variation among females may be more important to evolutionary processes than originally thought. Few species have been thoroughly studied with regards to female polymorphism (FP), and most studies have focused on single species, thus ignoring the broad effects of evolutionary history. I present anoles (Squamata: Polychrotidae) as a model for studying FP. This speciose lizard radiation contains several species with discontinuous variation in female dorsal patterns.

My overall question addressed the origination and maintenance of FP in anoles. As recommended for studies of possible adaptive traits, both pattern and process of its evolution were addressed by combining phylogenetic and geographic analyses with population studies of the female polymorphic anole *Norops humilis*. Phylogentic signal was determined to be moderate, resulting from independent evolution of FP in ancestors of multiple anole clades as well as in individual species, as indicated by parsimony and maximum likelihood methods. Combining phylogenetic and geographic distribution of FP showed a dichotomy in the evolution of this trait. Among the basal radiation of anoles, island species were commonly polymorphic, while mainland species were not. The opposite pattern was seen in the rest of the anole radiation. Comparative analyses revealed similarities in habitat use and especially perch use among female polymorphic species, indicating that FP may have evolved in response to selective pressures typical in those environments. Based on these results and because the dorsal patterns appear cryptic against their background, I examined the commonly accepted but virtually untested hypothesis that this polymorphic trait evolved in response to predator pressure.

Population level studies in *Norops humilis* examined predation on clay models, habitat selection, and survival of different female morphs in juveniles and adults. Possible predator associated mechanisms include frequency dependent predation (FDP) and morph specific microhabitat choice to reduce visibility to predators. Similar survival rates of morphs refuted FDP. Although a predation experiment indicated morph specific variation in predation depending on perch type, females were not found to choose perches in accordance with the lowest predation rate. I conclude that female dorsal patterns in *Norops humilis* at La Selva are not maintained by predation alone and I suggest alternative hypotheses.

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Table of Contents

Abstract ii

Acknowledgments iv

List of Tables vii

List of Figures viii

Chapter One: An Introduction to Female Polymorphism

A brief history of polymorphism 1

Female polymorphism – a further challenge to our understanding of evolution 3

Anoles 9

Chapter Two: The Evolution of Female Polymorphism: A Vertebrate Model

Introduction 11

Methods 15

Results 19

Discussion 24

Chapter Three: Dorsal Pattern Polymorphism and Habitat Use in Female Anoles (Squamata: Polychrotidae)

Introduction 39

Methods 42

Results 47

Discussion 48

Chapter Four: Survival of Alternative Dorsal Pattern Morphs in Females of the Anole *Norops humilis*.

Introduction 60

Methods 62

Results 65

Discussion 66

Chapter Five: Predation on Females with Alternative Dorsal Patterns in *Norops humilis*.

Introduction 73

Methods 76

Results 79

Discussion 80

Chapter Six: Female Dorsal Pattern Polymorphism in *Norops humilis* (Squamata: Polychrotidae): Perch Use and a Test of the Microhabitat Hypothesis.

Introduction 89

Methods 92

Results 94

Discussion 96

Summary and Conclusions 106

Literature Cited 112

List of Tables

Chapter Two, Table 1: Nomenclature applied for clades within anoles...........................33

Chapter Three, Table 1: Model selection steps to determine the relationship between macro and micro-habitat variables and the presence of female polymorphism................55

Chapter Four, Table 1: Goodness of fit tests for saturated model examining effects of morph on survival of juvenile and adult females of *Norops humilis*. 71

Chapter Four, Table 2: Modeling recapture (*P*) and survival (Φ) as a function of age (a) and dorsal pattern morph (m)..72

Chapter Six, Table 1: Model selection steps..102

Chapter Six, Table 2: Average perch heights 103

Chapter Six, Table 3: Model selection steps without leaf litter data 104

Chapter Six, Table 4: Average perch heights and standard deviations for 1982-1983 dataset without leaf litter observations 105

List of Figures

Chapter Two, Figure 1: Evolution of female polymorphism (FPP) in *Anolis* 34

Chapter Two, Figure 2: Geographic distribution of female polymorphism in anoles 38

Chapter Three, Figure 1: Phylogeny with patterns and habitat variables related to distribution of female polymorphism in anoles 56

Chapter Three, Figure 2: Distribution of female polymorphism among habitat types......59

Chapter Four: Figure 1: Frequencies of female morphs observed....................................70

Chapter Five, Figure 1: Clay models 85

Chapter Five, Figure 2: Bite marks categorized as predation 86

Chapter Five, Figure 3: Predation frequencies for pattern-background combinations from experiment 1...87

Chapter Five, Figure 4: Predation for different heights and diameters of woody stems from experiment 2..88

Chapter Six, Figure 1: Female morphs occurring in *Norops humilis* in the population of La Selva Biological Station, Costa Rica 101

CHAPTER ONE

AN INTRODUCTION TO FEMALE POLYMORPHISM

"If you come to any more conclusions about polymorphism, I shd be very glad to hear the result: it is delightful to have many points fermenting in one's brain"
Darwin, C. R. to Hooker, J. D., [25 Feb 1846]

Much of modern evolutionary theory arose from the early interest in phenotypic polymorphism, as pointed out by Darwin (1871). Polymorphism is the occurrence of distinct phenotypes within one species. More specifically, it is the discontinuous variation between individuals of the same developmental stage within a population (Clark 1976; Huxley 1955). Although some of this variation can result from environmental effects, focus here is solely on genetically determined polymorphism (Clark 1976; Ford 1940). Evolutionary theory predicts that polymorphism should be rare, because selection is expected to favor one optimal morph and even without selection, drift would eventually lead to the fixation of one allele (Futuyma 1998). But, genetic polymorphism was found to be surprisingly abundant in natural populations (Harris 1966; Lewontin and Hubby 1966; Nevo 1978), thus challenging evolutionary theory.

A brief history of polymorphism

Much of our knowledge on origination and maintenance of phenotypic polymorphism finds its roots in population genetics. Theoretical models were developed to explain the occurrence of stable polymorphism. The concept of heterozygote advantage (heterosis) formed the first adaptive explanation, stating that polymorphism could be maintained as long as the fitness of the heterozygote was higher than that of either homozygote (Fisher 1922; Fisher 1930; Haldane 1955; Jones 1917; Rendel 1953). Within a homogenous environment, this would indeed be the only selective mechanism to maintain allelic variation within the population. Levene (1953), however, showed that polymorphism can also be maintained in heterogeneous environments without heterozygote advantage. Stable polymorphism was also shown to be possible under directional change in selective pressures (Haldane and Jayakar 1962; later revised by Cornette 1981). Thus, attention was drawn to selective pressures varying in space and time (Dempster 1955; Gillespie 1973; Gillespie and Langley 1974; Levins and MacArthur 1966). Later on, models also explored effects of changes in fitness of genotypes based on their relative frequency (Lewontin 1958; Wright 1948), resulting in soft selection (Wallace 1975). This was later refined for phenotypes, rather than genotypes (Clarke and O'Donald 1964). Wright (1931) stimulated thought on the importance of chance variation (mutation and drift) in maintaining polymorphism, and formed the inspiration for Kimura's work on neutral processes (Kimura 1983; Kimura 1991). Neutral and selective processes need not be mutually exclusive, and both can contribute to origination and maintenance of polymorphism (Craze 2009; Dobzhansky and Pavlovsky 1957; Wright 1948). The discussion is thus reduced to how much each mechanism contributes to the maintenance of polymorphism.

The study of color pattern polymorphism facilitated testing of these models and much work focused on the variation of colors and patterns on the shells of *Cepaea* land snails (Cain and Sheppard 1954a; Jones et al. 1977; Lamotte 1952). Selective pressures for color patterns are attractiveness to mates, thermoregulatory capacity and avoidance of predation (Brodie 1992; Endler 1995; Forsman 1997; Forsman and Shine 1995; Gibson and Falls 1979; Watt 1968), and color pattern polymorphism can persist in cases of spatial or temporal variation in these selective pressures (Hedrick 1986; Hedrick 1990; Schmidt and Rand 2001). A more specific form of fluctuating selective pressure for dorsal color patterns is frequency-dependent selection by predators (Ayala and Campbell 1974; Endler and Greenwood 1988). Initially introduced by Poulton (1884), the concept of frequency dependent predation was never explicitly addressed in early population genetic models on polymorphism. Mate choice too can be frequency dependent and thus maintain polymorphism (Ayala 1972). Other evolutionary mechanisms could be heterozygote advantage (Hedrick 1999), correlational selection (Brodie 1989; Brodie 1992; Forsman and Appelqvist 1998) or genetic drift (Hoffman et al. 2006).

Female polymorphism – a further challenge to our understanding of evolution

Although color polymorphism may occur in males and females alike, as in the popular examples of *Cepaea* snails, or peppered moths (Cain and Sheppard 1954a; Kettlewell 1955), variation in color pattern may also be limited to one gender. Many species show gender-based variation in color patterns or other ornaments – particularly in males but also in some females – and this is often ascribed to variation in quality and related mate choice (Amundsen and Forsgren 2001; Amundsen et al. 1997; Gross 1996; Roulin 2004). Most of this variation, however, is continuous (Hill 2006).

As with continuous variation, gender-based polymorphic traits have mostly been studied in males, and are often linked to alternative mating strategies. For example, in bluegill sunfish (*Lepomis macrochirus*) some males resemble females in color pattern and behavior, allowing them to fertilize eggs without building nests or defending territories like the other males (Dominey 1980; Gross and Charnov 1980). A well-known example is the side-blotched lizard (*Uta stansburiana*), where the three throat color morphs represent different degrees of territoriality and mate guarding in what is often referred to as a ‘rock-paper-scissor’ game (Sinervo and Lively 1996; Zamudio and Sinervo 2000). Similarly, the dark and white males of the lek-breeding ruff (*Philomachus pugnax*) represent territorial and sneaker courtship tactics (Lank et al. 1995), and a third, uncommon morph mimics females (Jukema and Piersma 2006).

For females, however, such alternative mating strategies are not expected, because males are generally the showy sex, while females are choosy (Bateman 1948; Darwin 1871; Trivers 1972). Moreover, female coloration patterns were long thought to be merely a byproduct of selection acting on males (Fisher 1930; Lande 1980; Lande 1987). It is therefore not surprising that female variation in color patterns has largely been ignored (Amundsen 2000a; Amundsen 2000b; Andersson 1994). In the last two decades, however, a renewed interest in females was sparked by the realization that variation among females within a population may be more important to evolutionary processes than originally thought (Amundsen and Pärn 2006; Svensson et al. 2009). Female polymorphism has been documented for a variety of species, but only a few have been subject to research on the possible evolutionary significance of its occurrence (see below). In spite of some sparse examples of extensive research, female polymorphism continues to challenge evolutionary biologist to test hypotheses that could explain the commonness of female polymorphism in some radiations of species. Here, I review examples of female polymorphism to provide a basis for current knowledge on this topic.

Invertebrates

One of the first studied occurrences of female polymorphism was in butterflies. The families Papilionidae, Nymphalidae, Pieridae and Acraeidae all have species for which female-limited polymorphism has been reported (Owen 1971; Wickler 1968). The explanation for the color pattern variation in female color patterns in butterflies was ascribed to the mimicking of various unpalatable species or of different morphs within those species as a protection against predation (Fisher and Ford 1929; Joron and Mallet 1998; Owen 1971; Wickler 1968). Male-like patterns may occur in some females, as is the case in *Papilio dardanus antinorii* (Wickler 1968). Genetically, the process resulting in female polymorphism in mimetic butterflies may be regulated by modifier genes linked to the female-specific chromosome or be controlled by autosomal genes (Clarke and Sheppard 1962; Clarke and Sheppard 1963; Sheppard 1967; Smith 1975). Female mate choice appears to restrict development of polymorphic males (Krebs and West 1988), but differential habitat use may also be important in the limitation of polymorphism to females (Joron 2005). Among moths, another interesting example of female polymorphism is provided by the British pyralid moth, *Acentropus niveus* (Huxley 1955). Females of this moth are either a normal, male-like form or they can be an aquatic and flightless form that exploits an ecological niche outside of the reach of normal morphs.

Within Odonata (dragonflies and damselflies) various species have been described as female polymorphic (Tillyard 1917), and several have been subject to extensive studies. Although some variation exists among species, generally two or three female morphs can be distinguished, and one of these color morphs tends to resemble the male coloration pattern (Robertson 1985; Tillyard 1917). More specifically, when male-like color patterns are the dominant form in females, these tend to be bright colors, while if the female-specific color patterns occur in higher frequency than the male-like form, colors tend to be dull (Tillyard 1917). In damselflies, female polymorphism is coded by serial dominance of alleles in an autosomal gene (Cordero 1990; Johnson 1964; Johnson 1966). Maintenance of female-limited polymorphism in damselflies has been explained by a balance between sexual conflict and predation, with support for frequency dependent and possibly temperature dependent variation (Bots et al. 2009; Cordero et al. 1998; Robertson 1985), but no hypothesis has succeeded in fully explaining it.

Fiddler crabs too contain at least a few species with female polymorphism. The often stunning coloration patterns in fiddler crabs vary within and across species. Colors may change in an individual throughout the ontogenetic cycle or as a more immediate change in response to the environment (Crane 1975). Generally, females vary more in color pattern than males and therefore, several species of fiddler crabs have been described with female polymorphism in color patterns. Color patterns may assist in individual recognition, and specifically in mate recognition by males (Detto et al. 2008). In jumping spiders (Salticidae) of the genus *Phiale*, discovery of female color polymorphism led to a revision of the genus (Galiano 1981), but its significance remains unstudied (Oxford and Gillespie 1998).

Diving beetles (Coleoptera: Dytiscidae) display a very different variation in morphology; here, females vary in dorsal structures used during mating (Bergsten et al. 2001). Similarly, females of the copepod *Paroithona pacifica* (Cyclopoida: Oithonidae) vary in some exoskeleton characteristics, such as the number of spines on their swimming legs (Ferrari and Bottger 1986). Neither polymorphism is well understood. Another example of structural variation in morphology of females is the African bat bug *Afrocimex constrictus* (Cimicidae) (Reinhardt et al. 2007). Female bat bugs differ in genital structures, apparently to reduce the number of traumatic copulations which are common in this and related species.

Vertebrates

Female polymorphs in vertebrates has been documented mainly for lizards, but amphibians and even birds include examples as well. The toad *Bufo periglenes*, now extinct, was an exceptionally bright colored species of its genus, and females showed some variation in color and in presence or absence of a vertebral pale stripe (Savage 1966). In the warbler *Wilsonia citrina*, males and females perch in slightly different microhabitats, but some females develop the melanistic male coloration as they mature and use a male-like microhabitat (Lynch et al. 1985). This female melanism develops as the individual matures (Rappole and Warner 1980), which could explain the somewhat continuous variation in the trait. Plumage color polymorphism also appears in adult females of some cuckoos where some are ‘barred red’ and some ‘unbarred grey’, supposedly as a mimic of the sparrow hawk (Voipio 1951; *fide* Huxley 1955).

A well-studied case for vertebrates is the side-blotched lizard *Uta stansburiana* (Phrynosomatidae). Mostly known for its polymorphism in males, the side-blotched lizard is now studied for the dual polymorphism in females: throat color and dorsal pattern. Alternative throat colors in adult females are associated with egg and clutch size (Sinervo et al. 2000). Throat color is regulated by a single locus with an apparent hierarchical dominance between alleles (Sinervo and Zamudio 2001; Sinervo et al. 2000).

Dorsal pattern was found to be regulated by interactions between yolk oestradiol levels and the social environment (Lancaster et al. 2007). The combination of throat color and dorsal pattern results in a complex system where benefits of dorsal pattern alone are difficult to study (Lancaster et al. 2007).

Some examples with only one female color pattern polymorphism can also be found in lizards. In the common lizard *Lacerta vivipara* (Lacertidae) different colored bellies of females reflect alternative reproductive strategies and determines aggression and avoidance behavior between females (Vercken and Clobert 2008; Vercken et al. 2007). Among several Australian scincid lizards of the genera *Saprocinus* and *Lampropholis*, dorsal patterns of females differ in the absence or presence of a white mid-lateral stripe (Forsman and Shine 1995; Sadlier et al. 1993). In *Lampropholis delicata* (Scincidae) this may be related to variation in predation pressure, especially of gravid females, between populations and combined with gene flow (Forsman and Shine 1995). In some species, like the striped plateau lizard *Sceloporus virgatus* (Phrynosomatidae) throat color female-biased polymorphism is seasonal, in which case it can be linked to seasonal activities such as signaling reproductive status (Smith 1946; Weiss 2002).

This review is by no means exhaustive, but points out a few remarkable features of female polymorphism: 1) invertebrates have been subjected to more thorough studies and fewer examples are available among vertebrates, 2) much emphasis has been placed on conspicuous coloration, which is likely the result of observer bias for such color patterns, 3) probably as a result of this focus on conspicuous color patterns, female polymorphism is often studied in light of mate choice or reproductive strategies

(Svensson et al. 2009), while other mechanisms could maintain polymorphism in females. In this dissertation, I highlight the occurrence of a common, non-conspicuous variant of female polymorphism in anoles.

Anoles

Anoles (Squamata: Polychrotidae) form a diverse, species rich and widespread group of Neotropical lizards. Female dorsal pattern polymorphism (FPP) has been described for several species of anoles (e.g. Savage 2002; Schoener and Schoener 1976). Anoles have been thoroughly studied and they have proven to be good model organisms for behavioral, evolutionary and ecological questions (Losos 1994). Hence, much information on their biology is available for comparative studies. The occurrence of FPP in species of anoles, even though understudied, is generally known and pattern descriptions are often included in species descriptions. Anoles could thus serve as a model for the study of FPP, and an understanding of the occurrence of FPP in anoles is an essential addition to current knowledge on these organisms. The overall goal of my dissertation research is to better understand the evolution of FPP in anoles.

Evolution of a polymorphic trait has rarely been studied in a phylogenetic context (Jose et al. 2008), even though knowledge of the evolutionary history is important in the interpretation of population based studies and comparative analyses (Cheverud et al. 1985; Felsenstein 1985). Although population based approaches may give insight in short-term mechanisms of maintenance, phylogenetic approaches address long-term evolutionary patterns among species and indicate whether traits are novel or ancestral (Harvey and Pagel 1991). A common critique to using phylogeny in the study of a possibly adaptive character is the misunderstanding that the apomorphic character (novel trait) alone is sufficient to infer adaptation (Coddington 1990). A recent review on the use of phylogeny in testing adaptation clarified different viewpoints and concluded that evolution should be studied at different levels, while recognizing limitations and advantages of each (Grandcolas and D'Haese 2003). The authors suggested three criteria for adaptation: the genetic, the phylogenetic and the selection criterion, and as such emphasized the need for studying traits in the context of both clades and populations. The selection criterion supplements the phylogenetic criterion; a common selective environment has to be demonstrated for species sharing the trait of interest (e.g. Harvey and Pagel 1991).

Considering the sparse knowledge of female polymorphism in anoles, and no understanding of its genetic basis, an appropriate approach is thus to combine phylogenetic and population-based levels of study. In chapter 2, I focus on the evolutionary pattern of FPP in anoles, revealing the occurrence of FPP across species in light of their phylogenetic history and geographic distribution. Chapter 3 investigates whether female polymorphic anoles share a common environment that could exert selective pressures that favor the evolutionary maintenance of FPP. The next three chapters address micro-evolutionary patterns of FPP in a population of a common mainland anole, *Norops humilis*, studying two of the major mechanisms proposed for maintaining color pattern polymorphism: frequency dependent predation and predation in heterogeneous habitats.

CHAPTER TWO

THE EVOLUTION OF FEMALE POLYMORPHISM: A VERTEBRATE MODEL

INTRODUCTION

The incidence of multiple morphs within a population – polymorphism – has inspired theories of evolution since early explorations into evolutionary biology (Darwin 1859; Darwin 1871). Variation in morphological characters such as size or color 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 (e.g., Andersson and Iwasa 1996; Houde 1997; Pradhan and Van Schaik 2009; Shine 1979; Shuster and Wade 2003; Sinervo and Lively 1996). Research on polymorphism among females has concentrated mostly on insects, but has generally remained understudied. In recent years, the number of attempts to better understand female polymorphism has noticeably increased (Stamps and Gon 1983; Svensson et al. 2009).

Female polymorphism has been documented mostly for species of Lepidoptera (butterflies) and Odonata, (damselflies and dragonflies) and rarely in vertebrates (Fisher and Ford 1929; Richards 1961; Tillyard 1917; Wickler 1968). Although polymorphism has been described for other species, only a few of these have been subjected to research on its occurrence. Studies indicate that multiple selective pressures may interact to maintain polymorphism limited to females (e.g., Joron and Mallet 1998; Sirot et al. 2003). Female color morphs in damselflies, for example, are thought to exert alternative techniques to balance predation and male harassment (Bots et al. 2009; Cordero et al. 1998; Robertson 1985). In spite of intensive field studies and molecular research, especially in Odonata, female polymorphism remains controversial (Andres et al. 2000; Svensson et al. 2009).

Surprisingly, most research has focused on single species. Although such contributions are valuable for our understanding of how female polymorphism is maintained, they largely ignore the question of origination. In contrast, macro-evolutionary approaches pose 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 (Dobson 1985). 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 and Pagel 1991; Larson and Losos 1996; Schluter 2000). In this case, the shared character can have evolved from different ancestral states (convergent evolution), or from the same ancestral state (parallel evolution) (Harvey and Pagel 1991; Zhang and Kumar 1997). Phylogenetic approaches thus provide direction for future research and indicate possible limitation of population based studies (Grandcolas and D'Haese 2003).

Analogous to effects of phylogenetic relationships, geographic distribution can promote or constrain evolutionary change. Wiens et al. (2009) emphasized the importance of combining phylogenetic with biogeographical analyses. Geographic isolation is thought 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, geographic isolation could further stimulate parallel evolution through release from this saturated environment into a similar, non-saturated 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 combined phylogenetic and geographical 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 on the phylogenetic context of female polymorphism in damselflies suggested that it was the ancestral state for two genera (Van Gossum and Mattern 2008). In this case, the reason for origination and for maintenance of the trait may each need 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 thoroughly studied lineages 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 their dorsal patterns is easily observable, and patterns are known to be heritable (Calsbeek et al. 2008). Females of polymorphic species generally show two or three variations in dorsal patterns within a population. Savage (2002) summarized female dorsal patterns into five distinct morphs: vertebral 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. With nearly 400 species and recent advances in research of their phylogenetic history anoles lend themselves well to macro-evolutionary approaches to studying female polymorphism. Furthermore, anoles are an excellent model system for the study of ecology, evolution and behavior (e.g. Beuttell and Losos 1999; Losos 1992a; Losos 1994). The presence of female polymorphism in anoles, however, has received surprisingly little attention, although its presence is commonly known (e.g. Fitch 1975; Savage 2002; Stamps and Gon 1983). Two studies found a relationship between morph and perch use (Schoener and Schoener 1976; Steffen 2009). A third study detected density effects in immuno-competence variation between morphs (Calsbeek et al. 2008). Differences between morphs found thus far fail to explain the evolutionary origin and the maintenance of female polymorphism.

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. Particularly, we tested whether FPP is a derived character and has evolved independently among anoles. Furthermore, we incorporated a geographical analysis to investigate whether geographic isolation could have contributed to the current distribution of FPP among species.

METHODS

Data

Species descriptions were used to determine the presence or absence of pattern polymorphism in females (Avila-Pires 1995; Campbell 1998 ; Dixon and Soini 1986; Duellman 1978; Duellman 2005; Fitch 1975; Garrido and Hedges 2001; Lazell 1972; Lee 1996; Lee 2000; Nicholson et al. 2001; Rivero 1998; Savage 2002; Schwartz and Henderson 1991; Stafford and Meyer 2000; Stejneger 1900; van Buurt 2005; Vitt and de la Torre 1996). This allowed only species level assessments, so that species were scored positive for female polymorphism, even if not all populations showed this. Presence or absence of dorsal pattern polymorphism was based on the vertebral zone alone. Geographical variation, subspecies variation and variation due to metachromatism (i.e. color change) were not considered as polymorphism for the purpose of this study.

Nomenclature

There are nearly 400 species of anoles and, in spite of extensive research on their evolutionary history, some phylogenetic relationships and the related nomenclature remain ambiguous. Most anoline lizards were placed in the genus *Anolis,* but the great diversity led to a division into groups and series (first by Etheridge 1960; formalized by Williams 1976), only some of which are monophyletic in recent phylogenies. Some species that were originally considered to belong to separate anoline genera (*Chamaelinorops*, *Phenacosaurus* and *Chamaeleolis*) were later found to have arisen from within *Anolis* (Hass et al. 1993; Poe 1998). A division of *Anolis* into multiple genera was proposed (Guyer and Savage 1986), but this remains controversial

(Cannatella and de Queiroz 1989; Guyer and Savage 1992; Williams 1989). Only the name *Norops* is regularly used as a genus name to refer to Etheridge's (1960) Beta section (See Nicholson 2002 and references therein), but recognition of this genus renders a group with the remaining anoles paraphyletic. Recent phylogenies, however, indicate that there are several rather well-established clades within anoles, even though the relationship between some of these major clades still remains somewhat unclear (Jackman et al. 1999; Nicholson et al. 2005; Poe 2004), and a more practical nomenclature system may result. Because in our study the use of one genus name for so many species is impractical and many clades are rather stable entities, we will refer to monophyletic clades and series within clades (Table 1). We will still use *Anolis* as the genus name to avoid any confusion with future names that are likely to arise now relationships among anoles are being resolved.

Phylogeny

No single phylogeny for all anole species was available. Therefore, we combined recent phylogenies, based on 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 (JCVI). The major differences between the phylogenies we used was 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 et al. (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 maximum likelihood 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 transformation are used when accurate estimates of branch lengths are lacking. Interestingly, ML does not necessarily favor 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 maximum likelihood 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. Considering the slightly more conservative approach of equal branch lengths to missing taxa and previous evolutionary studies on anoles applying this transformation (Ord and Martins 2006; Poe et al. 2007), only results for equal branch lengths are presented.

Unordered parsimony analysis was performed in Mesquite (Maddison and Maddison 2008). This assumes equal rates of forward and backward evolution. Maximum likelihood 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 (-Log Likelihood $_{(ER)}$ = -87.47, -Log Likelihood $_{(ARD)}$ = -85.07, P = 0.0286, AIC $_{(ER)}$ = 177, AIC $_{(ARD)}$ = 174). Particularly, forward evolution was found to be roughly two times faster than backward evolution (Gain: 0.227 ± 0.05, Loss: 0.097 ± 0.02). Maximum likelihood values for the ARD model were plotted onto the phylogenetic tree for further analysis.

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 ($\lambda = 0$, i.e. all phylogenetic structure removed) and a given phylogenetic structure ($\lambda = 1$, 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 if lambda is significantly different from zero, a maximum likelihood ratio test was used in R (Harmon et al. 2008; Yang 2006).

Geographic analysis

For the geographic analysis, 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 geographic 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 combine a geographic and phylogenetic analysis. Some species, however, were not included in any available phylogeny and could only be incorporated for the geographical analysis.

RESULTS

For 180 species of anoles a detailed description of dorsal pattern was found. Of these, over 50 species were described as having female dorsal pattern polymorphism (FPP). The majority of the species with female polymorphism were mainland species, even though island species constituted the larger part in the dataset. Only 162 of these species were included in the phylogenies we used for our analysis.

Phylogenetic signal

We found a significant phylogenetic signal in the presence of FPP among anoles (Log Likelihood phylogeny = -81.89, Log Likelihood unstructured = -90.61, $P < 0.0001$). 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 (Figure 1.D.). For the 162 species included, the evolutionary pattern of FPP required 28 steps. The entire carolinensis clade lacked FPP (Figure 1.C). Three other members of this group for which more detailed phylogenetic relationships were not known also lacked FPP. All other clades had at least one species with FPP. Overall, parsimony analysis indicated the independent evolution of FPP across clades, but FPP was also found in closely related species, signifying that FPP likely arose in their ancestor. This was the case for island dactyloa minus *A. bonairensis* (Figure 1.D). 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 losers 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 in the ancestor of the mainland species ranging south of Mexico (Figure 1.A.). In either case, the trait was lost in *A. lionotus*, *A. notopholis*, *A. townsendi, A. lineatus* and the ancestor of the petersii series, in which a reversal to FPP appeared in *A. woodi*. An alternative scenario described evolution of FPP after the split of the petersii series. In this case, the ancestor of *A. 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 *A. whitemani*, *A. armouri* and *A*. *cybotes*, or alternatively in an ancestor of these species, with losses in *A. shrevei* and *A*. *haetianus* (Figure 1.B). Within the cristatellus series of the ctenonotus clade, the alternatives were evolution of FPP independently in *A. cristatellus* and *A. ernestwilliamsi*, or in the ancestor of these with a reversal in *A. desechensis* (Figure 1.B.). All species of the bimaculatus series could have evolved FPP independently, with the exception of the ancestor of *A. marmoratus* and *A. sabanus*. There were three, equally parsimonious scenarios, with FPP evolving earlier in the clade and subsequent loss of this trait (Figure 1.B.).

Maximum Likelihood Estimates

The maximum likelihood analysis supported the majority of the parsimony analysis (Figure 1.A.- D.). 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 likely, the maximum likelihood parsimony analysis generally resulted in values near 50% likelihood. Similarly, presence and absence of FPP in ancestors based on parsimony mostly resulted in high and low maximum likelihood estimates, respectively. Some of the alternative scenarios, however, were resolved here and the ancestor of the roquet series had a high maximum likelihood 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, but 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 clade, 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.

Geographic analysis

FPP was found throughout the distributional range of anoles (Figure 2). Trinidad is the only island for which all anole species had FPP. None of the Trinidad anoles are endemic to this region; all are shared with South America and the other islands of the Lesser Antilles. Cuba, Hispaniola and most islands of the Lesser Antilles had endemic species with FPP.

Cuba Of 63 species living on Cuba, there were 11 for which presence of FPP could not be determined: *A. aguera*, *A. altitudinalis**, *A. birama*, *A. delafuenti*, *A. incredulus**, *A. litoralis**, *A. oporius**, *A. ruibali**, *A. terueli**, *A. toldo**, *and A. vescus*. The majority belonged to the carolinensis clade (*), a radiation for which currently no case of FPP has been reported. Of 52 remaining species, only three had FPP, two of which were endemic. Although this was the result of independent evolution of FPP, all female polymorphic species were members of the sagrei clade. *A. birami* and *A. delafuenti*, both members from this clade, may or may not have polymorphic females. This clade of Cuban anoles is more closely related to mainland anoles than to the other Cuban anoles. There was no pattern in the distribution of female polymorphic species across Cuba. *A. sagrei* is found throughout Cuba. *A. allogus* also occurs throughout Cuba, with exception of the islets off the coast. *A. birama* is restricted to the central-eastern part of the island.

Hispaniola In Hispaniola, 8 out 43 species were described with FPP, 7 of which were endemic. *A. alumina* could be an additional anole with FPP, but uncertainty led us to include this species as unknown. *A. breslini* was formerly a subspecies of the female polymorphic *A. whitemani*. The presence of FPP in *A. breslini* will have to be assessed. The female polymorphic anoles of Hispaniola belonged to four different clades, phylogenetically separated by species from other locations, but all are nested within other Hispaniola anoles (Figure 1.B.,C.). They all range mostly in the south-western peninsula (Grand'anse, Sud, Sud-est and Ouest in Haïti, and Pedernales in the Dominican Republic). *A. ricordi* ranges further into the area along the border between Haïti and the Dominican Republic and into the northwestern peninsula (Nord and Nord-Ouest of Haïti). One species with FPP, *A. etheredgi*, resides much farther east in the Dominican Republic. *A. cybotes* was the only species with FPP that occurs throughout Hispaniola.

Bahamas, Puerto Rico, Jamaica, Cayman Islands The Bahamas and Jamaica do not have native anoles with FPP. The Cayman Islands hosts the female polymorphic anole *A. conspersus*. All these islands share *A. sagrei*, a species with FPP. Species with FPP inhabiting Puerto Rico and the Virgin Islands are all shared between both locations. These are the three closely related anoles *A. cristatellus*, *A. acutus*, and *A. ernestwilliamsi*, all belonging to the same clade. The two latter species are restricted in range in Puerto Rico to the bank, while *A. cristatellus* is more widespread on this island. In addition, *A. cristatellus* species has been introduced to Hispaniola.

Lesser Antilles FPP was common in both radiations of the Lesser Antilles, the roquet clade in the south and bimaculatus series in the north. The northern islands are home to some species for which the presence of FPP was not known: *A. schwartzi*, *A. pogus* and *A. forresti*, all former subspecies of the female polymorphic *A. wattsi*, and *A. leachi,* a former subspecies of the non-polymorphic *A. bimaculatus*.

Remaining islands Two little islands, San Andrés and Providencia each contain one species. *A. concolor* occurs in the former and has FPP. For the species in Providencia, *A. pinchoti*, FPP is not known. No species have been described for Aruba. The island of

Bonaire is home to *A. bonairensis*, which does not have FPP. *A. townsendi* and *A. lineatus*, although nested within the mainland norops, are both island species: the former on Cocos Island off the Costa Rican coast, the latter on Curaçao. Both are nested within mainland anoles with FPP, but neither of these island species displayed female polymorphism.

Mainland Within mainland dactyloa, female polymorphism was rare (Figure 1.D.). For norops, on the other hand, polymorphism in female dorsal pattern occurred in the majority of known anoles of the mainland (Figure 1.A.). FPP occurred throughout the entire geographic distributional range of mainland anoles.

DISCUSSION

We asked the question whether female polymorphism in dorsal patterns (FPP) was a derived character in anoles and if it could have been the result of parallel evolution. These questions were approached phylogenetically and geographically.

Phylogenetic patterns in the evolution of FPP in anoles

Both parsimony and maximum likelihood (ML) methods supported the absence of FPP in the common ancestor of anoles and the consequent occurrence of multiple evolutionary events along the tree. The current pattern of FPP distribution among anoles resulted from independent evolution in multiple common ancestors as well as in individual species. The shared state of FPP by closely related species resulting from ancestral evolutionary events explains why a phylogenetic signal was found. Nevertheless, FPP arose in several ancestors independently, so that phylogenetic relationships alone could not explain the complete distribution pattern of FPP, as indicated by the moderate value of lambda.

Similar to forward evolution of FPP, some losses of FPP occurred in ancestors, while others happened in single species. In spite of the much slower rate of loss compared to gains, independent losses were seen in both mainland clades, and depending on the evolutionary scenario, losses were seen in other clades as well. These scenarios were well supported by the ML method. Once lost, FPP was not regained, except in *A. woodi*. The possibility to re-gain a trait after it was lost remains controversial (Cunningham 1999; Dollo 1893; Simpson 1953). Following the phylogeny of Poe (2004), the scenario where FPP evolves independently in *A. woodi* was not supported. Regardless of the opinion on reversals, or some differences between phylogenies, our major conclusion remains that multiple independent evolutionary events explain the current distribution of FPP among anoles. Based on our dataset, FPP has evolved at least fifteen times independently in anoles, and it has been lost at least five times. To reconstruct our full scenario of the evolutionary history of FPP, either the number of losses or the number of gains increases even further. In addition, the number of losses and gains are expected to increase as more species can be added to the analysis. The multiple independent evolutionary events suggest that FPP in anoles may have evolved in response to a common environment (Harvey and Pagel 1991; Larson and Losos 1996; Schluter 2000), a hypothesis that needs to be tested.

Any analysis based on evolutionary relationships among species relies on the accuracy of the available phylogeny. Future changes in phylogenetic inference could therefore affect the results presented here. 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 maximum likelihood estimates. Next, future changes to the hypothesis of evolutionary relationships in *Anolis* lizards are expected to be minor (Nicholson et al. 2005). Last, a large proportion of the anoles of the West Indies were included, and thus the number of independent evolutionary events is unlikely to change greatly. Presence of FPP could have been underestimated because it was only based on species accounts. Consideration of the thorough studies on Caribbean anoles with highly detailed descriptions of variations in dorsal patterns by multiple authors suggests that there will be few changes, so that the number of independent events would hold. For the mainland, conclusions are less certain, because fewer anoles are known. Nevertheless, mainland species are all members of the clades norops or dactyloa, so that new species found on the mainland are likely to belong to either of these clades (Nicholson et al. 2005). The high proportion of female polymorphism among known species or the norops clade suggests that more polymorphic species are likely to be found within this radiation and a polymorphic common ancestor for mainland norops is thus very probable. Any further occurrence of female polymorphic dactyloa, on the other hand, are likely the result of independent evolutionary events.

Location and timing of the evolution of female polymorphism

Our results show that FPP evolved in several ancestors and divergence estimates for those ancestors may provide an estimate for how long FPP has been present in those clades. Within dactyloa from the southern Lesser Antilles, for example, the deepest split was estimated between 15.5 and 17 MYA (Creer et al. 2001). The bimaculatus series from the northern Lesser Antilles was 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* were estimated to have diverged from their common ancestor ca. 1.8-3.6 MYA (Stenson et al. 2004). These estimates are based on molecular clocks and should be approached with caution (e.g. Bromham 2002; Crother and Guyer 1996; Graur and Martin 2004). Nonetheless, the estimates indicate that FPP has been present in the anole radiation for a few million years. Continued presence of polymorphism over such a long period of time is an indicator for the presence of stabilizing selection, as random processes or directional selection are expected to result in fixation (Futuyma 1998).

Geographic isolation and the evolution of female polymorphism

The geographic distribution of anoles should be particularly favorable for the occurrence of parallel evolution. Anoles inhabit nearly all islands in the West Indies, most of the Neotropical mainland and a few islands in the Pacific Ocean. As the phylogeny shows, anoles have mostly speciated within islands and within the mainland, so that closely related species often inhabit the same region. This pattern of geographic isolation is thought to increase the number of times a trait can evolve independently, if similar environments are encountered in the separate locations (Schluter 2000; Simpson 1953; Wiens et al. 2009). Moreover, anoles are known for their rapid evolution in response to their environment (Losos et al. 2006b; Malhotra and Thorpe 1991). Indeed, geographic distribution patterns of anoles have been used to explain repeated evolution of some of their morphological characteristics in response to habitat use and competition (Harmon et al. 2005; Losos 1992b; Losos et al. 2006a; Losos et al. 1998; Rand and

Williams 1969; Williams 1972). The phylogenetic and geographic distribution pattern of FPP indicates that geographic isolation may have also contributed to the number of times FPP arose in anoles; the trait evolved separately in the majority of the islands and on the mainland.

Current geographic boundaries, however, were not necessarily present during the early evolution of anoles and the evolution of FPP. Cuba, Hispaniola and Puerto Rico used to be part of a larger landmass called the proto-Antilles (Pindell 1985; Rosen 1975). Some debate revolves around the processes behind the current distribution pattern of anole species, due to apparent discrepancies between the timing of anole evolution and geological history (Reviewed by Pregill and Crother 1999). Overwater dispersal events form the central issue in the debate, especially for speciation on the Greater Antilles, which could have resulted from vicariance when the Proto-Antilles split or from overwater dispersal after the split (Burnell and Hedges 1990; Crother and Guyer 1996; Guyer and Crother 1996; Hedges 1996; Hedges 2006; Hedges et al. 1994; See also Pregill and Crother 1999). Regardless, at least a few overwater dispersals must have occurred. Jamaica, for example, was submerged until the late Oligocene or early Miocene (Buskirk 1985; Iturralde-Vinent 2006; Robinson 1994). Current anoles on Jamaica form a monophyletic clade and are thus likely the result of one recent overwater dispersal event (Crother and Guyer 1996; Hedges and Burnell 1990). The Cayman Islands, the Bahamas and St. Croix are oceanic islands that were never connected to the mainland and could thus only have been reached via water.

Overwater dispersal could help explain the distinct events of FPP evolution on many islands, and why it never arose on Jamaica, the Bahamas and St. Croix. To colonize islands, survival of a few individuals from dispersal events would suffice. Female polymorphism, on the other hand, would require 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. Although such scenario is not impossible, long distance overwater dispersal would likely lead to a small founder population and consequent loss of alleles (Gorman and Kim 1976; Gorman et al. 1978). This idea is supported by the absence of FPP on Cocos Island and Curaçao, two islands that were populated by descendants from mainland norops in which FPP was found to be common (Williams 1969). The abundance of FPP among mainland norops fits this theory, because mainland norops are thought to be the result of a single island-to-mainland overwater dispersal event (Jackman et al. 1997; Nicholson 2002; Nicholson et al. 2005). FPP likely evolved shortly after the ancestor had reached the mainland and was only lost in a few species, including those migrating to islands.

On the Lesser Antilles too, FPP was found to be maintained after it arose in an ancestor, although this was the result of two independent events. The female polymorphic island dactyloa only occupy 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 and Atkins 1969; Guyer and Savage 1986; Williams 1969). In both clades, FPP evolved in a common ancestor. Overwater dispersal between islands must have occurred here too, so why was FPP retained here? 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 thought to survive bottlenecks in anoles because females can store sperm of multiple males (Eales et al. 2008). Shorter migration distance would also facilitate multiple migration events, which can contribute to maintaining variation (Kolbe et al. 2007; Kolbe et al. 2004; Kolbe et al. 2008). To test these ideas, however, historical locations of the islands along with timing of speciation events are required.

The evolutionary history of FPP on Cuba, Hispaniola and Puerto Rico shows that FPP was absent in the common ancestor of the clades that established on these islands. Generally, FPP here evolved in species that diverged relatively recently compared to the first establishment of each of the clades. This 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 population. Either scenario is consistent with Simpson's (1953) hypothesis that presence of similar environments on geographically isolated locations would stimulate parallel evolution. Under this hypothesis, FPP would have evolved as speciation occurred and species occupied environments that were conducive of maintaining variation in dorsal patterns of females.

Geographic isolation may thus have contributed to the number of independent events in the evolution of FPP in anoles. The major question, however, becomes why it evolved (and disappeared) repeatedly. The repeated evolution of a similar trait is not unlikely with (relatively) closely related species, given their similar genetic composition and ecological environment (Haldane 1932). To distinguish between random processes and selective pressures resulting in parallel evolution, FPP will have to be approached through comparative studies to identify a possible common environment, and further investigation at the population level will be required to understand how FPP is maintained.

Another interesting pattern that emerged when combining phylogenetic and geographic analyses is the evolution of FPP in norops and dactyloa. Both clades contain island as well as mainland species. In norops, FPP is abundant among mainland species, but rare in island species. Nevertheless, the Cuban species of the norops clade are the only species known to have FPP on Cuba, even though more than 60 species, divided over several separate radiations inhabit Cuba. The pattern was opposite in dactyloa. Only one mainland dactyloan anole in our dataset was female polymorphic, while among the Lesser Antilles relatives (roquet) absence of FPP was rare. Interestingly, the distantly related anole radiation that occupies the Northern Lesser Antilles (bimaculatus) contains many female polymorphic species as well. The relatively sparse occurrence of female polymorphism in Cuba and abundant occurrence in the Lesser Antilles in two distantly related clades is consistent with the idea of a possibly shared environment. The absence of female polymorphism in dactyloa of the mainland, where the only other radiation is almost entirely polymorphic, poses a dilemma that deservers further investigation.

Summary

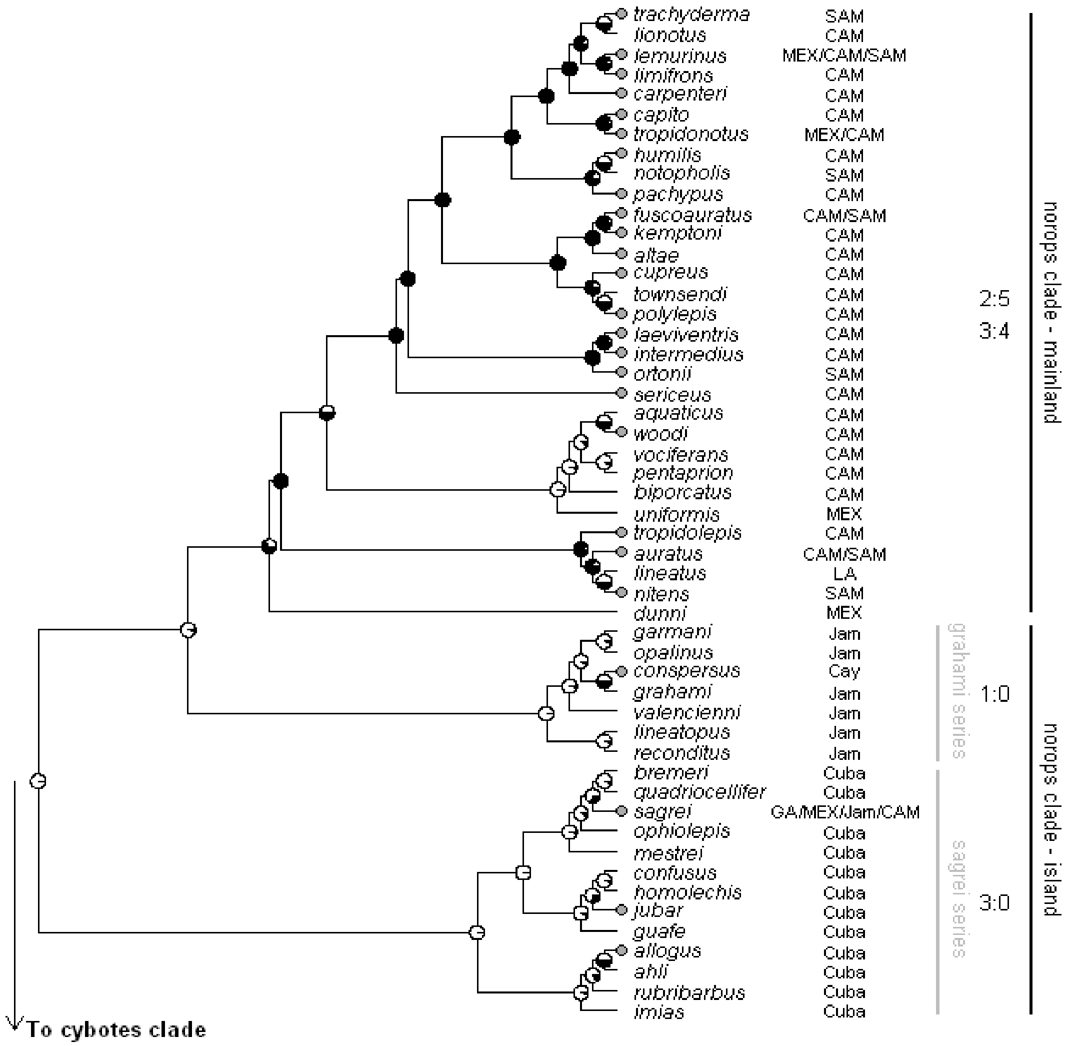
Our analyses presented a framework of opportunities and limitations for further study of female polymorphism in anoles. Female polymorphism of dorsal patterns in anoles was found to be partially associated with phylogenetic relationships between species, and further analyses should account for this dependence on evolutionary history. Phylogenetic relationships, however, did not fully explain the current distribution of female polymorphism among anoles; multiple independent evolutionary events occurred in nearly every geographically isolated location within the distributional range of anoles. In the Greater Antilles, 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 radiations in geographically isolated locations are indicative of an adaptive nature for FPP. If this pattern is indeed the result of parallel evolution in response to selective pressures, than 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, a hypothesis that remains to be tested.

Table 1. Nomenclature applied for clades within *Anolis*. Node numbers of the phylogeny of Poe (2004) are included to indicate the specific clade on the tree.

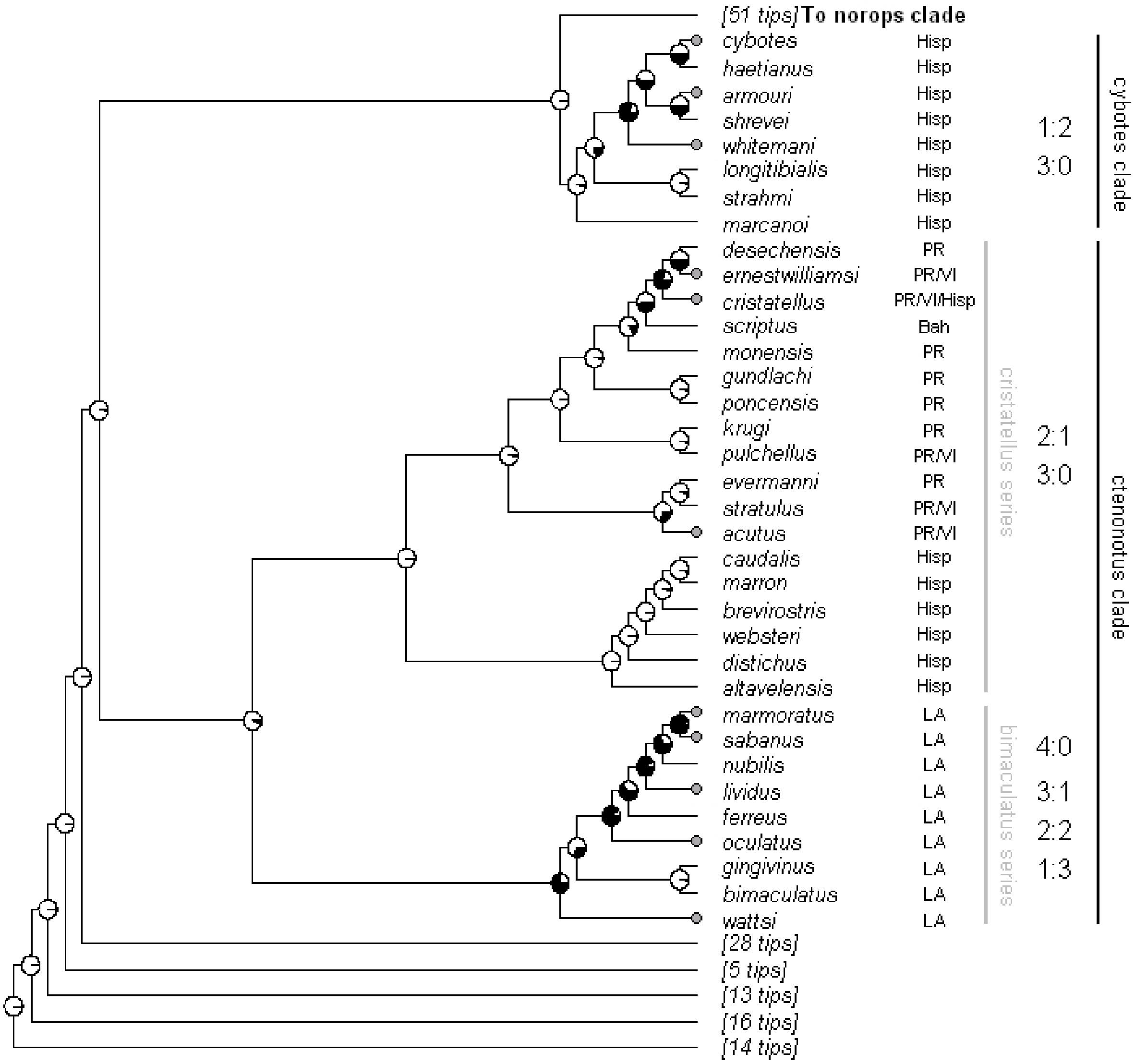
Clade name	Node number (Poe 2004)	Series
Norops = Beta anoles (Etheridge 1960).	286	Cuba: sagrei series (node: 225) Jamaica: grahami series (node: 284)
Cybotes	293	
Ctenonotus	216	Northern Lesser Antilles: bimaculatus series Greater Antilles: cristatellus series.
Carolinensis	309	
Chamaelinorops	197	
Xiphosurus	190	
Equestris	324	
Dactyloa	352	Southern Lesser Antilles: roquet series (node: 351)

Figure 1. **Evolution of female polymorphism (FPP) in anoles**. A. norops clade, B. cybotus and ctenonotus clades, C. carolinensis, chamaelinorops, xiphosurus and equestris clades, D. dactyloa clade. Presence of FPP is indicated with grey dots. Pie diagrams 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, 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’.

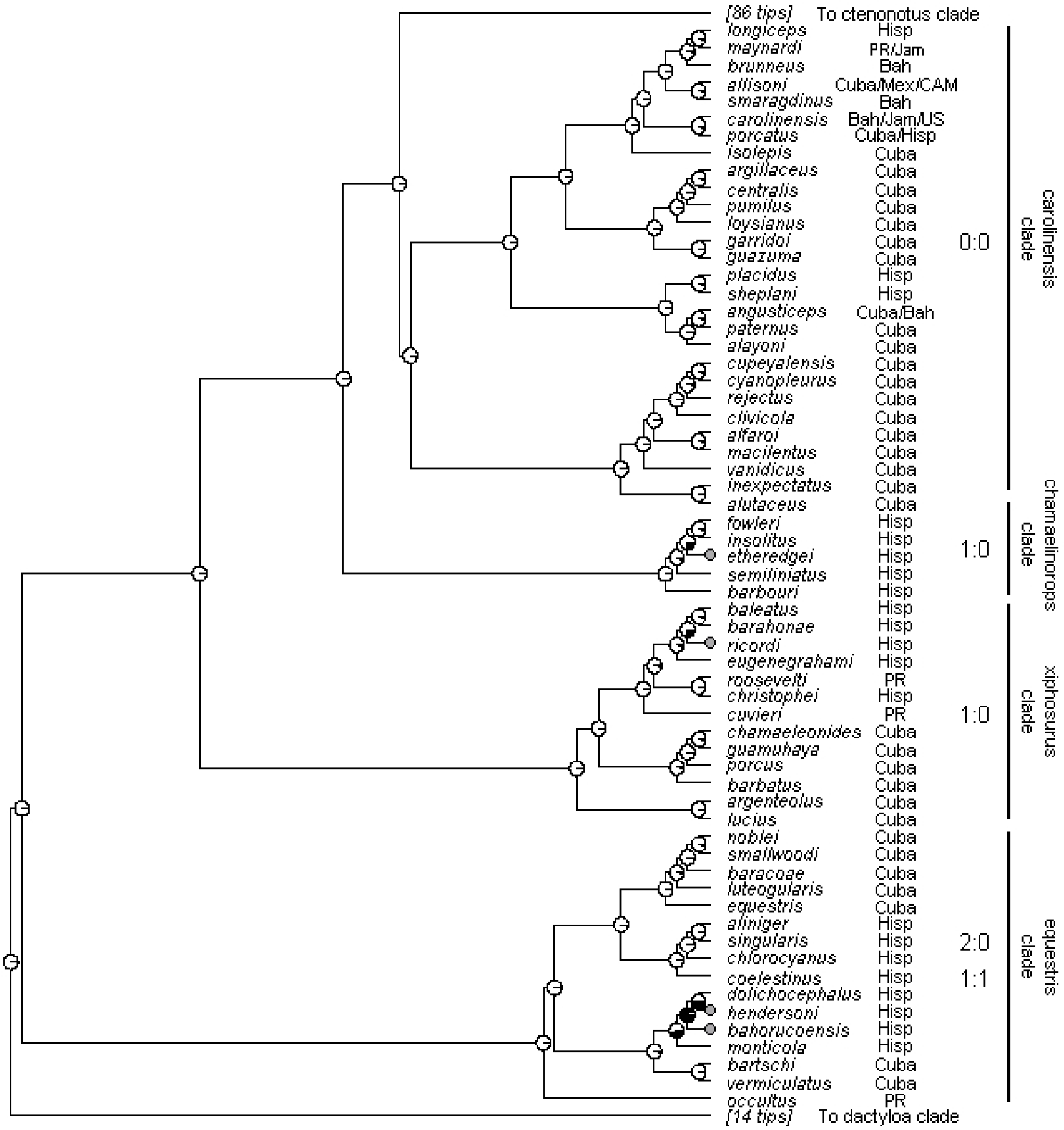
A.



B.


[51 tips] **To norops clade**
cybotes Hisp
haetianus Hisp
armouri Hisp
shrevei Hisp
whitemani Hisp
longitibialis Hisp
strahmi Hisp
marcanoi Hisp
desechensis PR
ernestwilliamsi PR/VI
cristatellus PR/VI/Hisp
scriptus Bah
monensis PR
gundlachi PR
poncensis PR
krugi PR
pulchellus PR/VI
evermanni PR
stratulus PR/VI
acutus PR/VI
caudalis Hisp
marron Hisp
brevirostris Hisp
websteri Hisp
distichus Hisp
altavelensis Hisp
marmoratus LA
sabanus LA
nubilis LA
lividus LA
ferreus LA
oculatus LA
gingivinus LA
bimaculatus LA
wattsi LA
[28 tips]
[5 tips]
[13 tips]
[16 tips]
[14 tips]
1:2
3:0
cybotes clade
2:1
3:0
cristatellus series
4:0
3:1
2:2
1:3
bimaculatus series
ctenonotus clade

C.


[86 tips] To ctenonotus clade
longiceps Hisp
maynardi PR/Jam
brunneus Bah
allisoni Cuba/Mex/CAM
smaragdinus Bah
carolinensis Bah/Jam/US
porcatus Cuba/Hisp
isolepis Cuba
argillaceus Cuba
centralis Cuba
pumilus Cuba
loysianus Cuba
garridoi Cuba
guazuma Cuba
placidus Hisp
sheplani Hisp
angusticeps Cuba/Bah
paternus Cuba
alayoni Cuba
cupeyalensis Cuba
cyanopleurus Cuba
rejectus Cuba
clivicola Cuba
alfaroi Cuba
macilentus Cuba
vanidicus Cuba
inexpectatus Cuba
alutaceus Cuba
fowleri Hisp
insolitus Hisp
etheredgei Hisp
semilineatus Hisp
barbouri Hisp
baleatus Hisp
barahonae Hisp
ricordi Hisp
eugenegrahami Hisp
roosevelti PR
christophei Hisp
cuvieri PR
chamaeleonides Cuba
guamuhaya Cuba
porcus Cuba
barbatus Cuba
argenteolus Cuba
lucius Cuba
noblei Cuba
smallwoodi Cuba
baracoae Cuba
luteogularis Cuba
equestris Cuba
aliniger Hisp
singularis Hisp
chlorocyanus Hisp
coelestinus Hisp
dolichocephalus Hisp
hendersoni Hisp
bahorucoensis Hisp
monticola Hisp
bartschi Cuba
vermiculatus Cuba
occultus PR
[14 tips] To dactyloa clade
0:0
carolinensis clade
1:0
chamaeleolinops clade
1:0
xiphosurus clade
2:0
1:1
equestris clade

D.

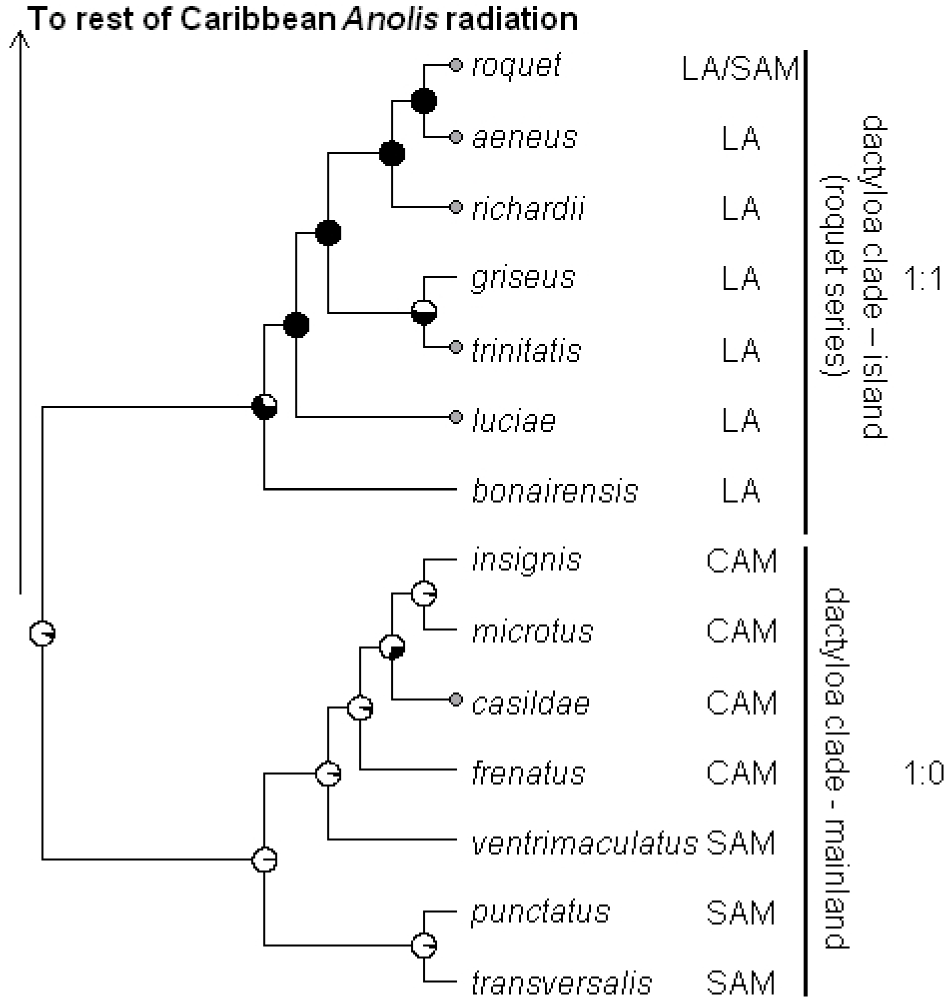
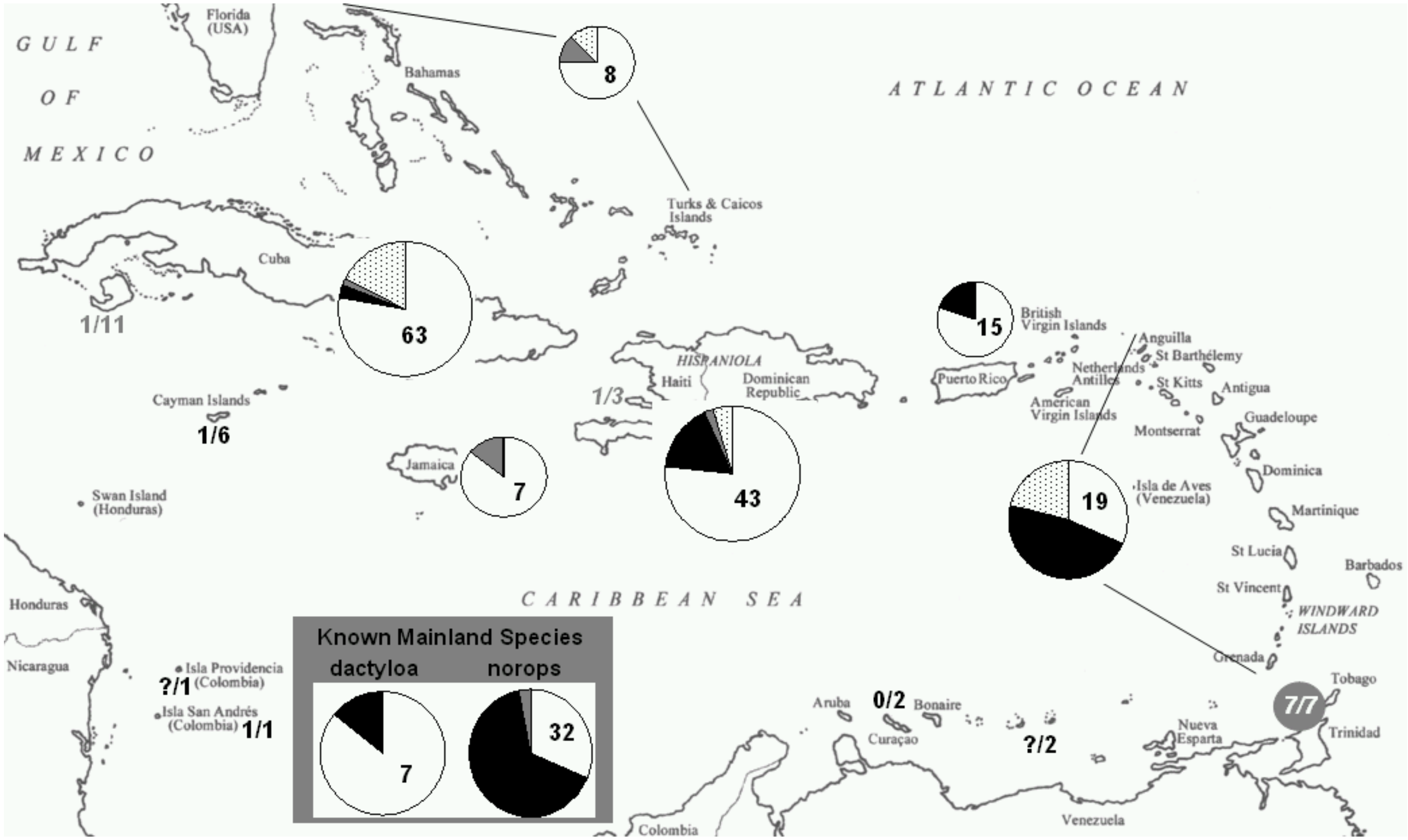

To rest of Caribbean *Anolis* radiation
roquet LA/SAM
aeneus LA
richardii LA
griseus LA
trinitatis LA
luciae LA
bonairensis LA
dactyloa clade – island (roquet series)
1:1
insignis CAM
microtus CAM
casildae CAM
frenatus CAM
ventrimaculatus SAM
punctatus SAM
transversalis SAM
dactyloa clade - mainland
1:0

Figure 2. Geographic distribution of female polymorphism in anoles. The total number of species per location are given along with the proportion of polymorphic (endemic: black, non-endemic: dark-grey), proportion of species for which the presence of polymorphism was unknown (light yellow) and proportion of non-polymorphic species (white). For the two radiations of mainland anoles, the proportion of polymorphic species is given relative to the number of species for which the presence of polymorphism was known.



CHAPTER THREE

DORSAL PATTERN POLYMORPHISM AND HABITAT USE IN FEMALE ANOLES (Squamata: Polychrotidae)

INTRODUCTION

Color pattern polymorphism has long been the classic model for tests of natural and sexual selection (Darwin 1859; Darwin 1871). Because we expect selective pressures to favor a particular morph, selection should lead to one optimal male and female morph (Charlesworth 1984; Charlesworth 1987; Fisher 1930). Even without selective pressures, however, variation is expected to disappear through chance events. Thus, intra-sexual polymorphism challenges evolutionary theory, and understanding mechanisms for the evolution and maintenance of alternative morphs provides insight into the processes of natural and sexual selection and drift. Because color patterns can be readily observed, they provide ideal study subjects to address these challenges.

Much research has been devoted to color pattern polymorphism (e.g. Basolo 2006; Galeotti et al. 2003; Gray and McKinnon 2007; Hoffman and Blouin 2000; Houde 1997; Jones et al. 1977; Roulin 2004; Seehausen et al. 1999). Gender-based polymorphism, however, has mostly focused on males. Many occurrences of male color polymorphism are explained by mate choice and mating strategy (Shuster and Wade 2003). A popular example is the rock-paper-scissor game of male color morphs in the lizard *Uta stansburiana* (Sinervo and Lively 1996). Female color polymorphism was studied intensively in the early 20th century, with regards to Müllerian mimics in butterflies where males were monomorphic, but females displayed a variety of patterns to mimic different non-palatable species (Fisher and Ford 1929; Owen 1971; Wickler 1968). It was not until the last few decades, however, that female polymorphism re-gained interest, much due to work on damselflies (Svensson et al. 2009). Female damselflies vary in the color of their abdomen, and often one color pattern resembles the male's (Abbott and Svensson 2005; Tillyard 1917). Several hypotheses have been proposed and tested, such as male harassment, frequency or density dependent mating success and balancing predation (Andres et al. 2002; Cordero 1992; Cordero et al. 1998; Hinnekint and Dumont 1989; Miller and Fincke 1999; Robertson 1985; Sherratt 2001). In spite of extensive research, much remains to be investigated. Interestingly, a recent study found that female polymorphism is the ancestral state for at least two genera of damselflies (Van Gossum and Mattern 2008). This, of course, changes the conclusions that can be drawn from population based studies. Even though female polymorphism in damselflies appears to be adaptive (Abbott et al. 2008; Andres et al. 2000), only current mechanisms for maintenance can be addressed. Moreover, studying the loss of this trait should be more informative when the trait is primitive.

The only other organisms for which the evolutionary history of female polymorphism has been investigated are anoles (Chapter 2). Female polymorphism in anoles consists of multiple dorsal patterns within a population (Savage 2002). Unlike many other cases of female color pattern polymorphism, the females do not differ in color. Moreover, the patterns appear cryptic, without colors that contrast with natural backgrounds and patterns that are formed by the same colors as seen on the rest of the body. Contrary to findings for damselflies, female polymorphism in anoles was shown to result from multiple independent events, although some closely related species share a female polymorphic ancestor (Chapter 2). This suggests that female polymorphism might be the result of parallel evolution, a hypothesis that needs to be tested. Parallel evolution occurs when distantly related species share a common environment that allows for a shared trait, in this case female polymorphism, to evolve. This is similar to convergent evolution, except that the new trait evolves from a similar ancestral state in parallel evolution (Zhang and Kumar 1997).

In explaining polymorphism of cryptic color patterns, habit use is an important central issue, because visibility of color patterns is determined by the background against which they are seen (Endler 1978; Merilaita and Jormalainen 1997). Visibility of an individual is determined by its color pattern, its behavior and the background; and also by the visual scanning behavior of the observer (Endler 1978). Light environment plays an important role in the visibility of color patterns, as well as time of day, cloud cover and vegetation cover; all affect the light environment (Endler 1993). Within a particular habitat, light environment can differ spatially with type of vegetation, and seasonally. An individual can “control” the light environment behaviorally through micro-habitat choice. Additionally, color patterns can serve three functions in animals: thermoregulation, inter and intra-specific communication, and evasion of predators (Cott 1940; Endler 1978). Thermoregulation, communication and predator avoidance can interact, and the resulting color pattern is not necessarily optimized for only one of these factors (Endler 1978; Endler 1980; Merilaita et al. 2001). Because color patterns are visual signals, habitat use can play an important role regardless of the functions of the color patterns. Thus, if female polymorphism is adaptive, we would expect to see a relationship between the presence of this trait and habitat use.

We investigated the relationship between female polymorphism and habitat use in anoles, using comparative methods. The need for comparative approaches to study maintenance of color pattern polymorphism has been emphasized by Gray and McKinnon (2007), but only few studies have done so (Galeotti et al. 2003; Seehausen et al. 1999; Van Gossum and Mattern 2008). Due to the complexity of habitats, we incorporated micro-and macro-habitat variables, and expected to find an association between the presence of female polymorphism and at least one habitat aspect.

METHODS

Anoline lizards (Squamata: Polychrotidae) form a radiation of nearly 400 species. Due to the standing debate on nomenclature of anoles and the need for a practical approach, we applied the original genus name *Anolis* for all species, but referred to specific clades as detailed elsewhere (Chapter 2). Anoles range as far north as the southeastern United States and are found on the Carribean islands and the Neotropical mainland. Many species, on the islands as well as on the mainland, are female polymorphic (Chapter 2). Females of these species vary in distinctive dorsal patterns and typical female patterns in those species include a light vertebral stripe, diamonds or dark chevrons. Although some variation exists, the same general patterns occur across species (Savage 2002).

Data on dorsal patterns, body size, distribution and habitat use were compiled from books, review papers and the primary literature (Avila-Pires 1995; Campbell 1998 ;

Cast et al. 2000; Dixon and Soini 1986; Duellman 1978; Duellman 2005; Estrada and Hedges 1995; Fitch 1973; Fitch 1975; Garrido and Hedges 2001; Irschick et al. 1997; Knox et al. 2001; Lazell 1972; Leal and Losos 2000; Lee 1996; Lee 2000; Lenart et al. 1997; Losos and DeQueiroz 1997; Moermond 1979; Nicholson et al. 2001; Pinto et al. 2008; Rivero 1998; Savage 2002; Schwartz and Henderson 1991; Stafford and Meyer 2000; Stejneger 1900; Thomas et al. 2009; van Buurt 2005; Vitt and de la Torre 1996). Geographical variation, subspecies variation or variation due to metachromatism (color change) was not considered polymorphic. Because descriptions were at species level, polymorphism could not be assessed for separate populations.

Similarly, habitat use was assessed for the species as a whole. To represent the overall light environment individuals could be exposed to, we combined micro-and macro-habitat data with body size. The macro-habitat data reflected the overall light environment available to the species. Macro-habitats were based on habitat use descriptions or point occurrence data and vegetation maps. Habitats were categorized as: ‘old growth forest’, ‘secondary forest’, ‘open natural habitat’, ‘agriculture’ and ‘urban’. Open natural habitat included shrub, beaches, savanna and grassland. Agriculture included mostly plantations, e.g. coffee or cacao. Urban species dwelled in gardens, houses or other man-made structures. This habitat division was ranked in this order as a combined variable to represent openness and disturbance. Because one species can use more than one type of habitat, habitat use was summarized into two variables based on habitat: number of different habitats used and maximum level of disturbance. Clearly, these were collinear and only one could be used in our statistical model. Another variable, humidity, was also based on habitat use descriptions and consisted of ‘dry’, ‘dry to moist’ and ‘moist to wet’.

Using distribution maps, species were assigned to a rainfall pattern category. This variable was based on the Koppen-Geiger classification data and indicated the amount and timing of rainfall (Kottek et al. 2006). Rainfall pattern was included because some habitats change drastically throughout the lifetime of an anole based on rain patterns. The distribution of anoles in our dataset contained four major Koppen-Geiger classes: tropical rainforest climate with no natural seasons (Af), tropical monsoon climate with slightly more variation in precipitation (Am), tropical wet and dry or savanna climate with a clear wet and dry season (Aw), and a dry climate with even less rainfall (BSh). These were divided into four categories. The first category included non-seasonal environments only (Af). The second category included only wet-dry environment (Aw). Species were assigned to the third category when they occupied both non-seasonal and seasonal environments (Af+Aw). Species occupying areas with a dry climate were assigned to the fourth category (BSh). All species ranging into habitat with slight variation in rainfall (Am) also occupied either non-seasonal or seasonal environments and were assigned to one of those categories. In summary, macro-habitat use was divided into: maximum disturbance level, number of different habitat types occupied, rainfall pattern, and humidity.

Within a macro-habitat, a multitude of microhabitats are available. Microhabitat use reflects the specific light environment and background within the macro-habitat to which the species is exposed. In addition, body size indicates how much of the variation within a patch to which an individual can be exposed at one time. For body size, the maximum value for females was recorded. For microhabitat use of Greater Antilles species, ecomorph type (Williams 1972; Williams 1983) could be used. This represents habitat use as well as morphological and behavioral characteristics. For other species the relationships between these characteristics is often different (Irschick et al. 1997; Knox et al. 2001), so that many species have not been assigned to an ecomorph type. Therefore, we used perch use descriptions instead. The first category included species occupying tree canopies (ecomorphs: crown, trunk-crown). The second category consisted of trunk perchers (ecomorphs: trunk, trunk-ground, trunk-bush). Twig perchers were placed in their own category, because although they use thin perches, they could be perching low in bushes as well as high in the canopy. Species perching on bushy vegetation formed a fourth category (bush, grass-bush). Atypical perch users, such as aquatic species and rock dwellers were included in a fifth category. After collecting the data, it appeared that none of the anoles in the last category had female polymorphism and therefore this category was excluded from the analyses of polymorphism.

Statistical Analysis

Female polymorphism in anoles was shared by some closely related species. Therefore, the data were not independent and a phylogenetic correlation structure had to be incorporated. We used a combined phylogeny from the most recent and extensive works (Nicholson et al. 2005; Poe 2004). Equal branch lengths were assumed. Generalized estimating equations (GEE) with a binomial distribution and the phylogeny as a correlation matrix were applied to a model with the occurrence of female polymorphism as the response variable (Table 1). Model selection started with a complete model and proceeded by sequentially removing the term with the highest non-significant P-value. This process was repeated until all terms were significant. For comparison, a logistic regression with the same terms was run as well. This model did not incorporate the phylogeny, but was used to indicate whether phylogenetic relationships affected the occurrence of FPP across habitats. The model selection process was identical to the process in GEE, except that an AIC was used for dropping terms rather than the P-value. Because maximum disturbance and number of habitats were collinear, the model was run with each term separately. Maximum disturbance consistently resulted in a model with a higher Akaike's Information Criterion (AIC) than the model with number of habitats in the logistic regression. In GEE, maximum disturbance turned out insignificant as well. Thus, only the analysis with number of habitats is shown. Because many occurrences of FPP result from ancestral evolution in the mainland norops clade (Chapter 2), we repeated the analysis with a reduced number of species from the norops clade. In particular, we collapsed the node leading to *A. sericeus* and remaining norops species. This replaced 15 species of the norops clade by one species with the characteristics of *A. sericeus*.

A post-hoc Levene's test was incorporated to investigate whether variance in SVL between polymorphic and non-polymorphic species was significantly different. All analyses were performed in R (R Development Core Team 2008). The GEE was completed with the packages 'ape' and 'gee' (Carey 2007; Paradis et al. 2004). Levene's test was performed in the 'car' package (Fox 2009). Relevant habitat data were plotted onto a phylogeny using the 'geiger' package (Harmon et al. 2008).

RESULTS

Female dorsal pattern polymorphism (FPP) evolved in several clades of *Anolis* (Figure 1). In the norops clade, the lack of FPP was uncommon. Among 121 species included in the dataset, 37 scored positive for female polymorphism. The most common form of polymorphism, nearly 40% of the cases, was the occurrence of females with a vertebral stripe alongside females with the male pattern. About 25% of female polymorphic species had a male pattern-stripe-diamond combination of female patterns, but this was only found in mainland species, while a stripe-diamond combination without male pattern (16%) was only found in island species. Male patterns of female polymorphic species were often indistinct, without pattern or with dorsal blotches.

After removal of the non-polymorphic species in the category of atypical perches, 110 species were used to analyze FPP. The logistic regression model dropped humidity and snout-vent length, respectively, since they had little influence on FPP (Table 1). This led to a model with perch type, number of habitats and rainfall pattern. The number of habitats was included, because the model without this variable was not significantly better than the model with this variable. The GEE resulted in a similar model, but rainfall pattern became insignificant. Humidity, snout-vent length and rainfall pattern were dropped from the model consecutively (Table 1). The remaining model consisted of perch type and number of habitats used. Collapsing the node leading to *A. sericeus* and related mainland species of the norops clade led to similar results (not shown).

Plotting the data illustrated the results from the models (Figure 2). Female polymorphism occurred across different perch types, but was most common in the trunk perching species and was very rare in twig perching anoles. Among mainland species of the norops clade, FPP was not present in species that were not perching on trunks or on bushy vegetation (Figure 1). This pattern did not continue throughout the rest of the phylogeny and also anoles using other perch types were polymorphic (Figure 1). Among twig anoles, only one species was polymorphic in this study: *A. oculatus*. It is closely related to the polymorphic species *A. marmoratus* and *A. sabanus*, which perch low on trunks and bushes. Polymorphic canopy species were mostly members of the roquet series in the dactyloa clade (Figure 1.C). The mainland dactyloa in our analysis were also canopy species, but were not polymorphic.

Polymorphic species were most common in geographic areas without true seasons and in areas with a dry and wet season ('Mixed' in Figure 2). For the number of habitats, differences in the occurrence of female polymorphism were not as clear, but the lowest proportion of polymorphic species was found among species restricted to one or two habitats, while the highest proportion was among species using three or five different habitats. The latter category, however, was a small sample of species. Species occurring in three different habitats were mostly species found in both forest and natural, open areas. Female polymorphism was rare among species occupying only dry habitats, although proportions of female polymorphism were not significantly different across categories of humidity. Snout-vent length (SVL) did not differ between species with and without female polymorphism, but species with polymorphism showed less variation in snout-vent length. ($S.D._{(No\ FPP)} = 39.7$, $S.D._{(FPP)} = 20.2$, $F_{(1,111)} = 4.80$, $P = 0.0306$).

DISCUSSION

We found a strong association between the occurrence of FPP and some aspects of habitat use, even though FPP showed significant phylogenetic signal (Chapter 2). In particular, our strongest result supported by all analyses indicated that anoles perching on trunks were more likely to be female polymorphic. Furthermore, FPP was more common among species occupying three different habitat types and occurring in both environments with and without seasonality in rainfall. The latter was phylogenetically associated, and patterns with rainfall disappeared when phylogenetic relationships were accounted for. Rainfall patterns were based on Köppen-Geiger classifications, which encompass large regions, without accounting for smaller regional variation. Because closely related species often occur on the same island or in the same area, it is not surprising that the effect of rainfall disappeared when effects of phylogeny were removed. To discern whether the relationship between rainfall pattern and polymorphism is solely due to phylogeny, rainfall patterns and polymorphism could be studied at a smaller scale. For the purpose of the current analysis, however, effects remaining after incorporating phylogeny provide an indication for a similar environment among female polymorphic species, regardless of their affiliation. Such association is expected if FPP is adaptive.

There was a trend of increasing occurrence of polymorphism with increased number of habitats occupied. Proportion of polymorphism was highest for species occupying three habitats and most of these species used forests as well as open habitats. This hints at a connection between variety of habitats occupied and presence of FPP, supporting the hypothesis that species occupying spatially or temporally heterogeneous habitats are more likely to be polymorphic (Cain and Sheppard 1954b; Ford 1945; Hedrick et al. 1976). When incorporating human-altered habitat (i.e. 4 or 5 habitats occupied), however, there was no consistent trend. Likely, FPP evolved before habitats had been altered. In addition, human altered habitats may consist of elements similar to natural habitats when considering light environments. The variation in light environment may thus be more important than the level of disturbance, but assessment of similarities between human-altered and natural habitat would require more detailed measurements of habitat use.

Perch use appeared to influence the occurrence of FPP, regardless of phylogenetic relationships. None of the species on rocks, in aquatic environments or other atypical perches were female polymorphic. For analytical purposes, these species had to be removed for analysis, and thus the statistical results may have underestimated the relationship between FPP and perch use. The majority of FPP was seen in anoles perching on trunks. Interestingly, in the mainland radiation of the norops clade, FPP only occurred in anoles perching on trunks or bushy vegetation, and was lost in all others. These anoles share a common ancestor that was likely already female polymorphic (Chapter 2). The loss of FPP in this radiation thus provides a stronger indication of any association with habitat variables than the mere presence of FPP. Among the remainder of anoles, however, the relationship between perch use and FPP was not as strict, although the association of FPP with habitat (including perch type) remained after removing the FPP-rich radiation of the mainland norops clade. Among island anoles, not all trunk perching anoles were polymorphic, and FPP was also found for other perch types, mostly in the dactyloa radiation. Species from both the mainland and island dactyloa radiations in our analysis were canopy species, but only among the island radiation was FPP found to be common. The mainland lineage of dactyloa has at least one polymorphic member, *A. casildae*, not included in the analysis for lack of detailed habitat data. Unlike the other species, however, this species appears to be a low perching anole (Nicholson et al. 2001).

For some species, perch use varies between or within populations and classification may be somewhat misleading. Here, we highlight a few examples that are relevant to our analysis. Some Lesser Antilles species that are considered canopy species, are also found on lower perches. For example, *A. marmoratus* and *A. sabanus* morphologically resemble canopy species (Losos and DeQueiroz 1997), but perch behavior is more similar to trunk-ground species, although some variation exists between populations of *A. marmoratus* (Schwartz and Henderson 1991). *A. oculatus* is a diverse species and some populations seem to be closer to trunk-crown anoles (our canopy category), while others classify closer to trunk-ground species (our trunk category) (Knox et al. 2001). Here we classified it as 'twig' and it would be interesting to check whether female polymorphism differs between populations in this species. Females of *A. conspersus* behave more like trunk-ground anoles with regards to perch choice (Schoener 1967), even though this species is generally considered a crown anole. *A. aeneus*, classified as a trunk-crown anole ('canopy') (Losos and DeQueiroz 1997), is also found in scrub habitat, which may be closer to our 'bush' category.

The pattern of evolution of FPP in association with habitat, in particular perch type, suggests that FPP requires a particular environment for FPP to evolve and be maintained. The main question becomes why it evolved mostly in trunk perching species. Predation has been suggested to explain the multiple dorsal patterns in female anoles (Macedonia 2001; Schoener and Schoener 1976). Anoles are preyed upon by mammals, birds, snakes, lizards including congeners, spiders and other invertebrates (e.g., Guyer

1988a; Henderson and Crother 1989; McLaughlin and Roughgarden 1989; Reagan 1996). Perhaps anoles perching on trunks are more exposed to predators. A predation hypothesis is further supported by the presence of a vertebral stripe as one of the patterns in female polymorphic anoles. In fact, the vertebral stripe was the most common alternative pattern in female polymorphic anoles, while males of these species generally had indistinct patterns or vertebral blotches. The vertebral stripe is a common alternative dorsal pattern in polymorphic reptiles and often related to habitat use as a concealing or disruptive pattern (Cott 1940; Duellman and Trueb 1986; Hoffman and Blouin 2000; Patterson and Daugherty 1990; Schoener and Schoener 1976).

Based on a few examples, Schoener and Schoener (1976) assumed that female polymorphic species were small, and suggested that the vertebral stripe would only be effective as a predation avoidance mechanism in smaller species. We found no association, however, between SVL and the presence of FPP. Interestingly, SVL variation was much smaller in polymorphic species, suggesting that female patterns are only concealing within a range of sizes from about 40-100 mm. Females of the largest species with FPP, *A. ricordi*, grow up to 151 mm SVL. The dorsum of these females is either rather uniform or shows a dark reticulate pattern, but not the vertebral stripe as seen in most other polymorphic species. The next largest polymorphic species was *N. capito*, with females measuring up to 100 mm SVL. Here, a vertebral stripe is one of the alternative patterns. Thus, although FPP is not limited to small species, size appears to matter and perhaps Schoener and Schoener's (1976) hypothesis could be adjusted to apply to a vertebral stripe as being concealing only in anoles of certain sizes. Whether the stripe indeed reduces predation would have to be tested.

The other question arising from our results is why the association between perch use and FPP in island radiations was not as strict compared to the mainland anoles. This dichotomy between island and mainland anoles also exists in the origination of FPP, with mostly independent evolution of FPP in island clades and ancestral evolution of FPP for mainland norops species. It was suggested that the genetic variation associated with FPP disappears as a consequence of founder effects upon colonization of new territories (Chapter 2). Mainland norops species are the result of one colonization event event (Jackman et al. 1997; Nicholson 2002; Nicholson et al. 2005). For island anoles, the variation necessary for FPP to evolve may not have been present in all species that occupy habitats where we would expect FPP to occur.

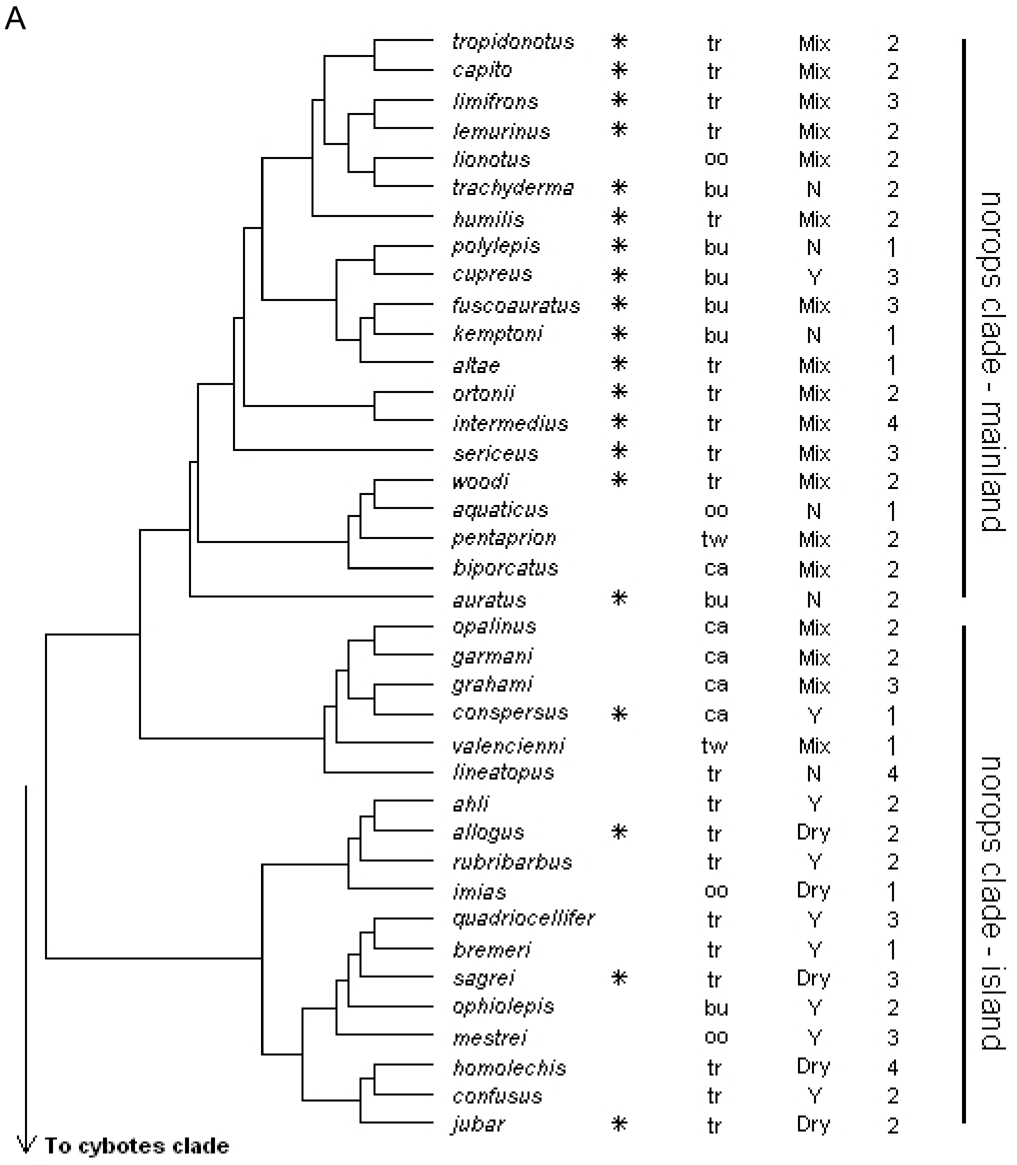
Selective pressures may also differ between the Neotropical mainland and the islands of the West Indies. The majority of the West Indies vertebrate fauna is composed of anoles, unlike the mainland where these lizards constitute only a minor part of the overall faunal biomass (Rand and Humphrey 1968), and biological interactions such as competition or predation are expected to differ (e.g. Andrews 1976; Andrews 1979; Wright 1981). Anoles on the mainland may experience higher predation than anoles on the islands (Andrews 1979; Andrews 1991; Schoener 1985; Schoener and Schoener 1982), because there is probably a wider variety of species preying on anoles (Losos 2009). Nevertheless, some island species may still experience high predation pressure. For instance, snakes of the genus *Alsophis* (Squamata: Colubridae) are anole specialists, and can be very abundant in the West Indies (Henderson and Sajdak 1996). In the Lesser Antilles most islands are inhabited by only one or two species, and predators are thus limited in their choice as to which species to prey on. Species on the Lesser Antilles could therefore experience high predation rates. Indeed, predation by pearly-eyed trashers on the female polymorphic *A. wattsi* was found to be high and this was related to moist habitats (McLaughlin and Roughgarden 1989).

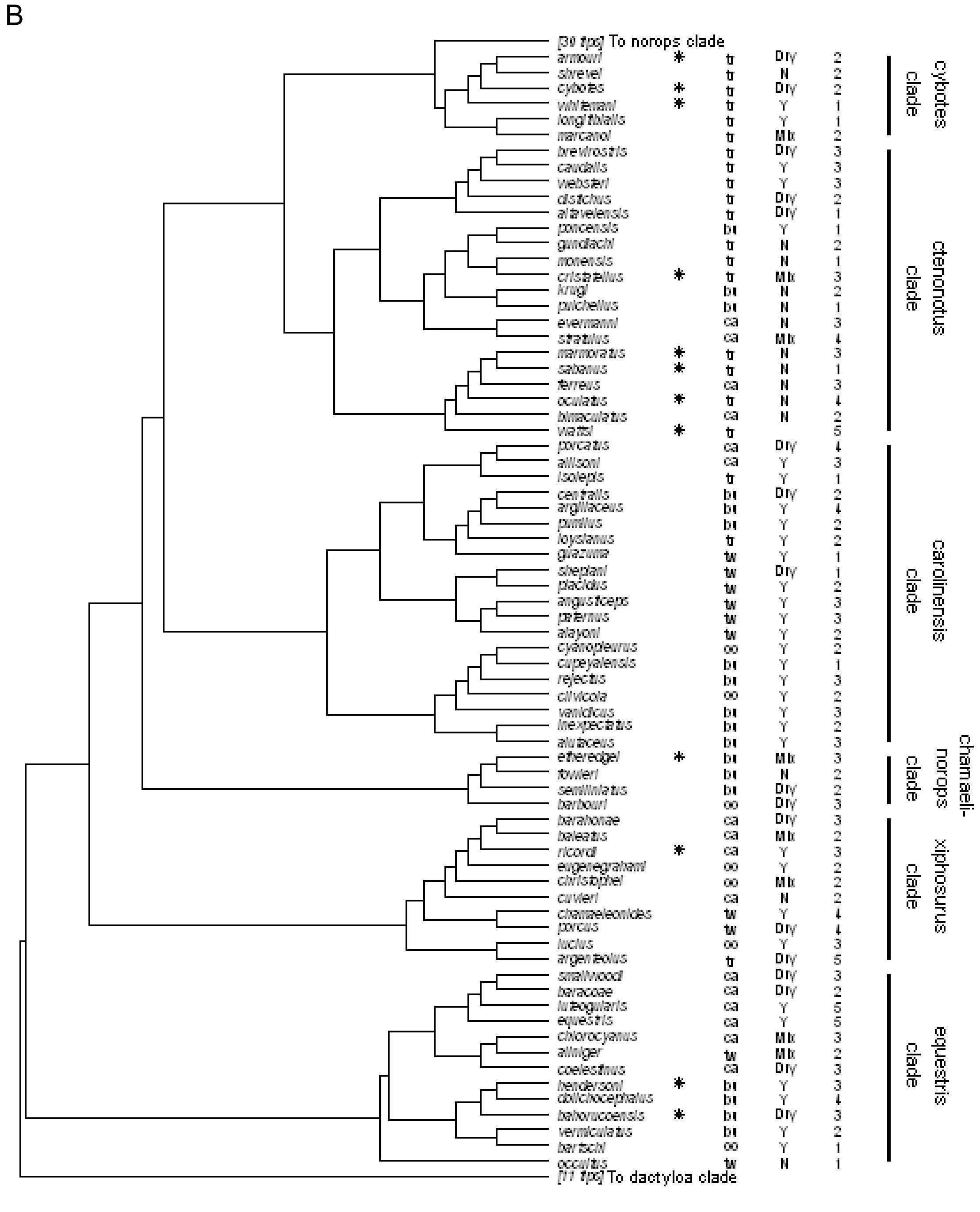
In summary, our results suggest that female polymorphic species share similar environments, but the broad variables incorporated in our analysis did not allow us to determine which elements within this environment are important for FPP. When combining our results with circumstantial evidence, we can hypothesize that predation is likely to be important in the maintenance of FPP.

Table 1. Model selection steps to determine the relationship between macro and micro-habitat variables and the presence of female polymorphism. Both the logistic regression model and the model based on generalized estimating equations are shown. The term with the highest P-value was dropped. The model was then run again without this term to select the next highest non-significant term. The process was repeated until the final model only contained significant terms. Drop-terms are listed in order of being dropped. AIC values represent values in comparison with the final model with only the respective term being dropped. Model selection with generalized estimating equations was based on P-values.

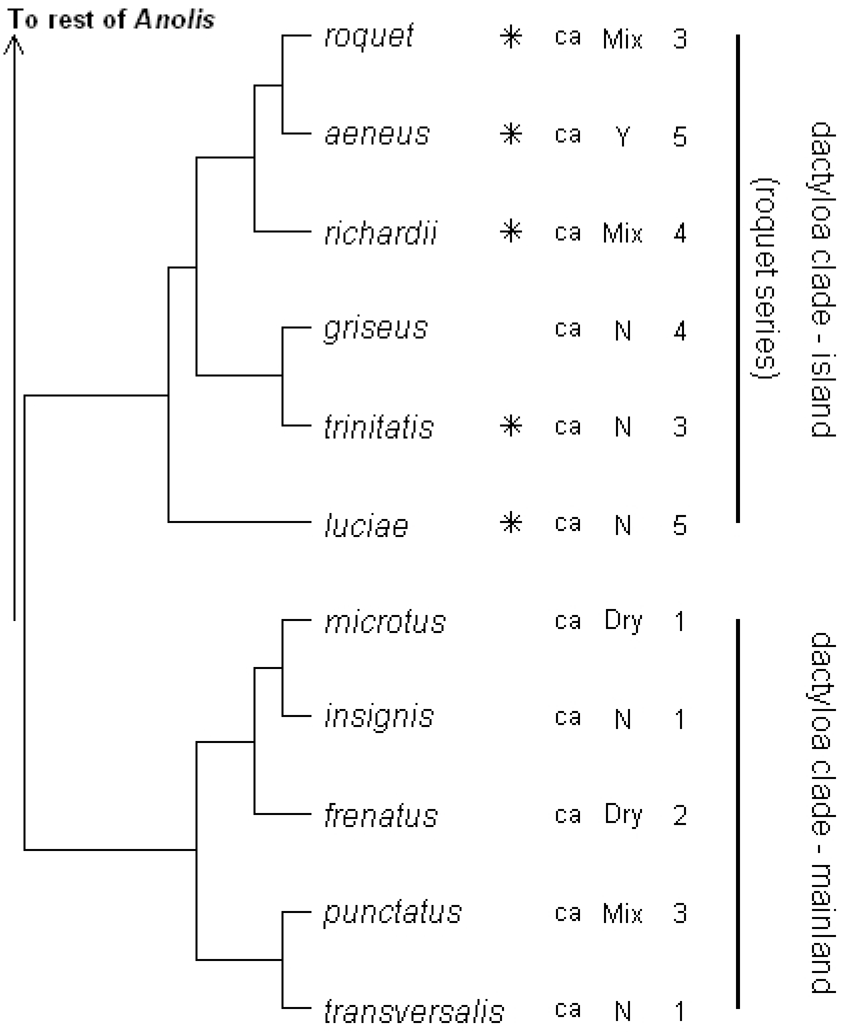
Multiple regression	**df**	**AIC**	**P**
Full model: FPP~svl+Perch+Humidity+Habitats+Rainfall		137.919	
Least significant term dropped:			
Humidity	2		0.685
Snout-vent length (svl)	1		0.474
Final model: FPP~Perch+Habitats+Rainfall		133.187	
Rainfall pattern (‘Rainfall’)	3	142.046	0.002
Perch	3	142.599	0.002
Number of different habitats	4	133.279	0.088
Generalized Estimating Equations - Incorporating phylogeny	**df**		**P**
Full model: FPP~svl+Perch+Humidity+Habitats+Rainfall			
Humidity	2		0.532
Snout-vent length (svl)	1		0.239
Rainfall pattern (‘Rainfall’)	3		0.272
Final model: FPP~Perch+Habitats			
Number of different habitats (‘Habitats’)	4		0.002
Perch	3		< 0.0001

Figure 1. Phylogeny with patterns and habitat variables related to distribution of female polymorphism in anoles. Female polymorphic species are indicated with a star (*). The second column indicates perch use: bushy (bu), twig (tw), trunk (tr), canopy (ca) and other (oo). Rainfall patterns are in the third column: no distinct season (N), wet and dry season (Y), N+Y (Mix) and dry regions (Dry). The last column presents the number of habitats used. A. norops clade, B. cybotes, ctenonotus, carolinensis, chamaelinorops, xiphosurus and equestris clades, C. dacyloa clade.



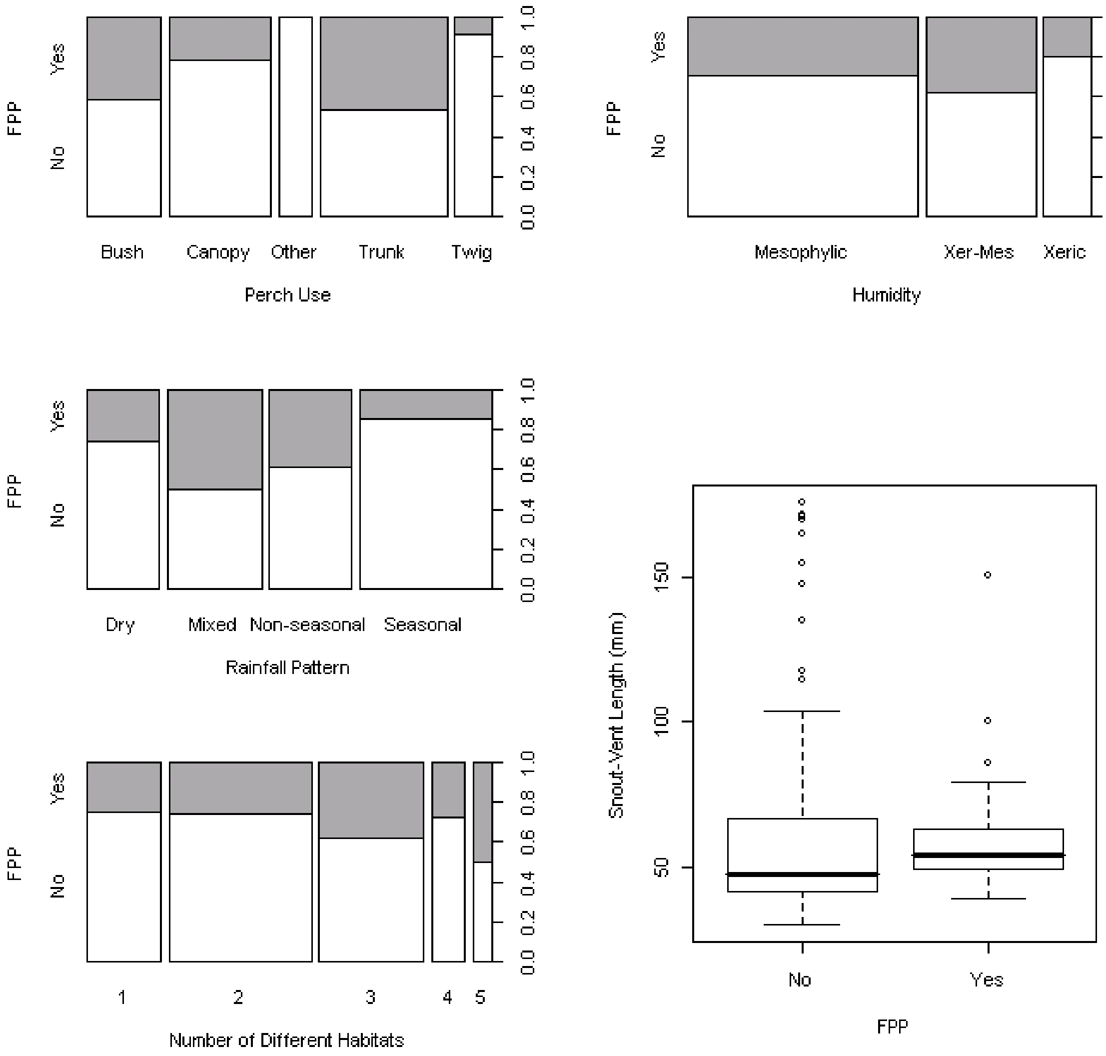

B
[30 tips] To norops clade
armouri * tr Dry 2
shrevei tr N 2
cybotes * tr Dry 2
whitemani * tr Y 1
longitibialis tr Y 1
marcanoi tr Mix 2
brevirostris tr Dry 3
caudalis tr Y 3
websteri tr Y 3
distichus tr Dry 2
altavelensis tr Dry 1
ponceusis bu Y 1
gundlachi tr N 2
monensis tr N 1
cristatellus * tr Mix 3
krugi bu N 2
pulchellus bu N 1
evermanni ca N 3
stratulus ca Mix 4
marmoratus * tr N 3
sabanus * tr N 1
ferreus ca N 3
oculatus * tr N 4
bimaculatus ca N 2
wattsi * tr 5
porcatus ca Dry 4
allisoni ca Y 3
isolepis tr Y 1
centralis bu Dry 2
argillaceus bu Y 4
pumilus bu Y 2
loysianus tr Y 2
guazuma tw Y 1
sheplani tw Dry 1
placidus tw Y 2
angusticeps tw Y 3
paternus tw Y 3
alayoni tw Y 2
cyanopleurus oo Y 2
cupeyalensis bu Y 1
rejectus bu Y 3
clivicola oo Y 2
vanidicus bu Y 3
inexpectatus bu Y 2
alutaceus bu Y 3
etheridgei * bu Mix 3
fowleri bu N 2
semilineatus bu Dry 2
barbouri oo Dry 3
barahonae ca Dry 3
baleatus ca Mix 2
ricordi * ca Y 3
eugenegrahami oo Y 2
christophei oo Mix 2
cuvieri ca N 2
chamaeleonides tw Y 4
porcus tw Dry 4
lucius oo Y 3
argenteolus tr Dry 5
smallwoodi ca Dry 3
baracoae ca Dry 2
luteogularis ca Y 5
equestris ca Y 5
chlorocyanus ca Mix 3
aliniger tw Mix 2
coelestinus ca Dry 3
hendersoni * bu Y 3
dolichocephalus bu Y 4
bahorucoensis * bu Dry 3
vermiculatus bu Y 2
bartschi oo Y 1
occultus tw N 1
[11 tips] To dactyloa clade
cybotes clade
ctenonotus clade
carolinensis clade
chamaeli-norops clade
xiphosurus clade
equestris clade

C



To rest of *Anolis*
roquet ✳ ca Mix 3
aeneus ✳ ca Y 5
richardii ✳ ca Mix 4
griseus ca N 4
trinitatis ✳ ca N 3
luciae ✳ ca N 5
microtus ca Dry 1
insignis ca N 1
frenatus ca Dry 2
punctatus ca Mix 3
transversalis ca N 1
dactyloa clade - island
(roquet series)
dactyloa clade - mainland

Figure 2. Distribution of female polymorphism among habitat types. The variables Perch Use, Rainfall Pattern and Number of Habitats were found to be significant determinants in the occurrence of female polymorphism (grey). The width of each column reflects the proportion of species (total =121 species) in each category. For details: see text.



CHAPTER FOUR

SURVIVAL OF ALTERNATIVE DORSAL PATTERN MORPHS IN FEMALES OF THE ANOLE *NOROPS HUMILIS.*

INTRODUCTION

The occurrence of multiple color patterns within a population has long fascinated evolutionary biologists (e.g. Bateson 1894; Cott 1940; Darwin 1871; Ford 1940; Huxley 1955). Color patterns provide a window to genetic variation, and thus provide a tool to study evolutionary patterns and processes (Gulick 1873). Generally, color patterns are thought to be adaptive, and function in thermoregulation, communication or predator avoidance (Cott 1940; Endler 1978; Poulton 1890). When color patterns appear cryptic, they are typically associated with predator avoidance (Owen 1980). Under selective pressure of predators, multiple color patterns can be maintained in a population, if there is temporal or spatial variation in predation, or a combination of both (Bond and Kamil 2006; Endler 1988; Haldane and Jayakar 1962; Hedrick et al. 1976).

One of the first mechanisms proposed to maintain color pattern polymorphism in species with visual predators was frequency dependent predation (FDP) or apostatic selection (Poulton 1884; Reviewed by Ayala and Campbell 1974). In FDP the fitness of a morph depends on its frequency relative to other morphs in the population (Clarke and O'Donald 1964), and is thus a mechanism of soft selection (Wallace 1975). FDP posits that a visual predator will select the most common morph (Allen and Clarke 1984), probably because development of a search image minimizes search time and thus increases foraging efficiency (Allen 1988; Dukas and Kamil 2001; Hubbard et al. 1982;

Staddon and Gendron 1983; Tinbergen 1960). This decreases the chance of detection of the alternative morphs, which will therefore increase their relative frequency within the population, after which the same process repeats itself (Allen 1988; Ayala and Campbell 1974; Endler and Greenwood 1988; Fisher and Ford 1929). Frequency dependent predation has been found to maintain polymorphism in a variety of cryptically colored species that are preyed upon by visual predators such as birds or fish in natural populations (Allen and Weale 2005; Olendorf et al. 2006; Reid 1987), as well as in experiments with artificial prey (Allen and Clarke 1968; Bond and Kamil 1998; Bond and Kamil 2002; Church et al. 1997; Fitzpatrick et al. 2009).

One of the main arguments against FDP concerns the process by which the predator would have to select its prey items; mainly questioning the existence of search image and continued switching behavior (Bond 2007; Punzalan et al. 2005). Experiments have documented, however, that predators may indeed continue switching to the most common prey item, even when familiarized with all prey types (Bond 1983; Bond and Kamil 2002). Ultimately, the major interest in frequency dependent predation arose from its role in maintaining color pattern polymorphism. Unless there is a frequency-dependent effect on survival of the morphs (Endler 1986), frequency dependent predation is unlikely to maintain multiple morphs in a population.

In anoles, several species have been documented to possess dorsal pattern polymorphism in females (Chapter 2). In such cases, one female pattern may resemble the male pattern, and one or two alternative dorsal patterns, usually a vertebral stripe or diamond pattern, are found only in females (Fitch 1975; Savage 2002). Little is known about the evolutionary basis for the occurrence of female polymorphism and only a few studies have addressed female polymorphism in anoles. The dorsal patterns in females are thought to have evolved in response to predation (Macedonia 2001; Schoener and Schoener 1976; Chapter 3). Anoles are preyed upon by a variety of species, including birds (Guyer 1988a; McLaughlin and Roughgarden 1989; Reagan 1996).

If alternative dorsal patterns in females evolved in response to predation, then survival of females should be affected by their dorsal patterns. Here, we tested whether frequency dependent predation could be maintaining female polymorphism in *Norops humilis*, which would be supported by fluctuations in morph frequencies over time, and lower survival of the most frequent morph.

METHODS

Study organism and data collection

Norops humilis (Peters 1863) is a small anole from lowland and pre-montane moist forests and rainforests in Costa Rica and Panamá. There is some indication that *N. humilis* may in fact represent distinct species among its geographic locations and the population under study would become *N. quaggulus* (Köhler et al. 2006; Köhler et al. 2003). The division, however, is mostly based on hemi-penis morphology, and further research is needed to determine whether this warrants a split of *N. humilis*. For the purpose of this paper, we will use *N. humilis sensu lato*.

Males and females measure up to 45 mm snout-vent length (SVL) although females average slightly larger than males (Fitch 1973; Fitch 1975). They perch low on trunks and roam the leaf litter. Generations overlap and a single egg is laid every ten to 21 days throughout the year (Guyer 1988b). Juvenile males and females reach sexually maturity after about four months, when they measure around 29 and 32 mm, respectively (Guyer 1986; Talbot 1979b). Males have a brightly colored dewlap that is missing in females. Lifespan of *N. humilis* is thought to be one year. Females of *N. humilis* can have one of three morphs: a dotted pattern like males (‘andromorph’), or one of two female patterns (‘gynomorph’): a tan to brown vertebral stripe or a reticulated pattern.

Norops humilis was studied between December 1982 and July 1983 at the La Selva Biological Station in Costa Rica (Guyer 1988a; Guyer 1988b). The study site consisted of three 15 X 15 m plots in former cacao/pejibaye/laurel plantations within a premontane rainforest. *N. humilis* individuals were captured, toe-clipped and re-captured during surveys with two to three day intervals between capture periods. At first capture, individuals were measured to the nearest millimeter. The same site was surveyed for *N. humilis* in 1988, 1993 and 2007, each time for several weeks.

Morph frequencies

Number of individuals per morph were calculated for both studies, separating juvenile and adult females. Because sex determination in juveniles is difficult (Guyer 1988a), gender of some andromorph individuals was uncertain and juveniles included were only those that lived long enough for the gender to be determined (1982-1983 data only). Although observations occurred in multiple plots during all years, numbers were too low for statistical analyses in all but the 1982-1983 data, and observations from different plots were pooled. For the 1982-1983 dataset, data were presented per plot to assess spatial variation in frequencies. Contingency tables were applied to the number of individuals observed per morph for adult females of all years as well as for juvenile females of 1982-1983.

Survival analysis

For the survival analysis, we used the long-term dataset of 1982-1983. The capture history of that study consisted of 88 events at which an individual could be captured (1) or not (0). Recapture of individuals was based on re-sighting, and thus susceptible to missing individuals that were present. When an individual was not captured, it could have been dead, or simply remained unseen. Because we used an open population model, individuals that remained undetected, could have temporally or permanently emigrated the plots. Survival analyses estimate recapture rates based on individuals that were known to be present at a specific time but were not recaptured during that time. Survival estimates are then calculated while controlling for recapture probability (Lebreton et al 1992).

I tested for differences in survival between female morphs in juveniles and in adults. I started with a saturated model (i.e., including all terms and interactions for both survival and recapture) as recommended by Lebreton et al (1992). The live capture model to investigate effects of dorsal patterns on female survival included effects of time (t), pattern morph (m), age (a), and interactions between these variables on capture (p) and survival probabilities (Φ). In this analysis time was not found to affect recapture probability or survival, but statistics indicated that insufficient data were available to estimate time effects. The analysis was repeated without this variable.

First, the saturated model was examined with a Goodness-of-Fit (GOF) test in the program RELEASE (Burnham et al. 1987). The GOF test examines the underlying assumptions that the probability of both recapture and survival of every marked individual in the population is equal, regardless of their capture history. The saturated model fitted the data for each test well (Table 1). Subsequent models were derived, dropping one term at a time for recapture probability, and then comparing models using Akaike's information criterion (AICc) and likelihood ratio tests (Lebreton et al. 1992). After modeling recapture rate, the same process was repeated for survival rates. Model selection with logit transformation of variables was performed in the program MARK version 5.0. for Windows (White and Burnham 1999).

RESULTS

Morph frequencies

Similar proportions of each morph were seen for juveniles and adults in the 1982-1983 study: 50-60% andromorph females and 20-30% of each gynomorph pattern (Figure 1). In the 1982-1983 study, the relative proportion of each morph in the population did not change from juveniles to adults ($X^2 = 0.1873$, d.f. = 2, $P = 0.9106$). Data recorded in 1988,1993 and 2007, resulted in a similar proportions of adult female morphs (Figure 1), and no significant difference was found in morph frequency between years ($X^2 = 2.4183$, d.f. = 6, $P = 0.8775$). Data were thus pooled to compare frequencies between morphs. Andromorph females constituted a significantly higher proportion of female morphs in juveniles $X^2_{juv} = 31.9644$, d.f. = 2, $P < 0.0001$) as well as adults ($X^2_{ad} = 21.3849$, d.f. = 2, $P < 0.0001$).

Survival rates

I examined survival rates of females for effects of dorsal pattern and age, while controlling for recapture rate. A GOF test showed that the fully parameterized Cormack-Jolly-Seber model fit the data for all tests (Table 1). The model selection process for effects of dorsal pattern in juveniles and adults on recapture and survival is detailed in Table 2. From AICc values, we determined that recapture rate varied among dorsal patterns for both juveniles and adults. In juveniles, recapture rate was lowest for the dotted females ($p = 0.31 \pm 0.01$) and highest for the striped females ($p = 0.41 \pm 0.02$). In adults, on the other hand, striped females had the lowest recapture rate ($p = 0.16 \pm 0.03$), and the highest rate was seen in reticulated individuals ($p = 0.32 \pm 0.03$). Thus, effects of morph and age on survival were modeled with recapture rate variation in age and morph.

Monthly survival probability was lower for juvenile than for adult females ($\Phi_{(juvenile)} = 0.46 \pm 0.03$, $\Phi_{(adult)} = 0.63 \pm 0.04$, $X^2 = 11.807$, d.f. = 1, P = 0.0006). In juveniles, monthly survival was lowest for reticulated and striped morphs and highest for dotted ones ($\Phi_{(dot)} = 0.47 \pm 0.04$, $\Phi_{(retic)} = 0.44 \pm 0.06$, $\Phi_{(stripe)} = 0.44 \pm 0.06$), while in adults survival was lowest for striped and similar for dotted and reticulated females ($\Phi_{(dot)} = 0.65 \pm 0.05$, $\Phi_{(retic)} = 0.65 \pm 0.10$, $\Phi_{(stripe)} = 0.52 \pm 0.12$). These differences, however, were not significant; the model incorporating morph effects as well as age effects did not differ significantly from the model incorporating only age effect on survival probability ($X^2 = 1.364$, d.f. = 4, P = 0.8504).

DISCUSSION

We compared frequencies of female morphs between years, and tested for differences in survival rates between female morphs to assess whether frequency dependent selection could be maintaining female polymorphism in *N. humilis* at La Selva. In all years, dotted females were the most common morph. Frequency dependent predation should thus have resulted in lower survival of the dotted morph. Our data, however, did not support this hypothesis. On the contrary, dotted morphs were found to have slightly higher monthly survival rates than the other morphs in juveniles as well as adults, although this difference was not significant.

The long-term nature of the 1982-1983 study along with comparable findings for adults in three additional years by different observers warrants the conclusion that morph frequencies are rather stable, and that they are not affected by observer bias (Rivera and Andrés 2001). The higher frequency of dotted morphs could also not be attributed to morph specific differences in recapture rate, as these were not found to be higher for dotted females compared to the other two morphs in the 1982-1983 dataset. As with frequencies between years, morph frequencies did not appear to change from the juvenile to the adult stage. Juvenile morph frequencies and survival should be approached with some caution, because sex determination in juveniles is difficult, due to the matching patterns of andromorph females and males. Both the constancy of the morph frequencies and the similar survival rates of morphs, however, suggest that frequencies may indeed remain stable from the juvenile to the adult stage.

Under the frequency dependent selection we expected fluctuations of frequencies over time. Fluctuations can occur over very short or very long intervals due to, for example, the predator's sensitivity to changing frequencies of the morphs (Bond and Kamil 1998; Merilaita 2006). Given the great similarity in morph frequencies over four years, long-term fluctuations in these preliminary results seem unlikely. In addition, survival was found not to differ significantly between morphs, thus agreeing with stable frequencies over time.

Although frequency dependent predation is a commonly proposed mechanism to explain color polymorphism, the complexity of food webs may reduce the chance for frequency dependent predation to operate. Indeed, with an increased number of predators, FDP is less likely to maintain polymorphism (Merilaita 2006), probably because of differences in predator response to morph frequencies (Endler 1988). *N. humilis* is preyed upon by a wide variety of predators (Guyer 1988a), and it was thus not surprising that frequency-dependent predation was not supported by our results. Additionally, search images for the most common morph are less likely to develop in heterogeneous environments, or when predators prey on a wide variety of species (Kono et al. 1998).

Furthermore, survival is affected by factors other than predation. In *N. humilis*, survival of adults increased when food was added to the habitat (Guyer 1988a), suggesting that starvation affects mortality in this species. Similar to food limitations, desiccation is also a possible cause of mortality in anoles (Hillman and Gorman 1977), although this may be less important in our rainforest population of *N. humilis*. Disease and parasites can affect survival too, although this seems to play a minor role in anoles (Dobson et al. 1992; Schall and Pearson 2000). Because of the multiple factors affecting mortality, survival analyses are not an ideal approach to study frequency dependent predation (Van Gossum et al. 2004). Equal survival rates, however, suggest that frequency dependent predation alone is not responsible for the occurrence of multiple female dorsal patterns in our study population of *N. humilis*.

Similar survival rates of morphs in our study can thus result from several scenarios. First, predation may actually differ between morphs, but is balanced by other parameters affecting survival. In *N. sagrei*, for example, female morphs have been shown to differ in immuno-competence (Calsbeek et al. 2008), and morphs may exert alternative strategies to balance predation risk and immuno-competence. Second, morphs may experience similar predation rate. This could result if there was no effect of morph on predation. If morphs are selectively neutral, however, drift should lead to fixation of one morph (Endler 1978). Similarly, morph frequencies could have reached equilibrium, resulting in equal fitness (survival) of the morphs (Bond and Kamil 1998). When selection results in equilibrium, drift can be compensated by rather weak selection (Oxford 2005), which may be difficult to detect and experimental manipulation of morph frequencies are required to test this hypothesis. Alternatively, equal survival probabilities of female morphs could be achieved through morph-specific background matching (Endler 1988; Hedrick et al. 1976; Stamps and Gon 1983).

Figure 1. Frequencies of female morphs observed. Top:. Observations of juvenile and adult females in 1982-1983. Bottom:. Observations of adult females between 1982 and 2007. Dots (●),Reticulated (◊), Stripe (*)

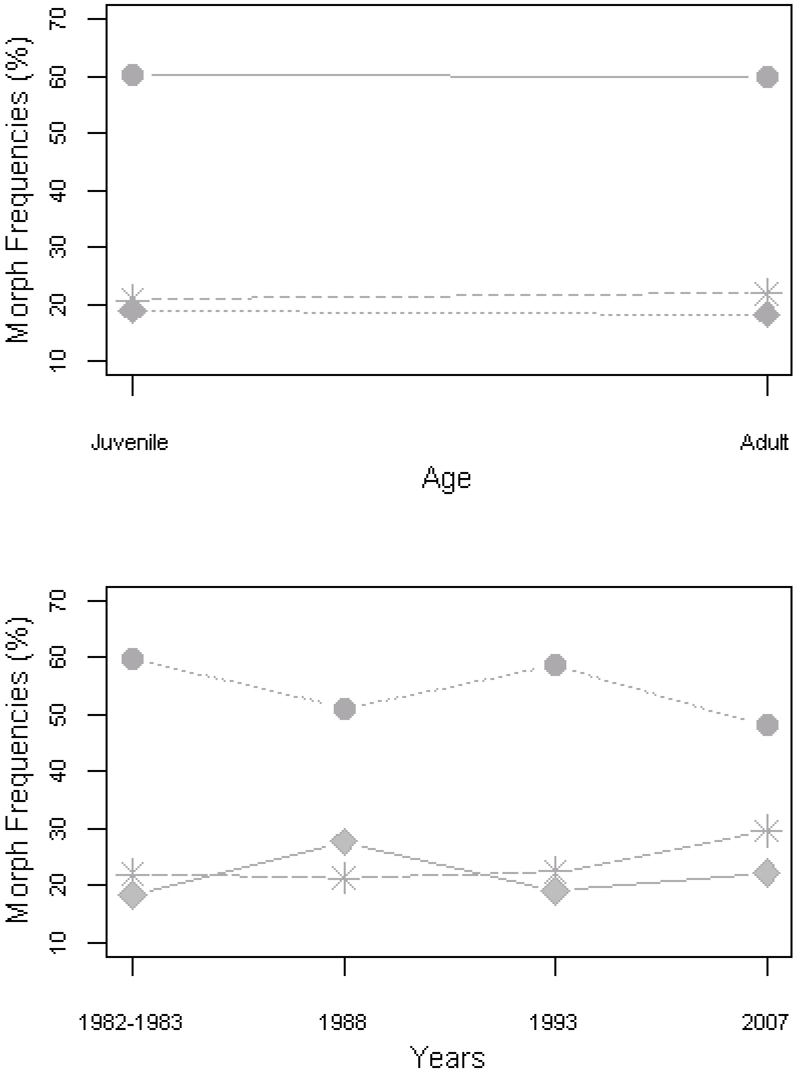


Table 1. Goodness of fit tests for saturated model examining effects of morph on survival of juvenile and adult females of *Norops humilis*.

Category	X^2	d.f.	P
Juvenile dot	211.0486	198	0.250
Juvenile retic	62.8323	97	0.997
Juvenile stripe	69.1363	109	0.984
Adult dot	31.5678	104	1.0
Adult retic	5.092	53	1.0
Adult stripe	1.8724	23	1.0
TOTAL	381.5494	584	1.0

Table 2. Modeling recapture (*P*) and survival (Φ) as a function of age (a) and dorsal pattern morph (m). The number of estimable parameters (np), deviance from the saturated model (DEV) and the Akaike's Information Criterion for small sample sizes (AICc) are given for every model. LogLikelihood Ratio Tests were used to test for effects of time, age and dorsal pattern, first on recapture rate and then on survival probability.

Model	np	DEV	AICc	Comparison
Saturated model:				
1. Φm*a, *P*m*a	12	5714.5	**5949.5**	Starting model fits the data
Modeling Capture				Age effect on recapture:
2. Φm*a, *p*m	9	5782.0	6010.9	4 vs 3: X^2 = 60.871, d.f. = 1, P < 0.0001
3. Φm*a, *p*a	8	5745.1	5971.9	Morph effect on recapture:
4. Φm*a, *p.*	7	5805.9	6030.8	3 vs 1: X^2 = 30.527, d.f. = 4, P < 0.0001
Modeling Survival				Morph effects on survival:
5. Φm, *p*m*a	9	5726.20	5955.0	6 vs 1: X^2 = 1.364 , d.f. = 4 , P = 0.8504
6. Φa, *p*m*a	8	5715.90	**5942.7**	Age effect on survival:
7. Φ, *p*m*a	7	5727.70	5952.5	6 vs 7: X^2 = 11.807, d.f. = 1, P = 0.0006

CHAPTER FIVE

PREDATION ON FEMALES WITH ALTERNATIVE DORSAL PATTERNS IN *NOROPS HUMILIS*

INTRODUCTION

In many animals, dorsal color patterns are associated with protection from predation. Bright coloration in prey species often functions as a warning signal for the predator, while drab color generally decreases visibility (Cott 1940; Edmunds 1974; Poulton 1890). Perception of color patterns, however, depends on the background against which the animal is seen (Bond 2007; Endler 1978; Ruxton et al. 2004), so that visibility is not inherent to a color pattern. Reduced visibility to predators (camouflage) can actually be obtained through color patterns that blend in with the background (crypsis) or patterns that deflect the predator's vision from the contours of its prey in which case the colors need not be similar to the background (Cott 1940; Cuthill et al. 2007; Endler 1978; Merilaita and Lind 2005). In a heterogeneous habitat, a camouflaging color pattern can be the result of compromising for the variety of backgrounds to which an individual is exposed; this pattern provides camouflage against a variety of backgrounds, but does not maximize camouflage for each background separately (Merilaita et al. 2001; Merilaita et al. 1999). Alternatively, individuals may select different microhabitats within the heterogeneous environment and maximize camouflage for this particular microhabitat, so that a variety of color patterns can be maintained within a population (Edmunds 1974; Endler 1978; Endler 1984; Hedrick 1986). Therefore, predation in heterogeneous environments may result in color polymorphic populations (Cain and Sheppard 1954b; Ford 1945).

Anoles (Sauria: Iguanidae) are known to vary in dorsal patterns within populations (e.g. Fitch 1975; Schoener and Schoener 1976). Moreover, these pattern variations are mostly limited to females, and the same patterns re-occur in many species (Savage 2002). The patterns vary in shape and do not appear to differ in color. A common female-only morph is the cream-colored vertebral stripe. Another common morph in female polymorphic species is a series of dorsal diamonds. The coloration pattern of these anoles consists of varieties of brown and green, suggesting that these patterns help reduce visibility to predators (Collette 1961; Fitch 1975; Macedonia 2001).

A comparative study found that female polymorphism in anoles is associated with perch use (Chapter 3). Moreover, the vertebral stripe is thought to provide camouflage on thin perches (Schoener and Schoener 1976). Previous studies indicated that female morphs select different perches (Schoener and Schoener 1976; Steffen 2010). In particular, striped females appear to select thinner perches in *Norops sagrei* (Schoener and Schoener 1976) and higher perches in *N. polylepis* (Steffen 2010). These studies were testing the hypothesis that dorsal pattern polymorphism in anoles is maintained through alternative morphs selecting different backgrounds that provide the best concealment for their particular pattern. Although perch use appears to differ between female morphs, no study has addressed predation.

To determine visibility to predators of each pattern against different backgrounds, experiments would be required. Methods have been developed to quantify how easily an individual is seen by a predator depending on the background it is seen against (Endler 1990; Endler and Mielke 2005). While background matching is relatively easily quantifiable for color polymorphism, such techniques have not been well developed for pattern polymorphism (Endler and Mielke 2005). To test whether visibility of morphs to predators is affected by perch type, I exposed modeling clay replicas of a common anole species to free ranging predators. Clay models have gained popularity to assess the interactions between predator and prey because predation is difficult to study under natural circumstances (Bittner 2003; e.g. Brodie 1993; Howe et al. 2009; Noonan and Comeault 2009; Steffen 2009). The advantage of clay models is that individual variation, such as size and behavior, can be removed. Under the hypothesis of background matching by morphs, I expected to find different predation rates for a variety of pattern-background combinations. Specifically, I expected each morph to match at least one background for which predation of this morph was lower than for other morphs. The species under study, *Norops humilis*, has three morphs in females: vertebral dots, as in males, a vertebral stripe or a series of diamonds. This species is found on the leaf litter and low on trunks (Fitch 1975; Talbot 1979a). Backgrounds for this species can thus consist of leaf litter and stems, and occasionally live leaves. Visibility of a pattern could vary with the diameter of the stem or the height at which an individual perches. Based on idea proposed by Schoener and Schoener (1976), I expected predation for striped morphs to be lowest on thin perches. Considering the pattern in males is the dotted form, and males perch higher than females (Fitch 1975; Talbot 1979a), I expected this pattern to experience less predation on higher perches. Remaining perch sites for the reticulated pattern are thus expected to be leaf litter and low perches with large diameter.

METHODS

Two experiments were carried out at the La Selva Biological Station, Costa Rica (10º26'N, 83º59'W). Several species of anoles are found at La Selva that are polymorphic in female dorsal patterns. The most common polymorphic species are *Norops humilis* (*sensu lato*), *N. limifrons and N. capito* (Guyer and Donnelly 2004). *N. humilis* measures up to 45 mm snout-vent length (SVL), and perches low on trunks and in the leaf litter. *N. limifrons* perches somewhat higher and females grow to 43 mm SVL. The larger *N. capito* measures up to 93 mm SVL and perches on tree trunks at heights similar to *N. limifrons* (Fitch 1973; Fitch 1975; Talbot 1979a). Predators of these anoles include spiders, birds, snakes, lizards and arthropods (Guyer 1988a). Females of the polymorphic anoles at La Selva can have one of three dorsal patterns: a male-like pattern, a reticulated pattern or a vertebral stripe that may vary from cream to brown depending on weather conditions (Steffen, pers. comm.). The male-like pattern consists of vertebral dots (sometimes no dots present) in *N. humilis* and *N. limifrons*. In *N. capito*, the entire dorsum has a lichenous pattern.

Replicas were based on *N. humilis*, but were made slightly larger to allow attachment to perches. Each model measured 50 mm SVL and the tails measured 70 mm, which was still representative of polymorphic species of the study site. Replicas were made from non-hardening, odorless, non-toxic modeling clay (VanAken ^{TM}), and constructed with a self-made mould (SELVA brand silicone rubber HB). The soft clay allowed observation of impressions resulting from predator attacks (Brodie 1993). The brown base color for the models was chosen to match *N. humilis* by human eye. The clay did not reflect UV, but UV radiation from the body has not been found in other species of anoles and was therefore not expected to occur in *N. humilis* (Macedonia et al. 2003). The three different dorsal patterns occurring in *N. humilis* were used in the models (Figure 1). To limit the effect of the amount of cream color on the dorsum, all morphs, including the dotted one, were based on a cream vertebral section. The outline of the reticulated pattern and the vertebral stripe were drawn with a black permanent marker. The same marker was also used for the vertebral dots and for the eyes. All models on perches were placed head down and kept in place by a metal wire through the ventral midsection.

The first study took place from 8 June, 2007 to 26 June, 2007. Clay models were placed on four different substrates that represented habitat elements where the polymorphic anoles were seen: leaf litter, green (live) leaves, stems less than 2 cm diameter, and stems more than 5 cm diameter. All stems were woody, to avoid effects of green versus brown stems. On live leaves and stems, models were placed as close to 60 cm high as possible, because this is the average perch height of adult *N. humilis* (Talbot 1979a). Each pattern-substrate combination consisted of 44 models, for a total of 528. Eleven study plots each contained four replications of each of twelve possible combinations of dorsal pattern and substrate. A random number was assigned to every combination using 'sample(48)' in R Version 2.8.1 (R Development Core Team 2008), which was then used as the order in which the combinations were placed within the plot. Models were placed in six rows. The minimum distance between models was two meters, but this distance increased if the pre-determined perch type was located at a slightly greater distance. Models were checked every third day. Models with predation were removed from the plot and damaged models were repaired by smoothing the surface. Because damage from ants increased over time, all models were collected after twelve days.

In July 2007, a follow-up study further investigated predation on models placed on stems that were chosen for perch height and diameter. Models were placed vertically on stems of different diameters and at different heights. The diameter of the stem was lower than 2 cm or thicker than 5 cm. Models were placed at 10 cm or 60 cm from the forest floor. Combinations were randomized and placement depended on the availability of perches as described above. For each of 12 combinations of pattern X diameter X height, 50 replicas were prepared for a total of 600 models. They were placed in plots as described above and left for four days.

Both experiments were carried out in disturbed forest (abandoned plantations, secondary growth). All three common polymorphic species were encountered in this type of habitat. Plots were separated by at least 100 m. Upon collecting the models, they were placed in Ziploc bags and transported to the lab where predation marks were recorded. Only V or U-shaped imprints and small symmetric slits and punctures were scored as predation (Brodie 1993; Saporito et al. 2007; Steffen 2009) (Figure 2). Ant damage was not scored as predation. When multiple predator marks were seen on one individual, a single predation event was scored. Occasionally tails were found to have fallen off of the model onto the ground. Marks on these tails were not included in the analysis. Models that were not retrieved were considered lost. Analyses were run with and without scoring the lost models as predation events.

In the first experiments, absence or presence of predation in the model was compared for the different pattern-background combinations. I used a randomization test of independence with 5000 iterations partitioned per background (McDonald 2009). This test was also used to determine differences in predation at differing heights and on differing diameters for each morph. A similar randomization test was also used to determine differences in predation rate on morphs, independent of the background they were on. All analyses were completed with proc freq in SAS/STAT ® software, Version 9.1.3 for SAS System for Windows.

RESULTS

Perch Substrate

Of 515 retrieved models, 111 (21%) showed signs of predation. Overall, predation was highest on dotted models (resembling males and females), moderate for female-only reticulated morphs, and lowest for female-only striped morphs ($X^2_{(2, N = 515)} = 9.0584$, $P = 0.0108$). For models placed on live leaves, the number of predation events differed significantly between morphs; striped morphs experienced less predation than expected, while the opposite was true for the reticulated morph ($X^2_{(2, N = 129)} = 6.45$, $P = 0.0398$; Figure 3). On stems with a diameter less than two centimeters, the reticulated replica had a lower attack rate and the dotted morph a much higher attack rate than expected ($X^2_{(2, N = 131)} = 8.30$, $P = 0.0158$). Predation in leaf litter was generally very low and did not significantly differ among morphs ($X^2_{(2, N = 123)} = 0.81$, $P = 0.67$). Similarly, no significant difference was found in predator attacks on models placed on stems greater than five centimeters in diameter ($X^2_{(2, N = 132)} = 4.26$, $P = 0.12$). When repeating the analysis with lost models scored as predation, results essentially remained the same (not shown here).

Perch diameter and height

Of 600 models, 593 were retrieved and, of these, 6.7 % showed signs of predation. No difference in predation was found for morphs placed at perches less than two or more than five centimeters diameter (Dotted: $X^2_{(1, N = 196)} = 0.88$, $P = 0.35$; Reticulated: $X^2_{(1, N = 198)} = 0.07$, $P = 0.79$; Striped: $X^2_{(1, N = 199)} = 0.00$, $P = 0.95$; Figure 4). When comparing predation between low and high perches, dotted and reticulated morphs did not differ in predation (Dotted: $X^2_{(1, N =196)} = 0.10$, $P = 0.76$); Reticulated ($X^2_{(1, N = 198)} = 1.73$, $P = 0.19$)). Striped morphs, on the other hand, were predated less on lower than on higher perches ($X^2_{(1, N = 199)} = 4.95$, $P = 0.03$). In this study, predation did not differ between patterns ($X^2_{(1, N = 593)} = 0.66$, $P = 0.72$). Repeating the analysis with lost models did not change the conclusions.

DISCUSSION

The microhabitat hypothesis for maintaining female polymorphism predicts that predation differs based on pattern-background combinations. Hence, survival would be highest for females selecting the background that provides the best concealment for their pattern. The prolonged survival and consequent higher lifetime reproductive output of these females could be sufficient for polymorphism to be maintained. Our study showed that clay replicas of *Norops humilis* differ in the rate of predator attacks based on the substrate they were placed on. The best perches were low stems or green leaves for the striped morph and thin high perches for the reticulated morph. For the dotted morph, none of the perches under study resulted in lower predation compared to the other two morphs.

The first study showed that the reticulated morph had a significant advantage over striped and dotted morphs on thin stems, at least when placed at 60 cm high. When low (10 cm) and high (60 cm) heights were combined in the second study, no effect of diameter was seen on predation rates for the reticulated morph. The striped morph had lower predation than expected on all substrates, but it had the advantage over the other two on green leaves. Although the brown coloration of all morphs stands out against the green background of these leaves, the stripe may function as a disruptive pattern (Cott 1940), rendering it more effective on backgrounds that are in strong contrast with the brown body color (Stevens and Cuthill 2006). *N. humilis*, however, is rarely seen on green leaves. Anoles are known to show a tight association between perch use and morphological characters, such as body size and shape, limb length and number of toe lamellae (Beuttell and Losos 1999; Losos 1990; Williams 1983). Morphology of *N. humilis* may thus not be well-equipped to use live leaves as a perch. For stems, the typical, elevated perch for *N. humilis*, striped morphs were found to experience significantly less predation on low stems, compared to higher perches. Predation on the dotted morph was generally higher than expected. The higher predation rate on the dotted morph in the first study suggests that this pattern may be the least concealing.

In the second study, no such difference was observed, but this could have resulted from the lower predation rate in the second study. Predation in the first study was high compared to the typical predation rate of 5-10% on clay models (Bittner 2003; Husak et al. 2006). This rate was found in studies leaving models in the field between four and seven days and thus the difference in predation rate may be due to the relatively long time period (twelve days) during which models in my first study were in the field. Indeed, predation rate per day was 1.75%, so that four days would result in a 7% predation rate. The second study, in which models were left out for four days, predation rate was 6.7%, and thus consistent with predation rates generally seen in clay model studies.

A higher predation on the dotted morph is surprising, considering it is the typical male pattern and the most common morph in females of *N. humulis* (Chapter 4). Males and females, however, differ in several characteristics and the patterns may affect predation differently on males and females. For example, males may not benefit from a protective pattern, at least not as an adult, because their visibility is increased through displays of their colorful dewlaps (e.g. Fleishman 1991). Males and females may also differ in the shape of their abdomen due to the eggs in the continuously gravid females, and this could lead to different visual effect from the dorsal patterns (Merilaita and Lind 2005). Indeed, a stripe pattern has been shown to reduce predation in gravid females, but not in other females or males in an Australian skink, *Lampropholis delicata* (Forsman and Shine 1995). The clay models in my study did not differ in shape and it would be interesting to test whether a bulging abdomen would reduce predation rates on female-only morphs even further. Alternatively, males may rely more on flight and females on camouflage, for example if movement of females is impeded by the presence of eggs (Bauwens and Thoen 1981; Lailvaux et al. 2003; Lee et al. 1996; but see Schwarzkopf and Shine 1992).

Furthermore, visibility of patterns is affected by movement (Stevens 2007). Thus, the variation in predation on the different morphs in this study is only applicable to motionless individuals. But, dotted morphs are expected to experience higher predation than the other morphs when moving, because the dots provide fixed reference points for predators (Brown 1931a; Brown 1931b). Dots are therefore associated with anti-predator techniques that do not rely on movement, such as remaining motionless or aggressive displays (Brodie 1992). This could explain why male anoles have the dotted pattern; dewlap displays may be used to deter predators (Leal and Rodriguez-Robles 1997). It does not, however, explain why the majority of females is dotted (Chapter 4). Perhaps, the high frequency of dotted females is the result of a dominant allele coding for vertebral dots. In female polymorphic damselflies, the pattern seen in males as well as females was found to be coded by a dominant autosomal allele (Andres and Cordero 1999). Alternatively, dotted females could benefit in other ways; for example a benefit might accrue through increased male attention based on their higher frequency in the population (Cordero 1992; van Gossum et al. 2001).

Females of *N. humilis* spend much time on the leaf litter and predation was low in the leaf litter for all morphs. The lower predation in the leaf litter could be because the different morphs are equally camouflaged in this diverse background. Alternatively, predation on the leaf litter could be lower due to an effect of height on predation rates. Anoles have been shown to experience lower predation at lower perch heights (Steffen 2009). This was confirmed by results of my second study, where all morphs experienced less predation on low versus high perches, although this was only significant for the striped morph. Lower predation on females in the leaf litter could result in relaxed selection on morphs. Because not all female polymorphic anoles frequently roam the leaf litter, this could not explain the occurrence of multiple morphs in those species.

Overall, my results supported the hypothesis of differential predation on morphs based on the background against which they were seen, but findings were not consistent with my predictions, which were based on perch use observations of female morphs in two other species that did not occur at my study site. The question arises if morphs of *N. humilis* at La Selva prefer the perch where they experience less predation.

Figure 1. Clay models. A. From top to bottom: dotted, striped and reticulated pattern. B. Model on leaf litter, C. Model attached to perch.

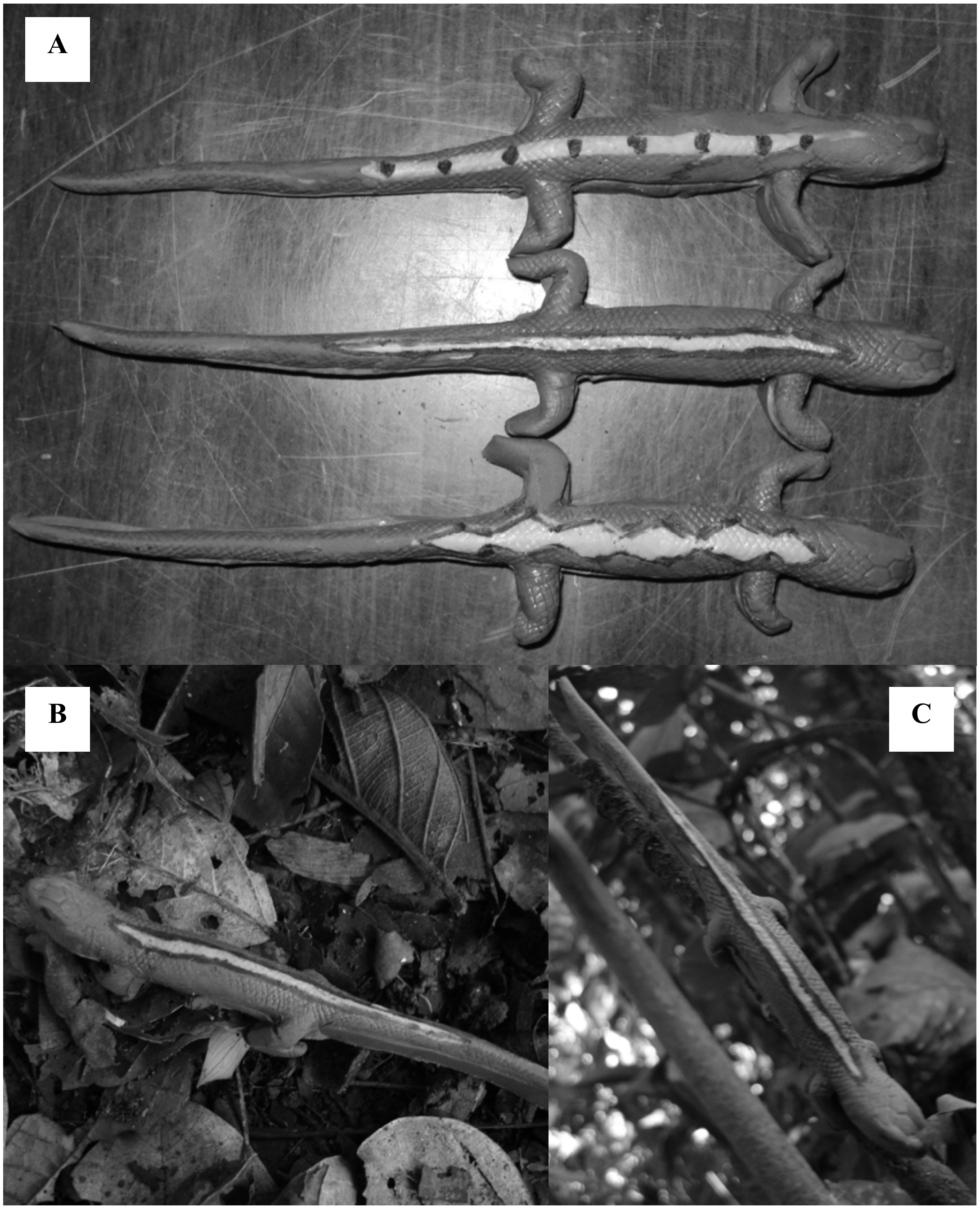
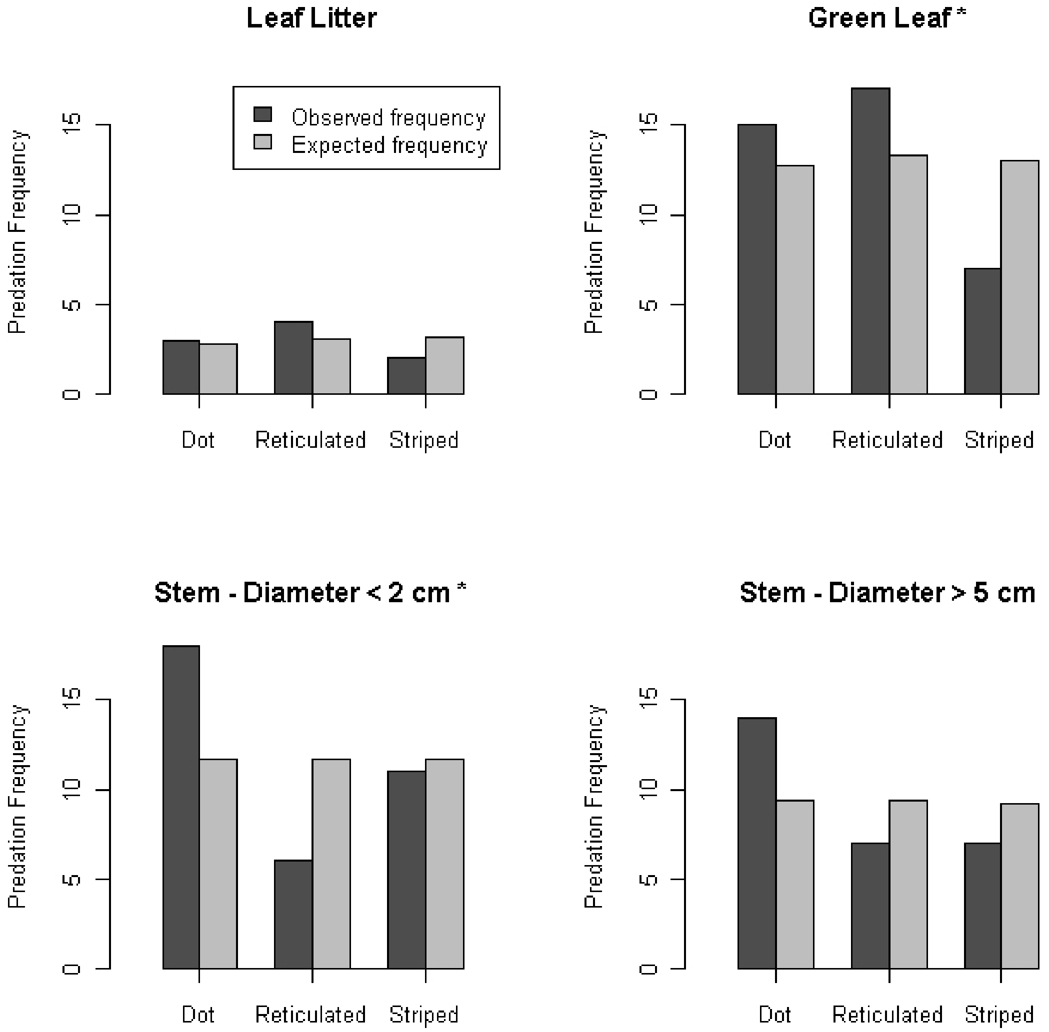


Figure 2. Bite marks categorized as predation.

Figure 3. Predation frequencies for pattern-background combinations from experiment 1. Each background is represented separately. Significant difference at 0.05 level are indicated with a star (*). Both observed and expected frequencies are shown to demonstrate how the patterns differed.



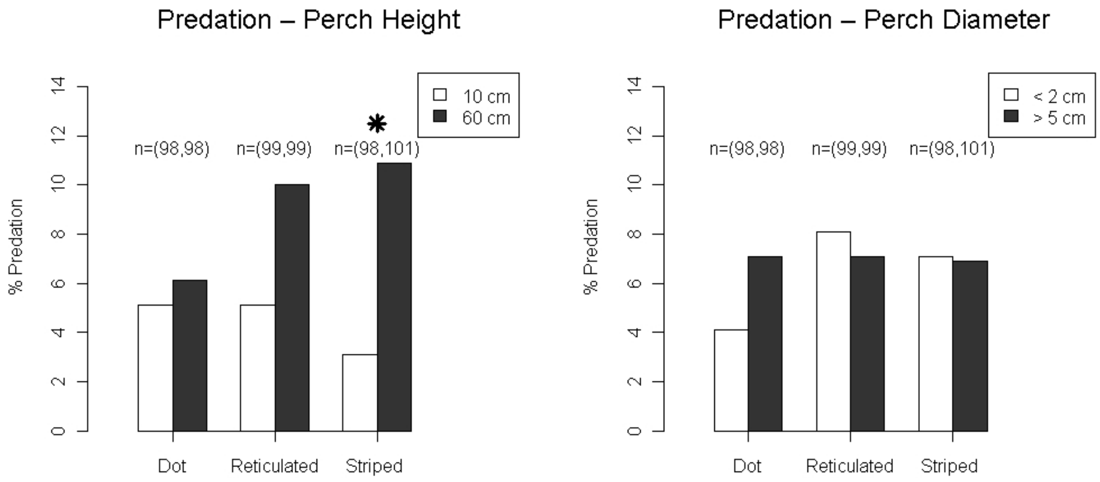
Leaf Litter

Green Leaf *

Stem - Diameter < 2 cm *

Stem - Diameter > 5 cm

Figure 4. Predation for different heights and diameters of woody stems from experiment 2. Significance is indicated by a star (*). Sample sizes are given above the bars.



CHAPTER SIX

FEMALE DORSAL PATTERN POLYMORPHISM IN *NOROPS HUMILIS* (Squamata: Polychrotidae): PERCH USE AND A TEST OF THE MICROHABITAT HYPOTHESIS.

INTRODUCTION

Intra-specific variation provides the evolutionary potential for evolution and speciation (Gray and McKinnon 2007). Research on mechanisms for maintaining intra-specific genetic variation in color and color patterns has led to a better understanding of how evolution proceeds in an environmental context. Classic examples in the study of color pattern polymorphism are *Cepaea* snails and the peppered moth *Biston betularia*, in which color morphs were associated with background matching for predator avoidance and thermoregulation in changing habitats (See Cook 1998; Cook 2003; Jones et al. 1977). They became important examples to elucidate the role of spatially and temporally heterogeneous environments in maintaining polymorphism. Theoretical approaches of how polymorphism can persist in a heterogeneous environment were introduced by Levene (1953). Elaborations on his work demonstrated that particularly spatial variation plays an important role in the maintenance of genetic polymorphism (Reviewed by Hedrick 1986; Hedrick et al. 1976).

Polymorphism under spatial variation is often related to cryptic color polymorphism, where alternative morphs choose specific microhabitats to reduce visibility to predators (e.g., Garciadorado 1986; Kettlewell and Conn 1977; Morey 1990; Sandoval 1994). Because microhabitat choice as well as predation risk may differ between males and females (Pocklington and Dill 1995; Slatkin 1984), the occurrence of multiple morphs may be restricted to one gender (Forsman and Shine 1995; Lynch et al. 1985; Merilaita and Jormalainen 1997). The microhabitat hypothesis for the maintenance of polymorphism in only one gender states that the polymorphic gender chooses backgrounds that optimize concealment of their color pattern, while the other gender may be using a smaller range of micro-habitats, thus restricting their options for concealing patterns (Stamps and Gon 1983).

In anoles (Squamata: Polychrotidae), a group of Neotropical lizards, females of many species vary in dorsal patterns, especially among mainland species (e.g., Fitch 1975; Chapter 2; Schoener and Schoener 1976). Most anoles are colored in variations of brown or green, with some blue in a few species. Dorsal patterns can consist of transverse bands, multiple longitudinal lines, indistinct patterns such as vermiculations or a lichenous pattern, or uniform coloration without any clear pattern. In addition, these dorsal color patterns may or may not incorporate one of the following middorsal patterns: blotches, a cream-to-orange-colored stripe with or without dark outlining, reticulated or diamond shapes or black X shapes resulting in a diamond-like pattern, or a herringbone pattern (Savage 2002; Chapter 3). These middorsal patterns consist of the same drab colors that are seen on the rest of their body. All middorsal patterns consist of similar colors. The middorsal stripe and the diamond pattern are often formed by a cream-colored tint of brown that is paler compared to dominant tints on the rest of the body.

The dorsal patterns have been shown to be heritable in one female polymorphic species, *Norops sagrei* (Calsbeek et al. 2008). Patterns are already clearly expressed in hatchlings, and are maintained throughout life. Females may be ‘andromorph’ (i.e. male-like), and an additional one or two ‘gynomorph’ (i.e. only in females) patterns occur (Fitch 1975; Guyer 1988a). Moreover, very similar patterns are recognized across species with roughly five categories of middorsal patterns and generally two or three varieties per population (Savage 2002). These five female middorsal patterns are mostly variations of the middorsal stripe and the diamond-like patterns described above. Overall, females differ only in dorsal pattern and not in color, as is more common in other species with female-limited color pattern polymorphism. The drab coloration of the patterns in female polymorphic anoles hints at the possibility for a link between the dorsal patterns and predator avoidance (Endler 1978). Furthermore, female polymorphism is most common among species that use trunks as one of their main perch sites (Chapter 3), indicating that perching behavior may play an important role in the maintenance of FPP. Indeed, relationships between morph and perch use have been found in one island and one mainland anole species (Schoener and Schoener 1976; Steffen 2010). The occurrence of spatial variation in predation based on combinations of pattern and perch characteristics was demonstrated with a study using clay models representing *Norops humilis* (Chapter 5). Studying perch use of this species in the same environment would provide more conclusive results regarding the role of predation and micro-habitat use in female polymorphism.

We investigated the microhabitat hypothesis of Stamps and Gon (1983) as an explanation for the maintenance of female polymorphism in a mainland anole, *Norops* *humilis*. This hypothesis predicts that females should perch at different heights. Specifically, we predicted that striped morphs would perch lower than reticulated morphs based on the differences in predation experienced by these morphs (Chapter 5). In relation to the limitation of polymorphism to females, the micro-habitat hypothesis states that females should use a wider spectrum of microhabitats than males. Hence, we expected to see greater variability of perch heights in females compared to males.

METHODS

Study organism

Norops humilis (Peters 1863, *sensu lato*) occurs throughout the lowlands of Panamá and Costa Rica. *N. humilis* perches low on trunks and on the ground. Juveniles roam the forest floor, while adults perch up to 200 cm high on stems (Fitch 1975; Talbot 1979b). Males and females are reproductive year round (Fitch 1973; Guyer 1986). The adult sex ratio is slightly male biased, and varies throughout the year (Guyer 1988a). Adulthood is thought to be reached around four to six months of age, when males have reached a snout-vent-length (SVL) of ca. 29 mm and females measure ca. 32 mm (Fitch 1970; Fitch 1973; Guyer 1986; Talbot 1979b). Individuals of *N. humilis* are thought to live up to one year.

Data collection

We used data from two separate studies of *N. humilis* at the La Selva Biological station in Costa Rica (10°26'N, 83°59'W). The first study was carried out in 1982-1983, the second one in 2007. Both studies observed individuals of *N. humilis* in abandoned plantations (cacao, pejibaye, laurel). At La Selva, female *N. humilis* exhibit three morphs within the population: a dotted andromorph, and striped and reticulated gynomorph patterns.

The 1982-1983 study consisted of capture-recapture data on six plots, of which three were supplemented with food for a different study (Guyer 1988a; Guyer 1988b). Only individuals from the three non-food-supplemented plots in this dataset were included. Individuals in this study were toe-clipped for identification. At each capture occasion, SVL, tail condition, perch height, perch substrate, perch location, gender (when possible), age category (juvenile/adult) and dorsal pattern were recorded. Individuals with missing data were omitted. In the 2007 study, six plots were surveyed three times over the course of three weeks in May. Individuals were not marked. The same variables were recorded as in the first study.

Data analysis

Data were analyzed with the software package R Version 2.8.1 (R Development Core Team 2008). Perch height data were not normally distributed for either dataset, mainly due to the long tail caused by the many leaf litter observations. Therefore, we used a Kruskal-Wallis rank sum test for the perch data from the 2007 study in which individuals were not marked and observations were assumed to be independent. In the 1982-1983 study, perch height of each (marked) individual was recorded at every observation and not all individuals were seen an equal number of times. Therefore, observations were not independent and could not be averaged over the number of observations. To account for varying numbers of repeated measurements per individual, this dataset was analyzed with generalized estimating equations (GEE) in the R-package 'geepack' (Yan 2002; Yan and Fine 2004). In GEE, distribution type is not a major influence and varying the distribution between normal and Poisson did not lead to different results. Results shown are for the Poisson distribution. For model selection, the Wald test was used (Zuur et al. 2009). The full model accounted for all possible variation and included the variables pattern, age, plot and gender, plus all interactions among these variables with the exception of the gender-pattern interaction. This interaction was irrelevant considering males only have one pattern (Table 1). Data were sorted based on date of observation per individual. The “exchangeable” correlation structure was used because there was no temporal factor; the correlation structure would be caused by individual perch height preference (Hardin and Hilbe 2003). To determine variation in microhabitat use for males and females, we applied a Levene test to perch heights to test whether deviations from the mean were larger for males than for females. The Levene test was carried out in the package ‘car’ (Fox 2009). Next, we tested for a difference in elevated perch use. Many of the observations on *N. humilis* were on the leaf litter. These observations were removed from the larger 1982-1983 dataset, and analyses of perch height differences between morphs and perch height variance for males and females were repeated.

RESULTS

Perch height with leaf litter observations

Perch height analysis from the 1982-1983 study showed that perch height was determined by age, gender, plot and the interaction between gender and plot and between gender and age (Table 1). Pattern or interactions with pattern were not significant. The estimated correlation parameter indicating individual preference for perch heights was low (alpha = 0.0858, S.E. = 0.0172). Perch height averages are shown in Table 2. Juveniles tended to perch lower than adults and males perched consistently higher than females in both juveniles and adults (Table 2). The 2007 study showed very similar results. Perch height of adult females did not differ significantly among morphs ($X^2_{(df=2)}$ = 3.534, N = 27, P = 0.172), but adult females perched lower than adult males ($X^2_{(df=1)}$ = 10.3, N = 60, P = 0.0013). Perch height also differed between adults and juveniles ($X^2_{(df=1)}$ = 12.6, N = 90, P < 0.001).

Next, we tested for a difference in variance in perch height between males and females to determine whether females showed a higher variability in perch height than males. In the 1982-1983 study the maximum recorded perch height for males was 200 cm, for females 130 cm. For female adults, much variation was seen among the three plots. Variation in average perch height for juvenile females appeared much lower. The Levene test for homogeneity of variance showed that male and female adults differed significantly in variance of perch height in this study ($F_{(1,1182)}$ = 48.903, P < 0.0001, $S.D._{males}$ = 29.6 cm, $S.D._{females}$ = 20.1 cm). Maximum recorded perch height for adult males and female in the 2007 study was 81 cm and 70 cm, respectively. No difference in perch height variance was found between males and females in this more limited sample of observations ($F_{(1,58)}$ = 1.98, P = 0.164, $S.D._{males}$ = 21.9 cm, $S.D._{females}$ = 18.4 cm).

Perch height without leaf litter observations

Juveniles as well as adults were often observed on the forest floor. In the 1982-1983 dataset, 70.8% and 64.3% of observations of juvenile females and males, respectively, were from the leaf litter. For adult females, leaf litter observations constituted 67.7% of the total, while for males this was only 45.8%. Observation of female morphs on the forest floor were very similar: 69%, 68% and 64% for dotted, reticulated and striped females, respectively. The analysis was repeated on a dataset without these leaf litter observations.

We found pattern, gender, age and plot as well as most interactions between these variables to explain perch height (Table 3). Although juveniles spent more time on the forest floor than adults, removal of these observations still led to lower perch height of juveniles compared to adults ($P_{age} < 0.0001$; Table 4). Males were found to sit higher on elevated perches than females ($P_{gender} < 0.0001$). For the three female morphs, perch height was variable among plots. Striped females were found to perch higher than dotted or reticulated females in all plots ($P_{pattern} = 0.0002$). Dotted females perched lower than reticulated females, except in the plot with only one reticulated female on an elevated perch. Variance in perch height of adult males and females on elevated perches alone did not differ significantly ($F_{(1,550)} = 1.42$, $P = 0.235$, $S.D._{males} = 31.0$ cm, $S.D._{females} = 25.5$ cm)

DISCUSSION

In heterogeneous habitats, dorsal patterns might be optimized to match a variety of patches within the habitat (Merilaita et al. 2001; Merilaita et al. 1999), or they might be optimized for a specific background, so that multiple morphs co-exist in a population (Edmunds 1974; Endler 1978; Endler 1980). In the latter case, individuals are expected to select micro-habitat patches that best fit their pattern to achieve concealment from predators (Edmunds 1974; Endler 1978; Endler 1984; Sandoval 1994). If males are more restricted in micro-habitat use than females are and dorsal patterns are related to micro-habitat use, then polymorphism should be more likely to evolve in females. This forms the micro-habitat hypothesis for the maintenance of female polymorphism (Stamps and Gon 1983).

We tested the micro-habitat hypothesis for *Norops humilis*, a low perching anole of Central America. We expected the three morphs observed in females to differ in perch height. Moreover, males were expected to use a narrower range of perch heights than females. We did not find a difference in perch height between female morphs when including leaf litter observations in perch use. In our analysis of elevated perches only, we found a significant difference in perch height among morphs. There were also interaction effects of pattern with grid and with age. All juvenile females appeared to perch at similar heights, regardless of pattern. Within adults, dotted females perched lowest and striped females consistently perched higher, on average, than the other two morphs. In another female polymorphic mainland anole, *N. polylepis*, striped females were also found to perch higher than other morphs (Steffen 2010). The finding that striped females perch higher than other morphs contradicts our prediction that striped females should be perching lower than the other two morphs to reduce predation (Chapter 5).

The vertebral stripe is a common female morph in many of the female polymorphic anoles is a cream-colored vertebral stripe, sometimes bordered by black (Savage 2002). This pattern may be beneficial to conceal females from predators as a disruptive pattern (Cott 1940). Perch diameter could therefore be an important factor in concealment, but a relationship between the presence of a vertebral stripe and perch diameter has found support in only one study on female polymorphic anoles and not in others (Schoener and Schoener 1976; See also Calsbeek et al., 2008; Steffen, 2010). In addition, a study of predation on female morphs at our study site found differences in predation rate based on perch height but not diameter (Chapter 5). Perch height is thus appropriate to test the microhabitat hypothesis and our results thus suggest that the this hypothesis may not explain the occurrence of multiple morphs in females of *N. humilis* at La Selva.

This conclusion is further supported by the great variation in perch use. Data in the 1982-1983 study indicated overdispersion, caused by large variation in perch height use. This could be expected if perch heights were random, because without restrictions to perch use, individuals are expected to move over the entire range of possible heights. In addition, perch height distribution was zero-inflated due to the large number of observations of individuals on the forest floor. Because possible perch heights for *N. humilis* range from 0 to about 200 cm high, and because more surface area is available on the leaf litter than on perches, the null-model predicts such a skew in perch height distribution. Furthermore, no individual preference for perch height was detected (very low alpha value in GEE). Also within morphs perch height was highly variable, even if leaf litter observations were not considered (Table 4). The high variation in perch use, the rather small differences in average perch heights between morphs and low individual perch height preference lead us to think that any perch height differences observed between females are unlikely related to concealment from predators. These results thus refute the micro-habitat hypothesis.

Stamps and Gon (1983) stated that the micro-habitat hypothesis can be refuted if males vary more in habitat use than females. Although our data showed that variance in perch height is indeed higher for males than for females of *N. humilis*, this need not be a prediction of the microhabitat hypothesis. Males and females often differ behaviorally and morphologically, and the lack of polymorphism in male dorsal patterns could be attributed to these differences. For example, an experiment in a scincid lizard showed that the striped female-only pattern did not increase male survival, but it increased survival of gravid females (Forsman and Shine 1995), leading the authors to suggest that body shape differences may affect visibility of the pattern to predators. Alternatively, female mate choice could limit variation in males, as is seen in female polymorphic butterflies (Krebs and West 1988).

In spite of the great variation in perch use, we found that males perched higher than females, and adults perched higher than juveniles. Similar patterns have been found for a variety of low perching species, including *N. humilis* (Fitch 1975; Talbot 1979b). Males and females have been shown to be adapted to different microhabitats (Butler 2007; Butler and Losos 2002), which could be attributed to differing resource needs. Males may perch higher to focus more on females as a resource, while females may focus more on food acquisition for reproduction (Andrews 1971; Davies 1991; Fitch 1975; Guyer 1988b; Guyer 1994; Parmelee and Guyer 1995; Perry 1996; Scott et al. 1976; Talbot 1979b). Resource access could also explain the lower perch height of juveniles. Availability of prey of suitable size for juveniles may be higher near the leaf litter. At the same time, juveniles still need to establish their home range and territory, and are confined mostly to the forest floor until they are large enough to do so. Perch height difference between morphs were much smaller than between the age and gender groups, and there is no clearly emerging relationship with resource use.

Inconspicuous color patterns are often related to predator avoidance (Endler 1978; Merilaita and Jormalainen 1997). The multiple dorsal patterns in female anoles were thus expected to be the result of morph-specific predation. More specifically, we expected morphs to choose microhabitats that would lower their chance of predation. Although we found a slight difference in perch height between morphs, these results were not consistent with predator avoidance. Another predator driven mechanism for maintaining polymorphism is negative frequency dependent predation, where the predator continues to switch his search image to the most common morph (Allen 1988; Ayala and Campbell 1974). The constancy of morph frequencies and similar survival rates of the female morphs in the juvenile, as well as in the adult stage, however, refute this alternative predator-based hypothesis (Chapter 4). We can thus conclude that multiple dorsal patterns in a population of *Norops humilis* are not maintained by predation, at least not by predation alone.

Figure 1. Female morphs occurring in *Norops humilis* in the population of La Selva Biological Station, Costa Rica. A. The andromorph dotted pattern, B. the gynomorph reticulated or diamond pattern, C. the gynomorph striped pattern.

Table 1. Model selection steps. Starting with the full model, one term (and any interactions including this term) was dropped. A Wald test was used to compare the models. A new model was then built with all terms except for the least significant one and the process was repeated until all terms were significant ('Final Model'). The process was repeated once more to ensure that all terms were significant. The degrees of freedom (Df), Chi Square value from the Wald test (X2) and P-levels from the Wald test are provided. The estimated scale parameter (Est. Scale Par.) and estimated correlation parameter (Est. Corr. Par.) are provided.

Full Model:	Perch ~ Pattern * Age * Plot + Gender:Age + Gender:Plot + Gender+Gender:Age:Plot					
Least significant term dropped:	**Df**	**X^2**	**P**			
Age:Gender:Grid	2	1.3914	0.4987			
Age:Pattern:Grid	4	9.1900	0.0565			
Age:Pattern	2	1.1246	0.5699			
Age:Plot	2	2.4307	0.2966			
Pattern:Plot	4	5.7495	0.2187			
Pattern	2	4.4468	0.1082			
Final Model:	Perch~Age+Plot+Gender+Gender:Plot+Gender:Age+Gender:Plot					
Age	2	31.179	<0.0001		Estimate	S.E.
Plot	4	26.618	<0.0001	Est. Scale Par.	34.31	1.956
Gender	4	43.898	<0.0001	Est. Corr. Par.	0.0858	0.01716
Gender:Age	3	13.8577	0.0031	Number of clusters: 499		
Gender:Plot	2	12.6217	0.0018			

Table 2. Average perch heights. Perch heights were first averaged per individual, then per category. A. Results from the 1982-1983 study per grid. Heights (in centimeters) are provided for each of the categories (grid, age, and pattern). B. Results from the 2007 study. Andro: the male pattern, Stripe: the middorsal stripe in females, Retic: the reticulated middorsal pattern in females. Standard deviation (S.D.) and sample size (n) are provided below the mean values.

Perch Height (cm)	Gender/ Age:		Female Juvenile			Female Adult			Male Juvenile	Male Adult
	Grid	Pattern	Andro	Retic	Stripe	Andro	Retic	Stripe	Andro	Andro
A	1	Mean	4.6	17.6	7.0	5.0	16.4	18	19.1	25.8
		S.D.	7.8	27.9	9.9	9.2	20.9	n/a	21.2	27.8
		N	(50)	(12)	(10)	(11)	(6)	(1)	(45)	(53)
	2	Mean	9.6	5.1	4.4	16.3	16.1	14.6	8.3	16.9
		S.D.	22.7	8.7	6.2	25.1	24.2	22	10.6	19.3
		N	(48)	(21)	(20)	(22)	(7)	(11)	(45)	(48)
	3	Mean	5.9	7.2	5.2	8.4	16.1	7.1	8.0	17.1
		S.D.	9.9	7.0	9.5	13.5	21.1	6.7	14.3	19.1
		N	(36)	(13)	(14)	(16)	(3)	(5)	(41)	(43)
B		Mean	6.9	0.6	6	9.5	21.3	11.8	8.89	29.4
		S.D.	6.7	1.5	8.5	6.7	1.5	8.5	11.6 (14)	21.9
		N	(7)	(7)	(2)	(13)	(6)	(8)		(33)

Table 3. Model selection steps without leaf litter data. For further details, see text and Table 1.

Full Model:	Perch ~ Pattern * Age * Plot + Gender:Age + Gender:Plot + Gender+Gender:Age:Plot					
Least significant term dropped:	**Df**	**X2**	**P**			
Age:Gender:Grid	2	2.72	0.2566			
Final Model:						
Age	10	55.4	$2.66.10^{-8}$		Estimate	S.E.
Plot	14	57	$3.84.10^{-7}$	Est. Scale Par.	18.0	1.63
Gender	8	43.3	$7.70.10^{-7}$	Est. Corr. Par.	0.0749	0.0312
Gender:Age	3	8.68	0.0339	Number of clusters: 318		
Age:Pattern:Grid	4	13.0	0.0113			
Age:Pattern	6	19.1	0.0041			
Age:Plot	6	20.3	0.0025			
Pattern:Plot	8	17.83	0.0225			
Pattern	12	37.5	0.0002			
Gender:Plot	2	8.51	0.0142			

Table 4. Average perch heights and standard deviations for 1982-1983 dataset without leaf litter observations.

Perch Height (cm)	Gender/ Age:		Female Juvenile			Female Adult			Male Juvenile	Male Adult
	Grid	Pattern	Andro	Retic	Stripe	Andro	Retic	Stripe	Andro	Andro
		Mean	21.4	26.3	25.7	30.0	20.0	43.3	37.0	46.7
	1	S.D.	12.7	13.6	18.5	31.6	n/a	29.4	26.7	38.1
		N	(51)	(16)	(23)	(7)	(1)	(6)	(97)	(133)
		Mean	23.0	27.3	21.0	27.2	41.2	67.0	23.4	31.2
	2	S.D.	22.0	16.2	12.2	26.1	22.9	38.7	19.1	24.1
		N	(87)	(41)	(31)	(44)	(21)	(5)	(97)	(178)
		Mean	21.1	21.8	24.5	20.9	26.9	30.0	23.5	37.5
	3	S.D.	15.1	14.0	14.7	12.0	22.2	10.0	18.2	29.2
		N	(39)	(11)	(39)	(23)	(8)	(3)	(70)	(123)

SUMMARY AND CONCLUSIONS

The abundance of polymorphism in nature poses an important problem for evolutionary biologists, because theory predicts minimal variation through the evolutionary mechanisms of drift or directional selection (Futuyma 1998). Because color patterns are easily observable, they provide an excellent tool for studying polymorphism. In spite of the large body of research on this topic, female polymorphism has received comparatively little attention and what studies there are focused mostlyon invertebrates. In a brief review on female polymorphism in my introductory chapter, I proposed that anoline lizards are an excellent model system to study female color polymorphism in vertebrates.

Chapter two revealed that female polymorphism has originated independently in several ancestors and in some single species, contrary to the well-studied damselflies where female polymorphism is an ancestral trait (Futuyma 1998; Van Gossum and Mattern 2008). Furthermore, several independent losses were observed. Thus, the study of anoles allows addressing both the origination and maintenance of female polymorphism. These results also provide support for the idea of phylogenetic inheritance of genetic variation (as opposed to inheritance of an individual trait). That is, variation at the population level can persist throughout the speciation process, occurring in both the ancestral and descendent species (Jose et al. 2008). This has implications for future research on female polymorphism in anoles; comparative analyses should incorporate phylogeny to account for phylogenetic signal in this trait (Felsenstein 1985; Freckleton et al. 2002). The pattern of phylogenetic inheritance of female polymorphism only occurred within geographically isolated areas, suggesting that geographic isolation may have been a prerequisite to the pattern of independent origination of female polymorphism in anoles. The Lesser Antilles formed the exception; female polymorphism likely resulted from a female polymorphic ancestor for each of two independent radiations inhabiting these islands, even though the different species inhabit separate islands. I hypothesized that the closer distance of these islands may have prevented loss of variation, but this needs to be tested.

The comparative study in the next chapter indicated that losses of female polymorphism in the norops clade of the mainland were associated with changes in perch use. This association was weaker for other clades, but analyses indicated that female polymorphism was more likely to evolve in species with certain habitat use patterns, particularly trunk perching anoles and species inhabiting a variety of different habitat types. The reason for these associations needs further investigation. An association with habitat was expected under an adaptive hypothesis, because visual signals, such as dorsal patterns, are affected by the light environment (Endler 1993). I addressed one of the possible adaptive hypotheses associated with habitat: female polymorphism is maintained through predation.

Species where female polymorphism of dorsal patterns (FPP) is the result of ancestral evolution, such as *Norops humilis*, are ideal to study maintenance (as opposed to origination) of FPP. In spite of the intuitive appeal to associate the drab and perhaps cryptic dorsal patterns with predation, my study could not support the hypothesis that female polymorphism in *Norops humilis* at La Selva was maintained by predation. The commonly invoked mechanism of frequency dependent predation could maintain polymorphism if predators continuously switch to the most common morphs, so that fitness is inversely related to the frequency of a morph (Ayala and Campbell 1974). Equal survival rates of morphs and similar morph frequencies in space and time refuted the hypothesis of frequency dependent predation in Chapter four. Equal survival rates would be expected, however, under the micro-habitat hypothesis. This theorizes that polymorphism can be maintained if alternative morphs differ in their visibility based on the background they are seen against, and anoles should thus choose perches that minimized predation (Hedrick et al. 1976; Stamps and Gon 1983). However, the differences in perch use I observed contradicted predictions based on predator avoidance determined by a predation study in Chapter five.

Anoles are preyed upon by a variety of predators, undoubtedly resulting in various predation techniques. The effectiveness of camouflage patterns thus depends on the relative importance of visually oriented predators. For *N. humilis*, observations suggested that ctenid spiders may be the most important predator (Guyer 1988a), but predation events by birds may just be more difficult to encounter. Ctenid spiders appear to have great visual capabilities including color vision and shape detection (Barth et al. 1993; Land and Barth 1992; Schmid 1998; Walla et al. 2009), although their ability to distinguish between dorsal patterns remains unclear. Drab dorsal color patterns may in fact counter selection pressure from predators, but without contributing to the maintenance of female color polymorphism. In other words, polymorphism might be influenced by other selection pressures, while predation itself simply ensures that all patterns will be drab.

Female color patterns could thus be a compromise between camouflage and another function (Endler 1978; Endler 1980; Merilaita et al. 2001). Besides serving as a predator avoidance mechanism, color patterns may function in thermoregulation and as a signal in communication such as attracting mates (Cott 1940; Endler 1978). Thermoregulation seems unlikely, because *N. humilis* is a thermo-conformer (i.e. no behavioral regulation of temperature) (Fitch 1973; Fitch 1975). A function in attracting mates seems unlikely given that females can probably store sperm (Fox 1963; Jeffrey and David 1980; Sever and Hamlett 2002), and thus limiting the need of acquiring multiple matings. Although the presence of eggs has not been investigated in relation to dorsal pattern, adult females are almost invariably found gravid (Fitch 1973; Guyer 1986). Genetic diversity of offspring increases with matings in anoles (Calsbeek et al. 2007), and attracting mates could therefore increase reproductive success through sperm competition, for example through increased genetic diversity of offspring (Jennions and Petrie 2000; Keller and Reeve 1995). But, there is little evidence for mate choice in anoles (Andrews 1985; Tokarz 1995; Tokarz 1998), and with the colorful dewlap displays of males, females rather than males are expected to choose (Stamps 1983; West-Eberhard 1983). This is further supported by a male-skewed adult sex-ratio in the population of *N. humilis* in this study (Guyer 1988a; Guyer 1994; Kvarnemo and Ahnesjo 1996). Alternative selective hypotheses for the maintenance of female polymorphism in anoles thus seem difficult to generate. Some similarities between female polymorphic species and differences between morphs could guide future research.

The comparative study of Chapter three showed that evolution of female polymorphism was associated with habitat use, in particular perch use. An association with perch use was further supported by the differences in perch use between female morphs in a population study of *N. humilis* addressed in Chapter six. Females differed slightly, but significantly in the use of elevated perches, with adult striped females perching highest and dotted females perching lowest in all plots. This finding was consistent with findings in another female polymorphic mainland anole (Steffen 2010). Differences in perch height in anoles are often ascribed to differing resource needs or competition (e.g. Andrews 1971; Lister 1976; Rummel and Roughgarden 1985; Schoener 1975; Schoener and Gorman 1968; Scott et al. 1976). The differences found between morphs in *N. humilis* were small, but consistent. If this is the result of competition between females, it is not clear what the females are competing for.

Furthermore, the difference in predation on morphs based on the background they are seen against (Chapter 5) combined with similar survival rates (Chapter 4) suggests the morphs may trade-off between predation and another aspect of survival, such as parasitism (Losey et al. 1997). Indeed, in another female polymorphic anole, density-dependent differences in immuno-competence were found between morphs (Calsbeek et al. 2008). Alternatively, morph frequencies may have reached equilibrium (Bond and Kamil 1998). Moreover, females with multiple mating produce genetically diverse offspring for which the combined genetic diversity approaches population variation (Calsbeek et al. 2007). Hence, maintenance of female morphs may not require strong selective pressures, and any selection acting on the morphs that contributes to their maintenance may prove difficult to detect. Before continuing research on possible selective pressures involved in maintaining female polymorphism in anoles, a worthwhile endeavor would be to develop theoretical models incorporating anole biology that allow exploring the relative role of neutral and selective processes.

In conclusion, several interesting patterns were revealed regarding the occurrence of female polymorphism in anoles. The geographic distribution of this trait, along with its association with habitat use deserves further investigation. Perch use differences between morphs appeared consistent, even when compared among species, and this may hold a clue to the processes involved in maintaining the morphs. The most striking pattern, however, was the constancy of frequencies of morphs over four sample periods in nearly thirty years. Because random processes are expected to lead to the extinction of at least one morph (Futuyma 1998), especially considering the low frequencies of the gynomorph patterns, selective pressures can be expected to re-establish the balance. Experimental manipulation of morph frequencies is therefore recommended. Further research could potentially have a wide-ranging impact on our ideas about the evolution of color pattern polymorphism, because drab color patterns as seen in female anoles are generally assumed to have evolved in response to predation. After testing the two predator-based mechanisms that could maintain polymorphism, however, I found no support that the three alternative morphs in females of *N. humilis* are maintained by predation. Until morph frequencies are manipulated, however, we should consider the possibility that predator effects may have remained undetectable.

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