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UNIVERSITY OF MIAMI

INTRALOCUS SEXUAL CONFLICT, ONTOGENETIC CONFLICT AND COLOR EVOLUTION IN THE IBIZA WALL LIZARD, PODARCIS PITYUSENSIS

By

Nathan B. Dappen

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Selection on the same trait may differ between the sexes and among age groups as a result of sex- and age-specific strategies in reproduction and survival. Antagonistic selective pressures on traits shared between the sexes can lead to intralocus sexual conflict, which occurs when selection favors the expression of particular alleles in one sex, but disfavors the expression of those same alleles in the opposite sex. Similarly, antagonistic selection on traits shared among age groups, can lead to intralocus ontogenetic conflict, which occurs when selection favors the expression of particular alleles in one age group, but disfavors the expression of those same alleles in another age-group. These two forms of conflict may result in individuals that deviate from their unique, sex- and age-specific optimal phenotypes. Display characters such as conspicuous coloration, may provide a prime example of this conflict because, while the reproductive benefits of expressing these traits are usually only realized by one sex (usually males) and at reproductive maturity, many of the costs of expressing these traits occur in both sexes and at all ages. Further, females and juvenile males share all, or at least most of the autosomal genes responsible for male-typical secondary sex traits. As a result, sexual selection on these traits in males can cause a correlated response on the

homologous trait in females and juvenile males, affecting a wide variety of evolutionary process.

In the context of intralocus sexual and ontogenetic conflict, this dissertation investigated the evolution of a display character (conspicuous coloration) between the sexes and among age groups of the Ibiza wall lizard, *Podarcis pityusensis*, a lacertid lizard species that exhibits striking color variation across its geographic range. Male *P. pityusensis* are generally more conspicuously colored than females, but color varies dramatically both within and between the sexes. Further, conspicuous color changes ontogenetically in this species. Juveniles in most populations are cryptically colored, but as they age and grow in size, color increases on their body in both saturation and coverage area. Variation in the degree of sexual dichromatism and ontogenetic color change observed within and among populations of *P. pityusensis* makes this species ideal for investigations on the evolution of color between the sexes and among age groups.

I investigated three issues regarding color evolution in *P. pityusensis*. First, I investigated the functional significance of color expression in males and females. I found that conspicuous color may be used by males as an honest signal of fighting ability in male-male contest competition. I was unable to identify a functional role for male-typical color expression in females, supporting the hypothesis that females express male-typical color due to an intersexual genetic correlation. Second, I set out to determine the role of predation in the evolution of color. I found that predators attack conspicuously color clay lizard replicas more than cryptic models suggesting that conspicuously color lizards may also be subjected to increased predation. The results from these first two experiments suggest that color may be subject to sexually antagonistic selection—it is favored in males by sexual selection, plays no role in females, and is disfavored in both sexes by predation. Lastly, I attempted to elucidate the adaptive significance of ontogenetic color change in this species. I found that adult and juvenile lizards occur in different habitats where these two age classes may be subjected to unique selective pressures that could influence the evolution of ontogenetic color change. It appears that juveniles and smaller adult males are forced out of high quality vegetated habitats into open habitats by aggressive males and cannibalistic adults. In this open habitat, the costs of being colorful may be greater due to increased conspicuousness to both cannibalistic lizards and avian predators. In summary conspicuous color may be subjected to a variety of selective pressures that differ between the sexes and among age groups of *P. pityusensis*. Research on the heritable basis of color expression is needed to determine whether these antagonistic selective pressures could drive intralocus sexual conflict and intralocus ontogenetic conflict over color expression.

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TABLE OF CONTENTS

LIST OF FIGURES

Page

CHAPTER 2

CHAPTER 3

CHAPTER 4

Chapter 1

Introduction

Natural and Sexual Selection

Darwin's theory of evolution by natural selection (1859) provided a mechanistic explanation for the existence of most phenotypic traits observed in living species. However, Darwin recognized that natural selection alone was inadequate to explain differences in shape, color, size, and behavior between sexes of the same species. Some sexually dimorphic traits, including conspicuous coloration, seemed maladaptive. The theory of sexual selection was put forth to explain these traits (Darwin 1859; 1871). Sexual selection, Darwin suggested, arises from variation in reproductive success due to competition for mates (Andersson 1994). This competition, Darwin observed, occurred more commonly among males rather than females, and accordingly, males more frequently express secondary sexual characters when compared to females throughout the animal world. Sexual selection is now considered to be another form of natural selection; however, because the evolutionary dynamics and outcome of sexual selection frequently differ markedly from other components of natural selection, the distinction between sexual and natural selection can be convenient (Endler 1986), particularly when discussing the evolution of weaponry or display characters.

The path with which these weapons or displays evolve depends greatly on the way that one sex competes for access to the other sex. In the context of sexual selection, competition broadly refers to the mechanisms by which one sex (generally males) competes, either directly or indirectly, for mating access to the other sex (usually females) (Andersson 1994). In general, sexual selection manifests itself broadly in two ways: intrasexual selection and intersexual selection. Intrasexual selection takes place when individuals of the same sex compete directly for access to mates, and can result in secondary sexual characters such as weaponry for battle, great physical endurance, increased size or aggressive display characters. In contrast, intersexual selection refers to indirect competition for mates through mate choice (Andersson 1994). Intersexual selection may result in showy colors or displays, complex songs or exaggerated ornaments. These two forms of competition may overlap, such that the weaponry or display characters reflect both intra- and intersexual selection.

Many times, ornaments, signals or behaviors evolve in opposition to other forms of natural selection. For example, male tungara frogs, *Physalaemus pustulas,* add chucks to a whine call that make them more attractive to females, despite the fact that fringe-lipped bats, *Trachops cirrhosus,* a major predator of the tungara frog (Rand and Ryan 1981; Tuttle and Ryan 1981), are more attracted to frogs that add chucks to their whine calls (Ryan et al. 1982). Likewise, conspicuous colors are often thought to represent a compromise between mate acquisition and the avoidance of detection by predators and prey. For example, conspicuously colored sticklebacks and guppies attain the highest mating success, yet their predators, trout and prawns, respectively, can find conspicuously colorful individuals more easily than cryptic individuals (Endler 1980; Zuk and Kolluru 1998). Similarly, male damselflies, *Hetaerina americana,* have large red spots at the base of each wing that function as honest signals of male-male fighting ability. The brightest males secure the highest mating success; yet these males also suffer reduced foraging efficiency because they are more conspicuous to their prey (Grether 1996; 1997; Grether and Grey 1996). As such, observed secondary sexual characters across taxa are often the results of sexual selection balanced by viability selection.

Intralocus Sexual Conflict

Darwin (Darwin 1871) was the first to describe how sex-specific selective pressures may operate differently on males and females due to their unique roles in reproduction and ecology. These divergent selective pressures can result in sexual conflict, which occurs when males and females have conflicting optimal fitness strategies (Arnqvist and Rowe 2005). In sexual conflict theory, sexually antagonistic selection can take two forms: interlocus sexual conflict and intralocus sexual conflict. In interlocus sexual conflict, alleles at one locus in males have conflicting interests with alleles that are at a different locus in females. This form of sexual conflict may result in an evolutionary arms race that produces such things as spiny genitalia and vaginal plugs in males, and females that are choosy and difficult to stimulate or have genital-plug removing mechanisms (Arnqvist and Rowe 2005). Interlocus sexual conflict has been extensively studied for more than a century. Intralocus sexual conflict, on the other hand, has received far less attention.

The theoretical foundations of intralocus sexual conflict were first developed by Fisher (1958), Lande (1980; 1982b; 1987) and Rice (1984). Fisher (1958) explained how divergent selection on a trait shared between the sexes can eventually lead to the accumulation of genes that are expressed differently in males and females. He suggested that most characters are initially expressed equally in males and females. Slowly, those characters diverge in each sex due to sex-specific selective pressures. Later, Lande (1980; 1982b; 1987) created mathematical models describing the evolution of sexual dimorphism by the interaction of sexual selection and other components of natural selection. Similar to what Fisher (1958) described, these models predicted that most sexually selected characters would initially be inherited in both sexes due to a strong intersexual genetic correlation. At first, the mean population value for the trait would change rapidly in the same direction in both sexes. This change would then be followed by an intensification of sexual dimorphism as the intersexual genetic correlation for the trait was gradually broken up by sex-specific natural and sexual selection. This sexually antagonistic selection throughout the transition to sexual dimorphism results in intralocus sexual conflict (Chippindale, et al. 2001; Rice and Chippindale 2001). Intralocus sexual conflict is defined as “the displacement of the sexes from their distinct phenotypic optima as a result of sex-specific selection on sexually homologous traits whose expression is regulated by shared genetic machinery” (Bonduriansky and Chenoweth 2009). Rice (1984) proposed multiple mechanisms by which this conflict may be resolved, ranging from genomic imprinting to sex-linked modifiers. Most of these mechanisms result in the evolution of sexual dimorphism.

Intralocus sexual conflict represents a unique evolutionary problem for sexual organisms. This problem is that males and females share an autosomal genome, yet the sexes themselves are defined by their divergent reproductive strategies (Clutton-Brock 2007) which result in sex-specific selection on many shared traits. Because most shared traits are assumed to be controlled by the same genetic machinery (Andersson 1994; Bonduriansky 2007; Bonduriansky and Chenoweth 2009; Chenoweth et al. 2008; Lande 1980; Rice 1984), intralocus sexual conflict arises when selection favors a trait in males, yet selects against that trait in females, and vice versa. Conspicuous ornaments, weaponry or displays may provide a prime example of this conflict because these traits are often subject to sexual selection in one sex (usually males), but not the other (usually females). Since most secondary sexual characters are controlled by much of the same genetic machinery in both sexes, sexual selection on these traits in males may cause a correlated response in the homologous trait in females (Bonduriansky 2007). As a result, females inherit all the costs of the secondary sexual trait, with none of the reproductive benefits that the trait offers males (Pischedda and Chippindale 2006). For example, sexual selection that favors the increased size of a trait in males can result in a correlated response in females, ultimately reducing female fitness, whereas viability selection opposing the increased intensity of that trait in females constrains males from reaching their adaptive optimum for that trait (Bonduriansky and Chenoweth 2009).

Intralocus Ontogenetic Conflict

Natural selection often differs among age classes of the same species (Anderson and King 1970; Stamps 1983). These differences in selective pressures are the result of an individual having age-specific interactions with the environment and with other organisms. Variation in selection among age groups may result in antagonistic selection on traits shared among age groups. This antagonistic selection may drive intralocus ontogenetic conflict. Intralocus ontogenetic conflict occurs when selection favors the expression of particular alleles in one age group, but disfavors the expression of those same alleles in another age group (Chippindale et al. 2001; Rice and Chippindale 2001; Sinervo and Calsbeek 2003).

Display characters such as conspicuous color may often be subject to intralocus ontogenetic conflict for many of the same reasons that these traits are often subject to intralocus sexual conflict – the traits often only benefit the reproductive success of adult males. (Folstad and Karter 1992; Sinervo and Calsbeek 2003). Therefore, while the costs of these traits may be outweighed by their reproductive benefits in adult males, display characters may decrease fitness when expressed in pre-reproductive individuals that suffer the costs of these traits with none of the reproductive benefits.

From these two forms of conflict (intralocus sexual/ontogenetic conflict), several major theoretical implications emerge. First, if selection on a shared trait differs between the sexes or among age groups, each sex, and individuals of different age groups cannot evolve to their optimum phenotype because high fitness parents will sire low fitness opposite-sex offspring and because high fitness juveniles may become low fitness adults. Intralocus sexual conflict is thought to drive the evolution of sexual dimorphism while intralocus ontogenetic conflict is thought to drive the evolution of developmental changes in traits subjected to conflict. The mechanisms that result in sex and age specific gene expression could potentially affect many other aspects of an organism’s morphology and physiology (Badyaev 2005; Cox and Calsbeek 2009; Day and Bonduriansky 2004). Further, evolutionary theory holds that genetic variation for traits under strong selection will continually diminish. The presence of high genetic variation for traits that are under strong selection (the “lek paradox”) has always been an evolutionary puzzle (Kirkpatrick and Ryan 1991). Intralocus sexual/ontogenetic conflict may be two mechanisms that maintain genetic variation for traits under strong directional selection (Foerster et al. 2007). Finally, these forms of conflict may provide explanations for observed variation or polymorphisms in both the form and quality of secondary sexual traits across a wide variety of animal taxa (Robinson et al. 2006).

Despite the potentially central roles of intralocus sexual/ontogenetic conflict on a wide variety of species, surprisingly few studies have identified these forms of conflict in natural populations. Therefore, my proposed research intends to identify intralocus sexual conflict and intralocus ontogenetic conflict on a putative display trait (conspicuous color), and to investigate how this conflict has affected the evolution of that trait in a lacertid lizard species, *Podarcis pityusensis*.

Study Organism

The Ibiza wall lizard, *Podarcis pityusensis*, is a diurnal terrestrial lizard that is endemic to the Spanish islands of Ibiza and Formentera and nearby rocky islets (Martinez-Rica and Cirer 1982; Pérez-Mellado 1998). A substantial portion of the larger islands (Ibiza and Formentera) and the majority of the smaller islands are protected by the Conselleria de Medi Ambiente Espais de Natura Balear from the Balearic Government under the title of "Natural Parks." While the Natural Parks on Ibiza and Formentera are open to visitors, most of the smaller islands are home to a host of endemic species, including lizards, and are thus strictly off-limits to tourists.

Podarcis pityusensis is found in high densities in vegetated areas, such as cultivated land and gardens, close to and around human habitats. These lizards also occur abundantly in rocky areas, especially in coastal regions and small islands. Individuals from populations on smaller and older islands tend to be larger, display a greater morphological homogeneity, and express darker dorsal coloring than individuals on larger and younger islands (Cirer and Martinez-Rica 1990; Martinez-Rica and Cirer 1982).

A host of animals prey on *P. pityusensis* including the common barn owl, shrikes, feral cats (Pérez-Mellado 1998), genets (Delibes 1977) and possibly seagulls, and rats

(Dappen Personal Obs.). Some authors have suggested that color variation among populations of *P. pityusensis* may be in part a result of differences in predator regimes among islands (Cirer and Martinez-Rica 1990) and research in other Balearic islands shows variation in predation pressure on lizard species (Cooper and Pérez-Mellado 2004; Pafilis et al. 2008).

Podarcis pityusensis begin their reproductive activity in late March and continue until August (Carretero and Llorente 1995; Salvador 1984; Salvador 1986; Salvador 2006). However, lizard activity begins to decline dramatically by July due to the extreme summer temperatures (Salvador and Pérez-Mellado 1984). Throughout the mating season, the males of many lacertid lizard species set up large overlapping home ranges and perform aggressive ritualistic territorial displays (López et al. 2002). In territorial displays, males raise themselves high up on all four limbs into a threatening posture, before strutting toward their opponent with their neck arched and snout pointed down (López et al. 2002). In many cases males will turn to show their competitor the side of their body, which may be colorful (Olsson 1992; 1994). If this display deters trespassers, the contest may be settled; however, if not, the encounter may escalate to a fight, ending in biting, chasing, and locking jaws (Olsson 1992; Verbeek 1972).

During courtship, on the other hand, a male lacertid lizard slowly approaches a female in a posture similar to the aggressive display (they raise themselves high up on all four limbs into a threatening posture, before slowly strutting toward the female with their neck arched and snout pointed down). Once near the female, a courting male begins to tongue-flick her near her tail, and then gently bites and shakes her tail. The male then bites the female's sides to hold her in place during copulation. Receptive females then allow courting males to mount them whereas nonreceptive females simply run away (López et al. 2002; Verbeek 1972). After copulation, which only lasts 1-4 minutes, some males engage in mate guarding for a period that lasts from hours to days. *Podarcis pityusensis* perform similar ritualistic displays (Dappen personal obs.). After fertilization, females bury 2-4 eggs in sandy or crumbly substrates (Carretero and Llorente 1995). Eggs hatch approximately 50 days after being laid (Carretero 2004). In captivity, females were observed to have up to 6 clutches in a single breeding season (Carretero 1995). Both males and females become reproductively active in their second year of life (Salvador 2006).

Lizard populations occur on at least 42 of the islands and islets in this archipelago and numerous subspecies have been named. Many characteristics vary among populations of *P. pityusensis* including lizards' size, degree of sexual dimorphism, number of femoral pores and lateral scales, and color expression (Martinez-Rica and Cirer 1982; Salvador 1984). This species expresses striking color diversity within and among island populations. Some islands host lizards that are green, whereas others host lizards that are bright blue, sandy brown, or even orange and black (Cirer and Martinez-Rica 1990; Salvador 1984; Salvador 1986). Further, lizard color on some islands is homogeneous with a single color, while on other islands populations may have multiple colors (Dappen, unpublished data). Like most species of lizards in the family Lacertidae, *P. pityusensis* are sexually dichromatic, with males being more conspicuously colored than females. However, color varies greatly within sexes, and the degree to which males and females resemble one another in the same population is highly variable—the sexes are almost indistinguishable on some islands, and are extremely dichromatic on others.

Conspicuous color expression in many lacertid lizards increases in both saturation and coverage area with age and size. Research on species in the same family of lizards suggests that conspicuous coloration may have evolved by sexual selection as an honest signal of competitive ability in male-male interference competition (Anderholm et al. 2004; Olsson 1994). This explanation, however, would not account for why female *P. pityusensis* partially or fully express male-typical color. Additionally, little is known about the factors that influence ontogenetic color changes in *P. pityusensis* or other lizard species. The extreme variation in color expression between the sexes and among age groups of *P. pityusensis* makes this species an excellent system for testing hypotheses related to the evolution of display traits between the sexes and among age groups.

Overall objectives

In the context of intralocus sexual and ontogenetic conflict, my dissertation research investigated the evolution of conspicuous color in *P. pityusensis*. This project had three main objectives: First, I performed a color manipulation experiment in semi-natural field conditions to determine the adaptive significance of color expression in male and female lizards. Second, I performed a clay model predation experiment using different colored plasticine clay lizard replicas to investigate how predation might influence the evolution of color in this species. These first two experiments were designed to help understand the evolution of color in male and female *P. pityusensis*. Lastly, I performed a habitat preference survey, a juvenile capture survey, cannibalism trials, and another clay model predation experiment to identify age-specific habitat settlement patterns and antagonistic selection on color expression among age groups of *P. pityusensis* to help understand ontogenetic color change in this species.

Chapter 2

The evolution of male-typical coloration in female Ibiza wall lizards (*Podarcis pityusensis*)

Summary

Display characters that increase male reproductive success are sometimes partially expressed in conspecific females; in such cases, the adaptive significance of the trait to females is often poorly understood. I conducted a color manipulation experiment in semi-natural field conditions to test the functional significance of conspicuous color expression in male and female Ibiza wall lizards, *Podarcis pityusensis*, a Mediterranean lizard species that expresses striking color variation within and between the sexes. In general, males are more conspicuously colored than females, but female color varies dramatically such that some females are more conspicuously colored than males. Results from this study suggest that, like closely related species in the same family, male *P. pityusensis* express conspicuous color as an honest signal of male fighting ability. In females however, I found no differences in any measurable fitness variable between color-enhanced and control females. These results suggest that females may express this male typical trait due to an intersexual genetic correlation with males rather than because the trait is selectively advantageous to females.

Background

Secondary sexual characters such as weaponry, behavioral displays, or bright coloration generally are more exaggerated and more variable in males (Andersson 1994; Darwin 1859). Consequently, research efforts have focused on how these traits evolve in males. Although females of many species partially express these male-typical characteristics, relatively little effort has been put forth to explain the expression of these male-typical characteristics in females.

Research suggests that secondary sexual characteristics increase male reproductive success in many species (Andersson 1994; Clutton-Brock 2007). For example, male red-winged blackbirds expose their red epaulets during territory defense and courtship, and experimental manipulation of epaulet conspicuousness affects both territory defense and female choice of mate (Yasukawa, et al. 2009). Mating success of male stalk-eyed flies positively correlates with eye-span size (Wilkinson and Reillo 1994). Male monogamous swallows with experimentally elongated tail ornaments obtain mates more quickly than males with shorter tails, have increased reproductive output, and also are preferred by females seeking extra-pair-bond copulations (Møller 1988). Such studies shed light on the evolution of these traits in males, yet females of all these species (and many others) partially express these male-typical ornaments. If these traits influence male reproductive success, why are they also expressed in females?

Over the last two decades, there has been increased interest in the evolution of female ornaments in insects (Watson and Simmons 2010), birds (Amundsen 2000; Amundsen et al. 1997; Griggio et al. 2003; Griggio et al. 2005; Irwin 1994; Komdeur

2005; LeBas and Marshall 2000; Mougeot et al. 2005; Muma and Weatherhead 1989b; Roulin 2004; Roulin et al. 2000), and reptiles (Baird 2004; Hager 2001; LeBas and Marshall 2000; Weiss 2005; Weiss et al. 2009). There are two non-mutually exclusive hypotheses on why females express these male-typical secondary sex traits: 1) females express male-typical traits due to an intersexual genetic correlation with males (*the genetic correlation hypothesis*) or 2) natural or sexual selection favors the expression of these ornaments in both sexes (*the mutual ornamentation hypothesis*).

Previously, most researchers attributed the expression of male-typical ornaments in females to an intersexual genetic correlation in males. This *genetic correlation hypothesis* states that because females share an autosomal genome with males, selection on traits in males may cause a correlated response on the homologous trait in females (Amundsen 2000; Lande 1980; Lande 1987; Lande and Arnold 1983; Muma and Weatherhead 1989a; Muma and Weatherhead 1989b; Rice 1984). Some research on the function of partially expressed male-typical traits in females supports this hypothesis (Cuervo et al. 1996; Muma and Weatherhead 1989b; Price 1996; Watson and Simmons 2010). Several quantitative genetic studies also show that ornamental traits can be genetically correlated between the sexes (Chenoweth and Blows 2003; Møller 1993; Price 1996; Price and Burley 1993; Roulin et al. 2001; Wilkinson 1993). Moreover, a few artificial selection experiments demonstrate that selection on male ornaments can cause a correlated response in the evolution of those ornaments in females (Harrison 1953; Wilkinson 1993).

The *mutual ornamentation hypothesis* proposes that these ornaments are favored in both sexes by natural and/or sexual selection (Amundsen 2000; Huxley 1914;

Johnstone et al. 1996; West-Eberhard 1979). For example, weaponry that helps males compete for access to females may also allow females to defend themselves from predators or to compete with conspecifics for resources (Cooper and Greenberg 1992). Male-typical color expression in females may aid in individual or sex recognition (Balph 1977; Shields 1977; Watt 1986). There also is robust evidence suggesting that male mate-choice for ornamentation in females occurs commonly in birds (Amundsen et al. 1997; Faivre et al. 2001; Jones and Hunter 1993; Kraaijeveld et al. 2004; Monaghan et al. 1996; Mougeot et al. 2005; Saether et al. 2001), fish (Amundsen and Forsgren 2001; Rowland 1989; Rowland et al. 1991; Werner and Lotem 2003; Wong et al. 2004), amphipods (Hua Wen 1993), and insects (Chenoweth and Blows 2003; Shellman-Reeve 1999). In reptiles, the partial expression of male-typical ornamentation in females is common. Nevertheless, mate-choice appears to occur less frequently among reptile species (Olsson and Madsen 1995; Tokarz 1995) and while mutual ornamentation may often be explained in many vertebrates by *the mutual ornamentation hypothesis* (Kraaijeveld et al. 2007), it is currently unclear which of the above hypotheses most commonly explains mutual ornamentation in reptiles.

I investigated the evolution of conspicuous color expression in both male and female Ibiza wall lizards, *Podarcis pityusensis*, a diurnal terrestrial lizard that is endemic to the Pityusic Archipelago in the Balearic Islands of Spain (Martinez-Rica and Cirer 1982; Salvador 1984; Salvador 1986). This species exhibits striking color variation across its geographic range (Figure 2.1). Some islands host lizards that are green, whereas others host lizards that are bright blue, sandy brown, or even orange and black (Cirer and Martinez-Rica 1990; Salvador 1984; Salvador 1986). Like most species of lizards in the family Lacertidae, *P. pityusensis* are sexually dichromatic, with males being more colorful than females. Color varies greatly within sexes, however, and the degree to which males and females resemble one another in the same population is highly variable. Furthermore, color expression changes developmentally with age and size. On most island populations, conspicuous color increases in both saturation and coverage area with snout-vent length and mass, both of which increase with age (Dappen unpublished data).

Research on closely related species in the same family suggests that conspicuous coloration evolved by sexual selection as an honest signal of competitive ability in male-male interference competition (Anderholm et al. 2004; Olsson 1994). This explanation, however, would not account for why female *P. pityusensis* partially or fully express male-typical color. The extreme variation in male and female color expression both within and among populations of *P. pityusensis* makes this species an excellent system for testing hypotheses related to the evolution of display traits in both sexes.

I conducted a color manipulation experiment in semi-natural outdoor enclosures to investigate how conspicuous color influences social interactions in male and female Ibiza wall lizards. This experiment tested the hypothesis that in males, conspicuous color is subject to sexual selection as a signal for male fighting ability in male-male contest competition. This experiment also tested whether male-typical coloration plays a functional signaling role in females (*mutual ornamentation hypothesis*). If conspicuous color is favored in males by sexual selection, yet plays no functional role in females, it's likely that females express this male-typical coloration due to a strong intersexual genetic correlation (*genetic correlation hypothesis)*. If color does play a function role in females, we cannot discount the possibility that color originally evolved due to genetic correlation and that subsequent selection shaped its current function. However, if conspicuous color has no functional role, the genetic correlation hypothesis is the most likely explanation for female expression of male-typical coloration in this species.

Materials and Methods

I performed this experiment using a natural population of lizards living on the island of Formentera (Figure 2.1). I captured 40 adult males and 40 adult females within the Ses Salines Natural Park during the first week of April 2010. Research suggests that reproductive behavior of both sexes may be influenced by female reproductive state (Ruiz et al. 2008). Therefore, lizards were housed individually in terraria for one month prior to the experiment to ensure that no females used in this experiment were pregnant. For each individual, I recorded snout-vent length and mass and sewed a unique combination of colored beads into the base of the tail for field identification (Fisher and Muth 1989).

I quantified color for each lizard using digital photographs in the programs ColourWorker^{TM} (Osorio and Anderson 2007; Stevens et al. 2006) and Adobe Photoshop (Dappen 2011). ColourWorker^{TM} can estimate the spectral reflectance of visible wavelengths (400-700nm) from digital photos. To ensure accurate measurements in ColourWorker^{TM}, I calibrated the program using spectrophotometric measurements taken with a UV-sensitive spectrophotometer (Ocean Optics USB-2000). I measured ten standardized points on captured lizards' backs and sides using the spectrophotometer. Spectrophotometer readings were entered into ColourWorker^{TM} as reference spectra. Points measured using the spectrophotometer did not have appreciable reflectance in the

UV spectrum, which permitted accurate reflectance estimates from photographs in ColourWorker^{TM}. Individuals were then photographed under standardized lighting next to a Macbeth color standard. The color standard in each image allows ColourWorker^{TM} to control for variation in ambient light conditions and exposure. By identifying the range of RGB values (in ColourWorker^{TM}) that correspond to lizard scales that peak in reflectance range in the green and blue wavelength (450 nm - 630 nm), I was able to use Adobe Photoshop to quantify the amount of surface area (in pixels) per lizard that peaks in reflectance in green and blue wavelengths. Lizard color increases in saturation and coverage area as lizards increase in size and age. Therefore, lizard color was quantified by two measurements: (1) green and blue saturation – as measured by reflectance estimates in ColourWorker^{TM}, and (2) by the proportion of pixels on a lizard's body with RGB values estimated in the blue-green range divided by the number of pixels that make up their total body. Using this process, I selected the most conspicuously colored male and female as "models" (Figure 2.2a). Lizard color varies dramatically among island population, so these models represented only the most conspicuous lizards on Formentera. However, while some island populations have brown, black, or orange lizards, most island populations are some shade of blue or green, so results from this study may be broadly applicable to many of these populations.

Using a process of mixing, measuring (in ColourWorker^{TM}), and remixing different colored human tattoo inks (Dynamic Color Co.), I created two ink mixtures that closely matched the spectral characteristics of the most colorful male and female "models" (Figure 2.2a). I then randomly selected half the captive males and females to be painted with these ink mixtures to match the spectral characteristics and coverage area of the colorful male and female models respectively (Figure 2.2c). Remaining males and females were sham-painted with water as controls (Figure 2.2b). Snout-vent length (SVL) and mass did not differ between the color-enhanced and control groups of males and females (males: P=0.27, N=40, SE=1.81; female: P=0.31, N=40, SE=1.8).

Experiments took place in two 7.5m x 7.5m ($56.25m^2$) enclosures built around naturally occurring lizard habitat. Enclosures were built using 0.5 m tall polyethylene boards that were partially buried in the ground. These enclosures had habitat that resembled natural conditions while facilitating observation and preventing lizard escape. I placed equal numbers of color-enhanced and control males and females into each enclosure (N=20). Lizard densities inside enclosures were not unrealistic as it is common to find patches of Ibiza wall lizards living at densities of approximately 1 individual/m^2 (Dappen unpublished data).

Like many Lacertid species, male *P. pityusensis* set up overlapping home ranges during the reproductive season and perform aggressive ritualistic territorial displays (López, et al. 2002). In territorial displays, males raise themselves high up on all four limbs into a threatening posture, before strutting toward their opponent with their neck arched and snout pointed down (López, et al. 2002). If this display deters trespassers, the contest may be settled; if not, the encounter may escalate to a fight, ending in biting, chasing, and locking jaws (López, et al. 2002; Olsson 1992). Most aggressive encounters end in a chase – the winner of which gains access to that territory by chasing the loser off. During courtship, on the other hand, male lizards slowly approach females in a posture that resembles their aggressive display. Once they are near enough to the female, they begin tongue flicking her tail or the ground around her tail, and then gently bite and shake the female's tail. Receptive females then allow courting males to mount them whereas non-receptive females simply run away. Copulation lasts between one and four minutes (Dappen unpublished data).

At the height of the 2010 reproductive season (May), I systematically observed the experimental enclosures for 50 hours over one week during peak activity hours (0900-1600 h) recording the details of all aggressive interactions and reproductive behaviors. I began recording data as soon as lizards were introduced into the enclosures. Aggressive interactions were defined as all interactions ending in chasing or biting. For each fight, I recorded the winners and the losers. A win was assigned to the individual that ultimately chased the other away. Fights began and ended quickly and it was always clear which lizard won. Whenever I observed a male in his ritualistic courtship display I counted it as one courtship event. Whenever I observed individuals copulating I counted it as one mating event and one courtship event.

Statistical Analysis

During observation periods I always was able to assign individuals involved in various behavioral interactions to sex and treatment group; however, due to the speed or location of the interaction, it was often impossible to identify the actual individuals involved. Therefore, I present my results in two ways. First, I present the unanalyzed pooled data for all interactions. I did not analyze pooled data statistically because to do so would violate the assumption of independent sampling. Instead, I present raw data for illustrative purposes. Second, I present results from analyzed data collected when I was able to identify the actual individuals involved. To test whether conspicuous coloration evolved in males as a sexually selected signal, I used a Mann-Whitney U-test to compare the outcome of aggressive interactions involving known color-enhanced and control males, an unpaired t-test to compare the mean number of courtship events involving known individuals between the two male groups, and a chi-squared goodness of fit test to compare unique copulation events between color-enhanced and control males. To determine whether increased reproductive performance was a result of male-male contest or female choice, I compared the proportion of courtship events that ended in copulation between color-enhanced and control males. To test between the *genetic correlation hypothesis* and *the mutual ornamentation hypothesis*, I used similar tests to compare the outcome of aggressive interactions involving color-enhanced and control females, and the courtship frequency and mating events of color-enhanced and control females. All statistical analyses were done in JMP 9.0 (SAS).

Results

I observed a total of 215 male aggressive interactions (each aggressive interaction involving two individuals). One-hundred thirty-eight of these interactions involved color-enhanced males aggressively interacting with control males. Considering all the 138 interactions regardless of whether individuals could be identified, color enhanced males won 121 encounters and control males won 17 (Figure 2.3a). For the subset of interactions in which both males could be identified, proportion of wins per male was significantly higher for color-enhanced males (0.75; SE ± 0.15) than for controls (0.17; ± 0.11; Z=2.32, N_{CE}= 7, N_{C}= 12; P=0.011; Figure 2.3a).

I observed a total of 181 courtship events. Considering all courtship events regardless of whether the individual male involved could be identified, color-enhanced males were seen courting females 123 times whereas control males were seen courting females 58 times (Figure 2.4a). Considering only those observations that could be assigned to individual males, mean courtship activity was higher for color-enhanced males (2.56 courtships/male; ± 0.43) than for control males (1.00 courtships/male; ± 0.58, $t = 2.94$, $N_{CE}= 9$, $N_C= 5$; P=0.0094; Figure 2.4b). Considering all copulation events, regardless of whether the individual males could be identified, color enhanced males were observed copulating with females 15 times whereas control males were seen copulating with females 3 times (Figure 2.5a). Considering only those observations that could be assigned to individual males, there was a non-significant tendency for color-enhanced males to copulate more that control males (color-enhanced=6; control=1; χ^2=3.57, DF=1, P=0.0588; Figure 2.5b). Finally, the proportions of all observed courtship events that ended in copulation were quite similar between color-enhanced and control males (color-enhanced=15/128; control=3/53).

In over fifty hours of observation I did not observe a single female-female aggressive interaction. Personal observations in the field (under non-experimental conditions) are consistent with this result (Dappen personal obs).

Considering all courtship events regardless of whether the individual males and females involved could be identified, males were observed courting color-enhanced females 68 times whereas males were observed courting control females 111 times (Figure 2.6a). Considering only those observations that could be assigned to individual females, mean courtship activity did not differ significantly between color-enhanced females (1.34 courtships/female, ±0.21) and control females (1.56 courtships/female, ± 0.17, t=0.81, N_{CE}=6, N_C=9, P=0.4346; Figure 2.6b). Finally, considering all copulation events regardless of whether the individual females could be identified, color-enhanced and control females were observed copulating 9 times each (Figure 2.7a). Considering only those copulation events that could be assigned to individual females, there was no significant difference in the number of copulation events between color-enhanced (3 observed copulations) and control females (4 observed copulations, $\chi^2=0.1429$; DF=1, P=0.71; Figure 2.7b).

Discussion

The objective of this investigation was to determine the functional significance of conspicuous color expression in male and female *P. pityusensis*. To accomplish this I performed a color manipulation experiment to investigate how conspicuous color influences social interactions within and between the sexes. The results from this experiment suggest that conspicuous color expression is subject to sexual selection in males as a signal for fighting ability. In females, however, conspicuous color expressed seems not to play a functional role in social interactions.

Color evolution in males – a signal for fighting ability:

Color-enhanced males outcompeted control males in aggressive interactions, they courted more females than control males, and they showed a non-significant tendency to copulate more than control males. Considering data from all the observed interactions regardless of whether individuals could be identified, these trends were in the same direction. The only fitness measurement that was non-significant when considering only those observations that could be assigned to individual males was copulation events;

however, data from all observed copulation events regardless of whether individuals could be identified show color-enhanced males copulating with five times as many females as control males. Further, courtship success is often used as a proxy for reproductive fitness in species with no female choice. Together these results provide strong evidence to support the hypothesis that conspicuous color is a sexually selected signal for fighting ability in male-male contest competition. These results are consistent with research on closely related species in the same family (Anderholm et al. 2004; Olsson 1994).

It is unlikely that female choice played a role in the observed differences in reproductive success between experimental and control males. While female choice for males with high quality resources is common, female preference for male ornaments is extremely rare in lizards (Olsson and Madsen 1995; Tokarz 1995). Furthermore, the proportion of observed courtship events that ended in copulation did not differ between the two groups, suggesting that females did not distinguish between male partners based on manipulated color differences. Research on *Lacerta agilis* suggest that females may show a matting preference for males with a major histocompatibility complex (MHC) genotype different from their own (Olsson et al. 2003). Research on the same species found that males with a particular MHC genotype could produce status coloration regardless of parasite load (Olsson et al. 2005); yet, little evidence suggests that females use coloration as an indicator of good genes in this family of lizards. Rather, the evolution of conspicuous male coloration appears to be driven by intrasexual selection (i.e. male-male contest competition).

Color evolution in females – a genetic correlation?

I was unable to determine any functional role of male-typical coloration in female lizards. Females were not observed in any aggressive interactions and, when considering the observations that could be assigned to individuals, there was no difference in the number of times color-enhanced and control females were courted by or seen mating with males. Data from all observations regardless of whether individuals could be identified suggest that, if anything, increasing conspicuous color in females reduces their attractiveness to males. Together, these results provide indirect support for the *genetic correlation hypothesis* - that females express male-typical coloration as a result of an intersexual genetic correlation with males.

Partial or full expression of male-typical secondary sex traits in females as a result of a genetic correlation with males may be common in many species. Muma and Weatherhead (1989b) performed a similar manipulation experiment with female red-winged blackbirds to investigate whether brightness of epaulette or chin plumage correlated with dominance status. Male red-winged blackbirds are black with bright red epaulettes on their shoulders while females are normally brown in color. However, females express a reduced version the male-typical epaulettes and the size, brightness, and saturation of this epaulette varies in both sexes. Muma and Weatherhead (1989b) found that brightness manipulation had no affect on dominance status in females and proposed that the male-typical epaulette and chin plumage was an indirect consequence of a genetic correlation with males. On the other hand, studies on related species suggest that female coloration may be used in sex recognition. In *P. hispanicus*, female coloration was shown to be a sex-recognition signal at long-distances, while at close distances, males used pheromone cue odors to identify sex, regardless of female color (López and Martín 2001). However, if males use color in sex recognition, selection should favor female-specific coloration. Why then is female color so variable within many populations of *P. pityusensis*? Galan (2000) found evidence that female color in *P. bocagei* became more male-like after females became pregnant and proposed that this color change may reduce unwanted male harassment during the breeding season for already pregnant females. Yet data suggest that female *P. pityusensis* do not change color throughout the breeding season (Dappen unpublished data). Instead, results from the present study favor the genetic correlation hypothesis to explain the observed color variation in female *P. pityusensis*.

In summary, conspicuous color in *P. pityusensis* appears to be subject to sexual selection in males as a signal for fighting ability in male-male contest competition and may be expressed in females due to a strong intersexual genetic correlation. To maintain honesty, male ornaments are thought to incur a cost (Zahavi 1975). Presumably, the reproductive benefits of these ornaments outweigh the costs in males. However, if these ornaments serve no purpose in females and are expressed due to a genetic correlation, there is a high potential for sexually antagonistic selection to drive intralocus sexual conflict over the alleles responsible for color expression. Intralocus sexual conflict occurs when the same set of alleles in males and females have different fitness optima (Rice and Chippindale 2001). This may be a mechanism that maintains variation for traits under strong directional selection in one sex (Bedhomme et al. 2008; Bonduriansky and Rowe 2005; Cox and Calsbeek 2009). Future work should investigate the heritable basis for color expression in this species and should determine whether conspicuous coloration is subject to sexually antagonistic selection. Additionally, color expression varies dramatically among island populations of *P. pityusensis*. This research may provide a basic explanation for the existence of green and blue color variation in *P. pityusensis*; however, nothing is known about why some populations are orange, black, brown or combinations of these colors. Much research is needed to understand the myriad of uniquely colored lizard populations in the Pityuses archipelago.

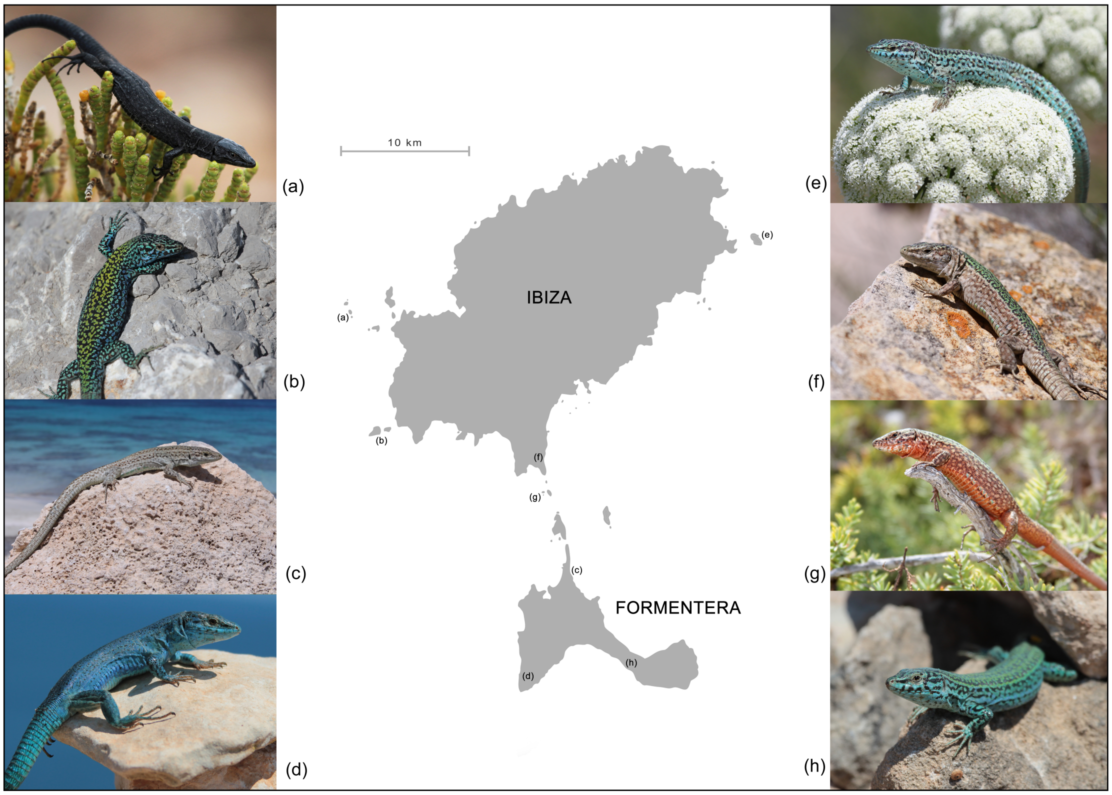

Figure 2.1. A map of the Pityusic Archipelago in Spain's Mediterranean Sea and examples of male Ibiza wall lizards from various island. This archipelago makes up the southernmost tip of the Balearic Islands. Ibiza and Formentera are the largest of the 42 islands and islets in the Pityuses that are home to populations of *P. pityusensis*. There is tremendous color diversity across this species range. Males from: (a) Bledes Plano; (b) Es Vedra; (c) Formentera, Es Trocadores; (d) Formentera, Cap de Barbaria; (e) Tagomago; (f) Ibiza; (g) Islas Negras; and (h) Formentera, central. In general, males are more colorful than females, but female color co-varies with male color among island populations.

Figure 2.2. Lizards used for the color manipulation experiment: (a) the most conspicuously colored males and females were used as models for which to base the color manipulation; (b) control lizards were sham-painted with water, thus dispayed their normal colors, while (c) color-enhanced lizards were painted to resemble the conspicuous male and female models (a).

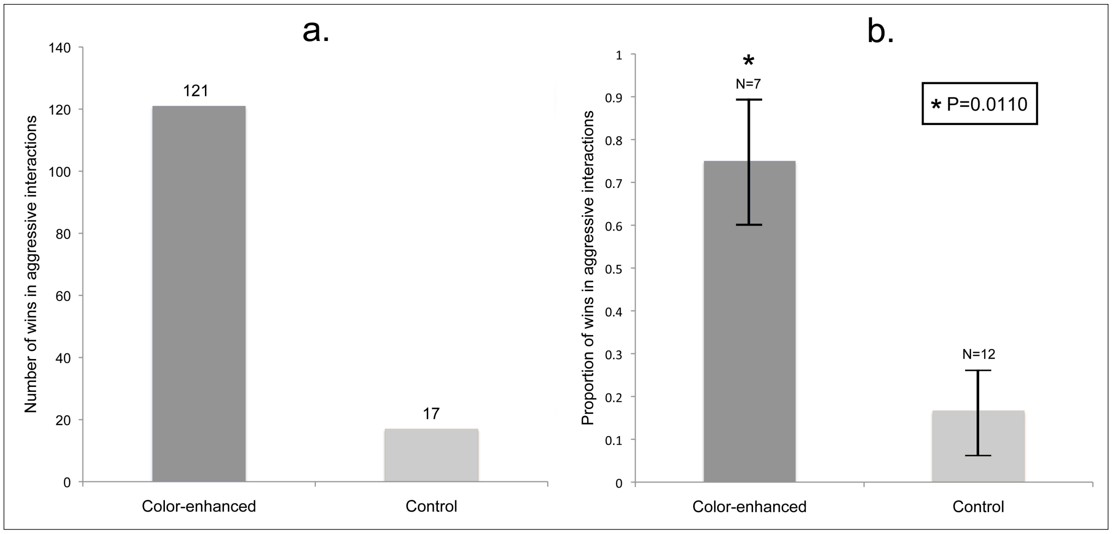

Figure 2.3. The effect of color on the outcome of aggressive interactions: (a) pooled data representing the outcome of all observed aggressive interactions in which color-enhanced males fought control males; (b) the proportion of wins when males fought unique individuals in the opposite experimental group.

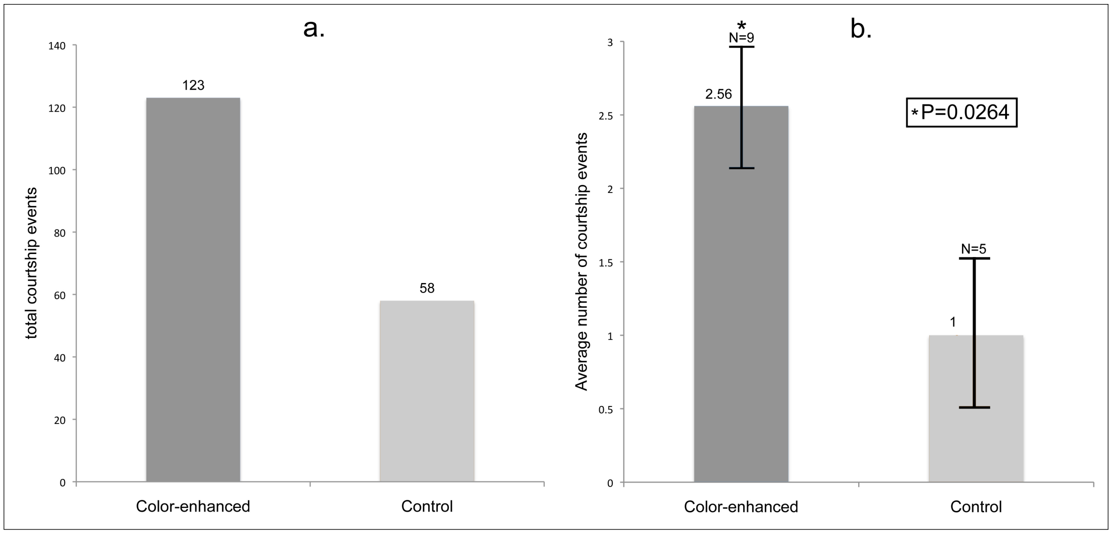

Figure 2.4. The effect of color on courtship occurrence in males: (a) pooled data representing the total number times color-enhanced and control males were observed courting females; (b) the average number of times individual color-enhanced and control males were observed courting females.

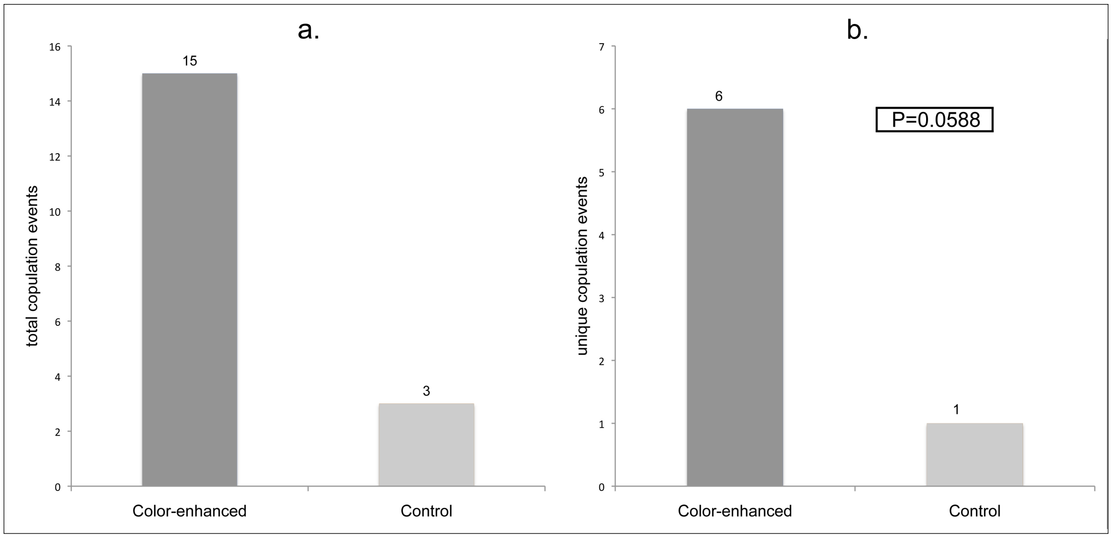

Figure 2.5. The effect of color on copulation occurrence in males; (a) pooled data representing the total number times color-enhanced and control males were observed copulating with females; (b) the number of times unique color-enhanced and control males were observed copulating with unique females.

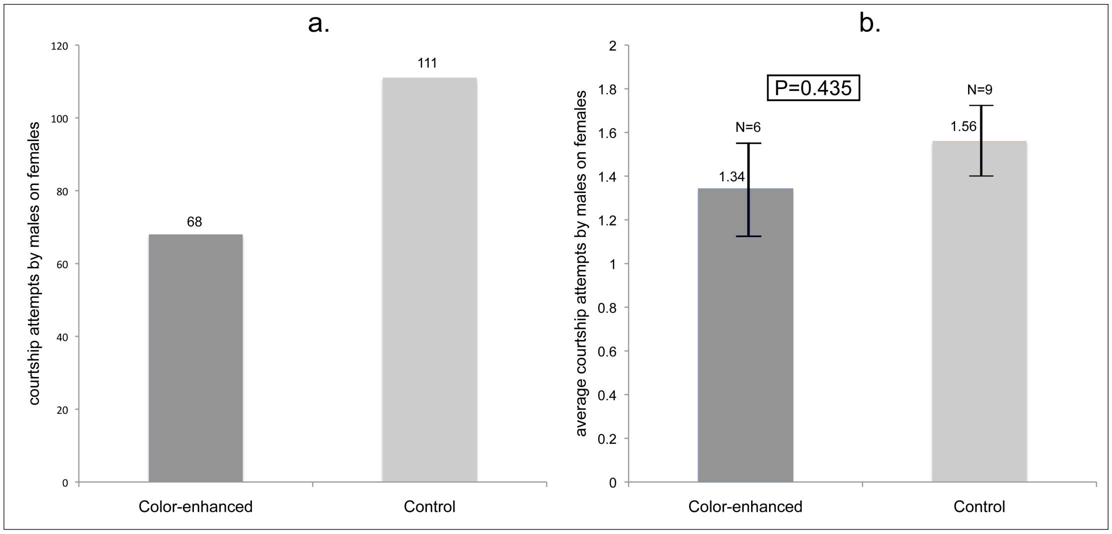

Figure 2.6. The effect of color on courtship occurrence in females: (a) pooled data representing the total number times color-enhanced and control females were observed being courted by males; (b) the average number of times individual color-enhanced and control females were observed being courted by males.

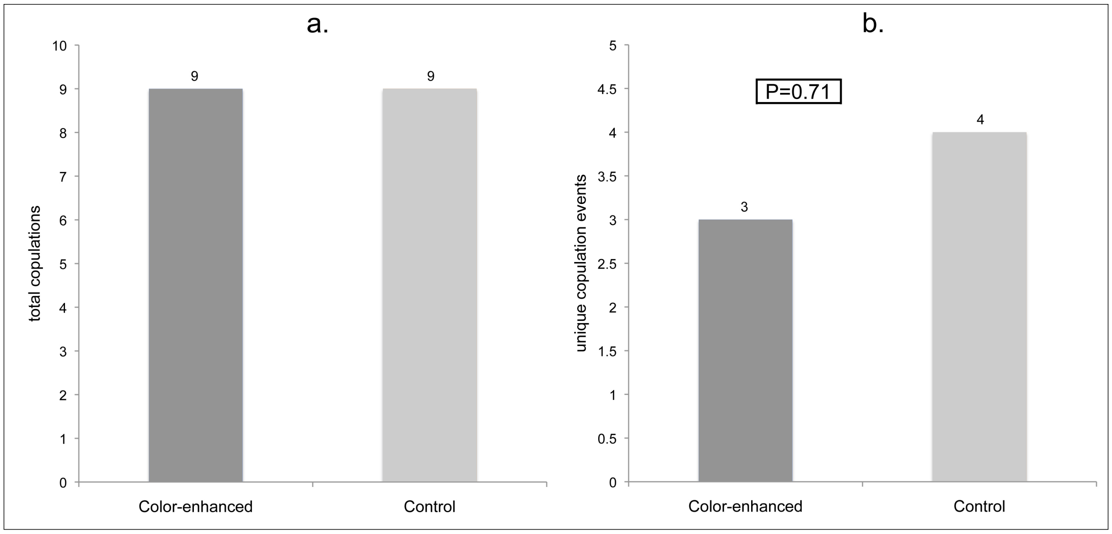

Figure 2.7. The effect of color on copulation occurrence in females; (a) pooled data representing the total number times color-enhanced and control females were observed copulating; (b) the number of times unique color-enhanced and control females were observed copulating with unique males.

Chapter 3

Predation and male-contest competition may drive intralocus sexual conflict over color expression in the Ibiza Wall lizard (*Podarcis pityusensis*)

Summary

Extravagant display characters increase adult male fitness in many species, yet the same traits can be detrimental when expressed in females due to sex-specific differences in selection. These antagonistic selective pressures may cause intralocus sexual conflict, in which the expression of particular genes have opposing fitness consequences between the sexes. Theory posits that over time, intralocus sexual conflict should drive the evolution of sexual dimorphism in these costly traits. Nevertheless, in many species, females partially or fully express male-typical display traits. The Ibiza wall lizard, *Podarcis pityusensis*, expresses striking color diversity across its geographic range. Males are generally more conspicuously colored than females, but sexual dichromatism varies dramatically within and among populations. Previous research suggests that conspicuous coloration is favored by sexual selection in male lizards, yet appears to have no functional role in females. I performed clay-model predation trials to determine whether conspicuous color evolves in opposition to predation pressure. My results suggest that more conspicuously colored lizards suffer higher predation rates than cryptically colored lizards. In light of previous research on the function of color in male and female lizards, these results suggest that conspicuous color is subject to sexually antagonistic selection that may drive intralocus sexual conflict.

Background

The evolution of the sexes presents a unique evolutionary problem: males and females share most of the same genes and express many of the same traits, yet the sexes themselves are defined by their unique reproductive strategies (Clutton-Brock 2007) resulting in sex-specific selection on many shared traits (Bonduriansky and Chenoweth 2009; Bonduriansky and Rowe 2005). This sexually antagonistic selection may generate *intralocus sexual conflict*, in which genes that are beneficial when expressed in one sex are detrimental when expressed in the other (Rice and Chippindale 2001).

Several major theoretical implications emerge from intralocus sexual conflict. First, if selection on a shared trait differs between the sexes, neither sex can evolve to its optimal phenotype because high fitness parents will produce low fitness opposite-sex offspring (Bonduriansky and Chenoweth 2009; Bonduriansky and Rowe 2005; Cox and Calsbeek 2009). Second, evolutionary theory predicts that genetic variation for traits under strong selection will continually diminish. The presence of high genetic variation for these traits has always been an evolutionary puzzle (i.e. the “lek paradox”) (Borgia 1979; Hamilton and Zuk 1982; Kirkpatrick and Ryan 1991). Intralocus sexual conflict may be one mechanism that maintains genetic variation for traits under strong directional selection (Bonduriansky and Chenoweth 2009; Cox and Calsbeek 2009; Foerster et al. 2007). Despite its potentially central role in various evolutionary processes, very little research has investigated how this conflict has influenced the evolution of natural history traits in natural populations of organisms (Brommer et al. 2007; Cox and Calsbeek 2010; Foerster et al. 2007; Merila et al. 1997).

Extravagant display characters have the potential to be influenced by intralocus sexual conflict for a variety of reasons. These traits are often subject to sexual selection in one sex (usually males), but not the other (Andersson 1994). Further, signals that have evolved for mate attraction or within-sex aggressive competition are frequently conspicuous to predators, and the sexual selection leading to these traits may be opposed by viability selection (Cooper 1999; Endler 1983a; Endler 1986; Hamilton and Zuk 1982; Morehouse and Rutowski 2010; Zahavi 1975; Zuk and Kolluru 1998). Conflict between mating success and survival is a tradeoff that occurs in a wide range of taxa and many sexually selected signals such as auditory (Cade 1975; Ryan et al. 1982), olfactory (Noldus et al. 1991a; Noldus et al. 1991b) and visual signals (Endler 1980; Endler 1983b; Endler 1986; Endler 1987; Endler and Greenwood 1988; Grether 1997; Grether and Grey 1996; Husak et al. 2006; Morehouse and Rutowski 2010) have been shown to represent this compromise. Further, intraspecific color variation for sexually selected traits is often attributed to variation in predation pressures across a species' geographic range (Breden and Stoner 1987; Endler 1980; Endler 1991; Endler and Greenwood 1988).

Most display traits are controlled by similar underlying genetic mechanisms in both sexes. As a result, sexual selection on these traits in males may cause a correlated response in the homologous trait in females (Bonduriansky 2007; Bonduriansky and Head 2007; Fisher 1930; Lande 1980; Lande 1982a). Therefore, females may inherit all the costs of the display trait, with none of the reproductive benefits that the trait offers males (Lande 1987; Pischedda and Chippindale 2006).

Theory posits that intralocus sexual conflict should drive the evolution of sexual dimorphism through the decoupling of the trait's expression between the sexes

(Chenoweth et al. 2008; Cox and Calsbeek 2009; Fisher 1930; Lande 1980; Lande 1982a; Lande 1987). Nevertheless, in many species, costly male secondary sex traits are partially or fully expressed in females. Little is known about how genetic correlations between the sexes influence the evolution of such traits in nature (Bonduriansky and Chenoweth 2009; Chippindale et al. 2001; Rice and Chippindale 2001).

In the context of intralocus sexual conflict, my research investigates color evolution in the Ibiza wall lizard, *Podarcis pityusensis*: a diurnal terrestrial lizard that expresses striking color variation across its geographic range. This species is endemic to the Pityusic Archipelago in the Balearic Islands of Spain (Martinez-Rica and Cirer 1982; Salvador 1984; Salvador 1986). On some islands these lizards are green, whereas on other islands they are bright blue, sandy brown, or even orange and black (Cirer and Martinez-Rica 1990; Salvador 1986). *Podarcis pityusensis* are sexually dichromatic, with males being more conspicuously colored than females. Color varies greatly within sexes, however, and the degree to which males and females resemble one another in the same population is highly variable. Previous research on this species suggests that conspicuous coloration is favored by sexual selection as an honest signal of competitive ability in male-male interference competition, yet color appears to play no functional role in females (Chapter 2).

Building on previous work that suggests conspicuous color benefits adult males, yet plays no signaling role in females, I performed a *clay-model predation experiment* to test the hypotheses that this conspicuous coloration evolves in the face of predation pressures and is thus subject to sexually antagonistic selection. Experimental studies of predation's role in color evolution often involve the manufacture of artificial prey replicas that vary in color or pattern (Gotmark 1996; Pfennig, et al. 2001). These replicas are then exposed to predators in an experimental arena or in nature and monitored to measure predation rates. I created clay-model lizard replicas that differed in color. I then exposed these models to predators in nature and compared attack rates among replica colors to investigate whether more conspicuously colored lizards suffer greater predation risk.

Materials and Methods

I performed this experiment in July 2010 at three different locations on the island of Formentera (Figure 3.1). Formentera is the southernmost, and smallest of the larger islands that make up Spain's Balearic Islands. This island is characterized by rocky terrain interspersed with rosemary and juniper bushes, and is home to dense populations of *P. pityusensis*. On this island it is possible to find three distinct color forms of *P. pityusensis*. On the Trocadors Penninsula in the north, the lizards are almost all completely brown (Figure 3.1c); on the Cap de Barbaria to the southwest, the lizards are mostly blue (Figure 3.1b); and in the central area and La Mola in the east, lizards are a bright green (Figure 3.1a). With the exception of the brown lizards on the Trocadors peninsula, the lizards on Formentera express tremendous variation in sexual dichromatism. In fact, it is often misleading to sex lizards in the field by color, as females are often as colorful as males (Dappen personal obs.).

A variety of animals may prey on *P. pityusensis* on Formentera. Potential avian predators include kestrels (*Falco tinnunculus*), booted eagles (*Aquila pennata),* seagulls (*Larus michahellis*) and shrikes (*Lanius* spp.) (Araújo et al. 1977; Catalá et al. 1990;

Cooper and Pérez-Mellado 2011; Cramp and Simmons 1980; Cramp and Simmons 1983; Gómez 1991). Additionally, feral cats (*Felis catus*) and the black rat (*Rattus rattus*) were introduced to many of the Balearic Islands and are now abundant on Formentera. Both of these mammals prey on lizards (personal observation).

Using a silica mold formed from a preserved specimen of *P. pityusensis*, I crafted lizard replicas from pre-colored, non-toxic SCULPEY III® brand plasticine modeling clay (Polyform Products Co., Illinois). Plasticine modeling clay has been used in previous predation experiments because impressions from the teeth, beak or claws of predators will remain identifiable on the clay (Saporito et al. 2007).

I created a total of 300 clay-model lizard replicas: 100 replicas that matched the spectral characteristics of conspicuously green lizards (Figure 3.1a); 100 models that matched the spectral characteristics of conspicuously blue lizards (Figure 3.1b); and 100 that matched the spectral characteristics of cryptic brown lizards (Figure 3.1c). As mentioned above, all three of these color-forms can be found on Formentera. Color-matching was done by mixing different clay colors together until the reflectance curves of those mixtures closely matched the reflectance curves of actual lizards as measured in the program ColourWorker^{TM}.

ColourWorker^{TM} can estimate the spectral reflectance of visible wavelengths (400-700nm) from digital photos (Osorio and Anderson 2007; Stevens, et al. 2006). I calibrated ColourWorker^{TM} using spectral data from these lizards collected using a UV sensitive spectrophotometer (Ocean Optics USB-2000) (Chapter 2). Once calibrated, ColorWorker^{TM} provided objective and accurate estimates of the spectral characteristics of lizards. Additionally, to the human eye, these clay-mixtures closely resembled the colors of real lizards (Dappen personal obs.). Therefore, lizard replicas closely matched the spectral characteristics of their real-life counterparts.

I conducted three 24 hr predation trials over six days at three different locations on Formentera. For each of these trials, I walked in a strait line through the habitat laying out 100 models of each color placed 5 m apart directly on the ground in strict alternation. After 24 hours in the field, I collected the models and inspected each one for evidence of predation.

Statistical Analysis

To test whether predators differentially attack lizards according to their color, I compared predation events on each model type using a chi-squared test of independence. I broke these analyses into two types: (1) predation events due to all predator types (i.e. avian, rodent, cat together) and (2) predation events due only to avian predators. All statistical analyses were done in JMP 9.0 (SAS).

Results

I recovered all 900 replicas placed at different locations on Formentera. Of all the recovered replicas, 120 (13.3%) were attacked. I attributed 112 attacks to birds, 7 attacks to rodents, and 1 attack to a cat. Lizards also attacked the models, but I do not include lizard attacks in my analysis. I compared predation rates among different colored replicas using data from all predation events and then using data only from avian predation events, as birds are typically visual predators. The single cat attack was on a green replica, and rodents attacked different colored lizard replicas at similar rates (blue=3, green=1, brown=3, χ^2= 1.14, DF=2, P=0.5647). Replica forms were attacked at different rates when considering all predation events (Chi-square test: χ^2 = 32.529, P <0.0001; Figure 3.2a) and when considering predation by avian predators alone (Chi-square test: χ^2 = 32.855, P <0.0001; Figure 3.2b). In both analyses, blue models were attacked significantly more than both green (All Predators: blue=61 vs green=37, χ^2= 5.88, DF=1, P=0.0153; Avian Predators only: blue=58 vs green=35, χ^2= 5.69, DF=1, P=0.0171), and brown models (All Predators: blue=61 vs brown=22, χ^2= 18.33, DF=1, P<0.0001; Avian Predators: blue=58 vs Brown=19, χ^2= 19.75, DF=1, P<0.0001), and green models were attacked significantly more than brown models (All Predators green=37 vs brown=22, χ^2= 3.81 DF=1, P=0.0508; Avian Predators: green=35 vs brown=19, χ^2= 4.74, DF=1, P=0.0295).

Discussion

The objective of this study was to investigate the role of predation in conspicuous color evolution, and in doing so, identify potentially sexually antagonistic selection on conspicuous color expression in male and female *P. pityusensis*. To accomplish this I performed a clay model predation experiment in which I created clay lizard replicas that differed in color, exposed these replicas to predators in nature, and then compared attack rates among different colored replicas. Blue models were attacked most often, green models next most, and brown models least often. In light of previous research, the results from this experiment suggest that conspicuous color evolves in opposition to predator pressures and that color expression may be subject to sexually antagonistic selection in this species.

Predators attacked colorful clay models significantly more than cryptic models when considering all predation events and only avian predation events. These results suggest that conspicuous color may evolve in the face of predation pressure and that both colorful males and colorful females likely suffer greater predation pressure than less colorful lizards. This result is not surprising. Many studies have found that conspicuous prey suffer from greater predation (Endler 1983a; Husak, et al. 2006; Stuart-Fox, et al. 2003).

Heightened predation risk as a result of increased conspicuousness may carry cost other than simply increasing mortality rates. For example, in the closely related *P. muralis*, López and Martín (2001) found that real lizards, painted to be more conspicuous suffered a significantly greater loss of relative body mass than controls painted to resemble drab lizards. While bright coloration did not increase mortality directly, the researchers concluded that this coloration may have resulted in increased predation risk, which forced lizards to use anti-predatory behaviors that have associated costs. In support of this idea, research on the same species suggests that predator avoidance behavior may vary with predation pressure (Diego-Rasilla 2003) and that variation in these pressures can result in decreased body condition and health state (Amo et al. 2006). Previous research on this species suggests that conspicuous color expression is favored in males as a signal for male-male contest competition, yet appears to serve no functional role in females (Chapter 2). Similar studies on closely related species support the hypothesis that conspicuous coloration evolved in this species by sexual selection as a signal for male fighting ability (Anderholm et al. 2004; Diaz 1993; López et al. 2009; López and Martín 2001; López et al. 2002; Olsson 1994).

Extravagant secondary sexual characters such as conspicuous color are often viewed as the products of countervailing sexual and natural selection (Endler 1983a; Grether 1997; Grether and Grey 1996; Morehouse and Rutowski 2010; Zuk and Kolluru 1998). Yet researchers have traditionally taken a male-centric view on how these countervailing pressures influence individual fitness and the evolution of extravagant secondary sexual traits. Selection on these traits in females may influence the evolution of these traits in unforeseen ways such as the effects of multi-generational inheritance (Bonduriansky and Chenoweth 2009; Lande 1980). That is, the fitness effects of a trait may be different between parents and offspring or between offspring and grandparents, ultimately influencing the persistence of the genes responsible for that trait in a population. For example, a female sired from a colorful father may have colorful sons despite the color of her mate. Alternatively, the fitness of colorful males that sire colorful daughters may be reduced as a result of increase predation on the daughters. The evolutionary dynamics of these traits are vastly different if selection acts on them in different ways in each sex.

In summary, conspicuous color in *P. pityusensis* seems to be favored in males by sexual selection as a signal for fighting ability, appears to play no social function in females, and is disfavored in both sexes by predation. Male *P. pityusensis* are generally more conspicuously colored than females; however male and female colors co-vary among island populations, suggesting that there is an intersexual genetic correlation for color expression between the sexes. If this genetic correlation exists, then sexually antagonistic selection on color may be generating intralocus sexual conflict.

Intralocus sexual conflict on life history traits such as secondary sexual characters may be common in many species and may provide an explanation for the partial or full expression of male-typical traits in females and the high amounts of variation in these traits despite apparently strong directional selection. A clearer understanding for how selection will influence the evolution of traits that are subject to intralocus sexual conflict will require detailed knowledge of a trait's additive genetic variance and the strength of the intersexual genetic correlation for that trait. Finally, more field studies on a wide variety taxa are needed to confirm the generality of these results in nature.

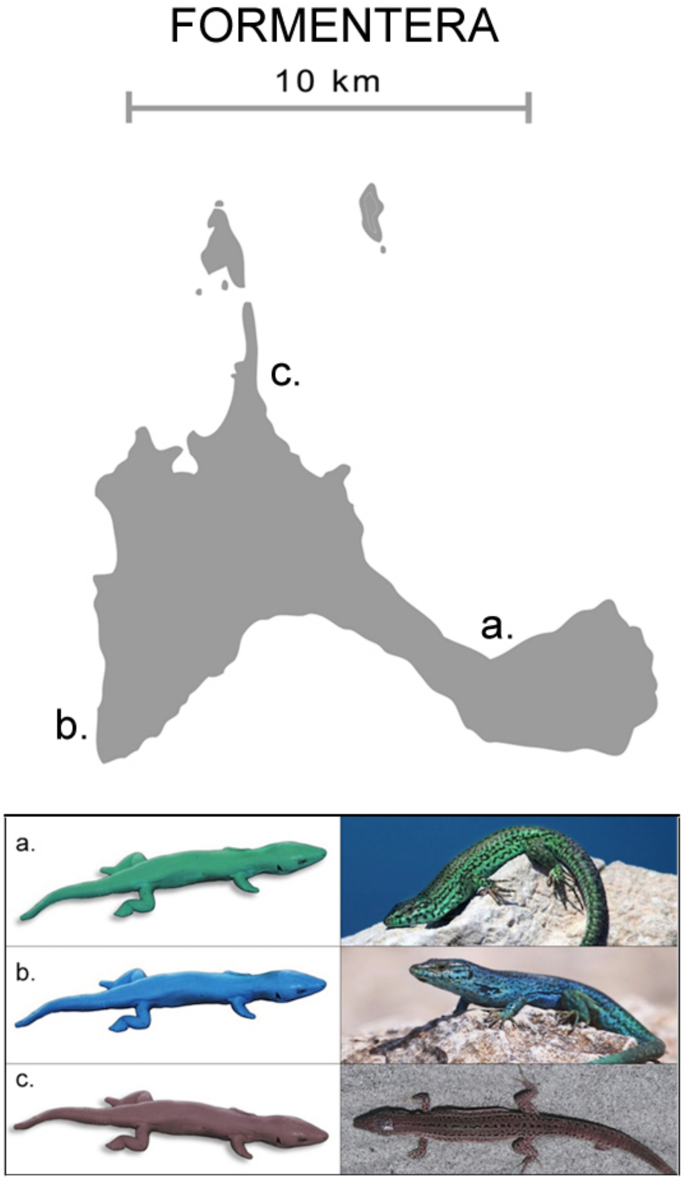

Figure 3.1 Clay model lizard replicas (left) and their real-life counterparts (right) from the island of Formentera. On this island it is possible to find three distinct color forms of *P. pityusensis*. I created plasticine lizard replicas to resemble these three color forms: (a) in the central area and La Mola in the east, lizards are generally bright green; (b) on the Cap de Barbaria to the southwest, the lizards are mostly blue; and (c) on the Trocadors Penninsula in the north, the lizards are almost all completely brown.

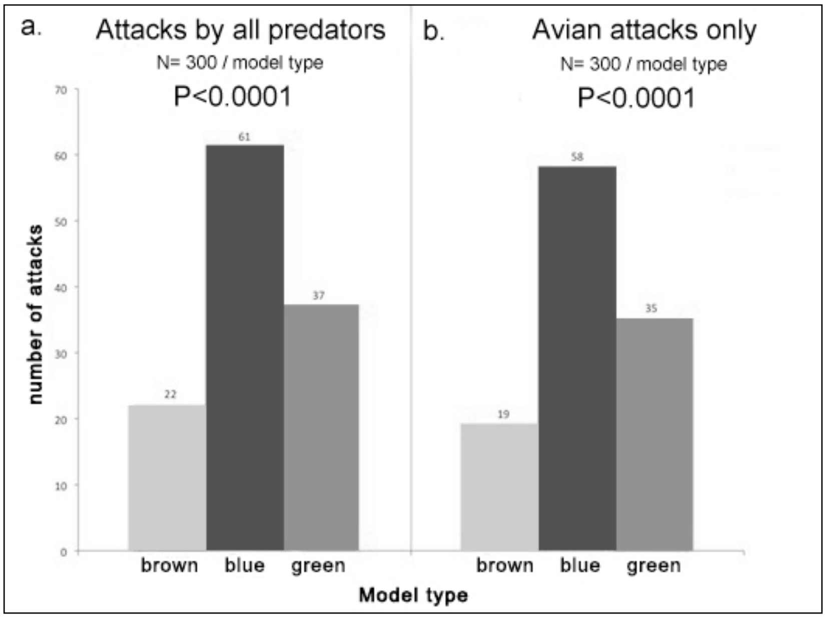

Figure 3.2 Results showing predation events on different colored clay lizard replicas: (a) attacks on different colored models by all predators and (b) attacks on different model colors by avian predators only.

Chapter 4

Intralocus ontogenetic conflict and the evolution of ontogenetic color change in the Ibiza Wall lizard (*Podarcis pityusensis*)

Summary

Extravagant display characters such as conspicuous coloration increase adult male reproductive success in many species, yet the same traits may be detrimental when expressed in juveniles due to differences in selection among age groups. This antagonistic selection on traits shared among age groups may drive intralocus ontogenetic conflict, in which selection favors the expression of particular alleles in one age group, but disfavors the expression of those same alleles in another age group. In this study, I investigated the factors influencing the evolution of ontogenetic color change in *Podarcis pityusensis*, a lizard species with striking ontogenetic color variation within and among populations. I conducted a habitat preference survey, cannibalism trials, and a clay model predation experiment that demonstrated: 1) adult and juvenile lizards are found in different habitats, 2) this difference is likely influenced by the high frequency of cannibalism, and 3) predation pressure is different between the habitats where adults and juveniles are found. Taken together with previous research demonstrating that conspicuous coloration is favored by sexual selection in adult males, these results suggest that color-expression is subject to antagonist selection among age groups in this species. Results from this study may help explain ontogenetic color change in *P. pityusensis* and other lizard species.

Background

Natural selection often differs among age classes of the same species (Anderson and King 1970; Stamps 1983). These differences in selective pressures are the result of individual's age-specific interactions with the environment and with other organisms. For example, as organisms get older and larger, their ability to capture larger prey or to compete with conspecifics might improve, allowing them to exploit resources in novel habitats. These ontogenetic (developmental) shifts in diet, habitat, and behavior can have large effects on how natural selection operates on individuals at different life stages and thus may have a profound influence on the evolution of life-history traits (Stamps 1983; Werner and Gilliam 1984). The study of how organisms interact with the environment and each other at different life stages is fundamental to understanding a species' ecology and evolution.

In most habitats, resources such as food, mates, and refugia are rarely distributed uniformly throughout an environment, but rather exist in patches. If these patches are limited resources, intraspecific competition may result in some individuals being excluded from high quality patches and thus forced to survive in marginal habitats (Duckworth 2006). Generally, larger older individuals will outcompete smaller younger individuals for high quality patches (Duckworth 2006; Forslund and Part 1995; Saether 1990; Wynne-Edwards 1962). Variation in selection between high and low quality patches may favor the expression of particular alleles in high quality patches yet select against the expression of the same alleles in low quality patches. Because the ability to compete for high quality patches often depends on age, antagonistic selection on traits shared among age groups may drive intralocus ontogenetic conflict where selection favors the expression of particular alleles in one age group, but disfavors the expression of those same alleles in another age group (Chippindale et al. 2001; Rice and Chippindale 2001; Sinervo and Calsbeek 2003).

Male display characters such as conspicuous coloration may often be subject to intralocus ontogenetic conflict because these costly traits usually benefit reproductively mature males only (Andersson 1994). Further, these characters often evolve in opposition to other selective pressures such as predation (Cooper 1999; Endler 1980; Endler 1983a; Endler 1986; Hamilton and Zuk 1982; Morehouse and Rutowski 2010; Zahavi 1975; Zuk and Kolluru 1998) Also, investment in the expression of display characters has been shown to negatively influence immune function (Folstad and Karter 1992; Sinervo and Calsbeek 2003). As such, while the costs of these traits may be outweighed by their reproductive benefits in adult males, display characters may decrease fitness when expressed in pre-reproductive individuals that suffer the costs of these traits with none of the reproductive benefits. Nevertheless, adult male-typical display traits, such as color, are partially expressed in juveniles of many species (Booth 1990).

Conspicuous colors and patterns are used as display characters for intraspecific communication in species from many different taxa (Andersson 1994; Hubbard et al. 2010; Mills and Patterson 2009), and many of these species exhibit ontogenetic color changes—nonreversible color changes associated with normal progressive development within individuals (Booth 1990; Bückmann 1984; Bückmann 1985). Most organisms must pass through a series of morphologically immature stages as they transition from being a zygote into a reproductive adult. Historically, researchers discounted ontogenetic color changes as part of this non-adaptive developmental epiphenomenon (Rohwer and

Butcher 1988). However, more than four decades of research on ontogenetic color changes in birds, fish, and insects suggests that these changes are often an adaptive life history strategy (Booth 1990; Hawkins et al. 2011). Many hypotheses have been proposed to explain the adaptive nature of ontogenetic color changes. In most cases, these changes are thought to be the result of a compromise between current and future reproductive efforts (Booth 1990).

There are five potential adaptive explanations for sub-adult coloration. These generalized hypotheses fall under: 1) thermoregulation, 2) interspecific mimicry, 3) intraspecific mimicry (i.e. female mimicry) 4) crypsis and 5) status signaling (Booth 1990; Clusella-Trullas et al. 2008; Hamilton 1973; Hawkins et al. 2011; Walsberg et al. 1978; Willmer and Unwin 1981). These adaptive explanations may help explain the evolution of ontogenetic color changes in reptiles, a group where these developmental changes are common. Despite the commonality of ontogenetic color changes in reptiles, few studies have investigated the adaptive significance of such changes in this group (Booth 1990; Mills and Patterson 2009; Wilson et al. 2007).

The Ibiza Wall Lizard, *Podarcis pityusensis* is a diurnal terrestrial lizard, endemic to the Pityusic Archipelago in the Spanish Mediterranean. As *P. pityusensis* increases in age and size, conspicuous green or blue color increases on its body in both saturation and coverage area. Therefore, the most conspicuously colored lizards are generally the largest lizards (Figure 4.1). However, ontogenetic color changes vary dramatically among populations such that juveniles from some populations closely resemble adults with respect to color, while juveniles from other populations are much more cryptically colored than adults. Further, ontogenetic color changes often vary dramatically among individuals of the same population. My previous research suggests that conspicuous color is favored by sexual selection in male contest competition (Chapter 2). Because conspicuous color expression correlates with lizards' body size and because size often influences the outcome of aggressive interactions, conspicuous color honestly signals male fighting ability. It is unclear, however, what factors might influence the dramatic variation observed in ontogenetic color change within and among populations of this species.

Podarcis pityusensis is observed at highest densities within and around densely vegetated habitat (Dappen unpublished data), presumably because it provides a variety of resources that are lacking in open habitats such as refugia from predators, shade for thermoregulation, food, and mates. Throughout the Pityusic Archipelago, lizard habitat frequently consists of open rocky areas interspersed with patches of vegetation. The high abundance of lizards in vegetated areas suggests that these habitats are preferred over open rocky habitats. These vegetated habitats may represent a limited resource that is fought over by this lizard species. If the outcome of male contests is influenced by size, which is strongly correlated with conspicuous color expression, then more conspicuously colored males should have a competitive advantage when competing for vegetated patches. Losers of these competitions would thus be excluded to the marginal open patches, where the cost of being colorful may be higher due to increased conspicuousness and vulnerability to predation (Selander 1965). Selander (1965) proposed that young male birds that delay the expression of adult plumage may have a greater lifetime reproductive fitness because they avoid the increased mortality risks associated with breeding. These risks may include energetic costs, risk of injury due to intraspefic aggression, or an increased risk of predation. This hypothesis may help explain ontogenetic color change in *P. pityusensis* as well.

A variety of birds prey on lizards (Chapter 3), yet it is also common to observe adult *P. pityusensis* cannibalizing juveniles—a behavior that is thought to occur more commonly in island lizard species as a result of the reduced resources, higher population densities and decreased dispersal abilities on islands (Carretero et al. 2010; Castilla and Van Damme 1996; Fox 1975; Møller, et al. 2008; Pafilis, et al. 2009). Birds are frequently considered the primary predators of Mediterranean island lizards, however observational evidence suggests that intraspecific predation (i.e. cannibalism) may also frequently result in mortality, at least among juveniles. Between the summers of 2010 and 2011, I observed 13 adult *P. pityusensis* eating juvenile lizards in the field (Figure 4.2). Meanwhile, I observed only three avian predation events during this same timeframe. Observation bias may be responsible for this large difference. Nevertheless, these observations, and the frequent mention of cannibalism in other studies of Mediterranean island lizards (Carretero, et al. 2010; Castilla and Van Damme 1996; Fox 1975; Møller, et al. 2008; Pafilis, et al. 2009) suggest that cannibalism may be a major factor contributing to juvenile mortality in *P. pityusensis*.

In this study, I investigate factors that may result in antagonistic selection on conspicuous color expression among age groups to help understand ontogenetic color changes in *P. pityusensis*. I test the overarching hypothesis that intraspecific competition among adults for high quality habitats, and cannibalism by adults on juveniles force smaller adults and juveniles, respectively, to occupy more exposed, lower quality, open habitats, where the costs of being conspicuously colored (as a result of avian predation) may be higher. I performed 1) a habitat preference survey to test the predictions that adults are more abundant in vegetated habitats, juveniles are more abundant in open habitats, and adult lizards that inhabit vegetated patches are larger than lizards found in open habitats; 2) a juvenile capture survey and cannibalism trials to test the predictions that adult lizards are highly cannibalistic and juveniles are frequently the recipients of this behavior; and 3) a clay model predation experiment to test the predictions that lizards experience increased predation in open habitats versus vegetated patches and that predator types differ between vegetated versus open habitats. I expected replicas to experience more attacks by lizards in vegetated habitats and more attacks by avian predators in open habitats.

Materials and Methods

Study Site & Habitat Definitions

This study was performed between 22 April and 10 June, 2011 in the Cap de Barbaria on the southwest tip of Formentera, the southernmost of the Balearic Islands (Figure 4.3). Patches of vegetation that are composed of rosemary and juniper characterize the Cap de Barbaria. These dense patches of vegetation are well defined and are interspersed throughout open rocky fields (Figure 4.3). For this experiment, I defined open habitat (low-quality habitats) as any habitat without vegetation, and that is 5 m from any patch of vegetation. I defined vegetated habitats (high-quality habitats) as patches of habitat that are directly under or within 1m from the perimeter of vegetation.

Habitat Surveys

I performed a capture survey to investigate whether lizards found in open versus vegetated habitats differ in sex, size, or age classes. To capture lizards, I created pitfall traps by cutting the tops off of two-liter plastic water bottles and sinking them into the ground. Over two weeks, I laid out 52 pitfall traps—26 traps were placed in unique vegetated habitats and 26 traps were placed in unique open habitats. Traps were never placed in the same locations and were never placed less than 20m from any other trap. Traps were baited with fresh fruit and were left in the field. After approximately two hours, I returned to each trap and recorded the sex, size (snout-vent length [SVL] in millimeters, and mass in grams) and age-class (adult or juvenile) of lizards found in each pitfall trap. Carretero et al. (1995) found that the minimum sizes of reproductively mature males and females were 49mm and 50mm respectively in an introduced population of *P. pityusensis* in Barcelona, Spain. Therefore, I considered all lizards less than 48mm to be juveniles and all lizards that were 49mm and above to be adults. Juvenile lizards are difficult to sex. Thus, I do not report the sex of lizards smaller than 48mm.

To test whether adults and juveniles were found in different habitats, I compared the number of adults (together and by sex) and juveniles found in open versus vegetated habitats using a chi-squared test of independence. To determine whether adult lizards that inhabit vegetated patches are larger than adult lizards in open habitats, I used an ANOVA to compare the SVL and mass of adult lizards found in vegetated areas to those found in open habitats.

Cannibalism Trials

To investigate the frequency of cannibalism in *P. pityusensis*, I performed both a capture survey quantifying the amount of bite-mark scars on juvenile lizards and cannibalism trials to investigate the cannibalistic propensities of adult lizards. In the capture survey, I collected 14 juveniles from the Cap de Barbaria area by hand and using baited pitfall traps. When adult lizards attack juveniles they leave distinct bite-mark scars that are easily identified (Figure 4.4). For each juvenile, I recorded SVL, mass, and the number of bite-mark scars on the body and tail, noting whether it had its original tail, had a new tail, or was missing a tail. Missing or new tails may suggest prior agonistic interactions with conspecifics or predators (Pianka 1970; Rand 1954; Vervust et al. 2009). I did not analyze these data statistically. Instead data are used to illustrate the frequency of aggression and/or intraspecific predation attempts on juveniles.

To estimate the rate of cannibalism by adult *P. pityusensis* I adapted a method first described by Castilla and van Damme (1996). For each trial a juvenile (from the juvenile capture survey described above) was fitted with a string harness around its back legs and torso. Harnessed juveniles were tethered to the end of a 3 m panfish pole using 1 m of sewing thread. I searched for adult lizards in a different location for each trial. Once I found an adult, I sat approximately four meters from that focal lizard for a three-minute habituation period. The tethered juvenile was then placed within 1 m of a resident lizard. Care was taken to ensure that the juvenile was placed within view of the adult focal lizard. Once the juvenile was placed near the adult, the trial lasted three-minutes or until the adult attempted to attack the juvenile. The time trial started when the juvenile was placed in front of the resident. Male *P. pityusensis* have ritualized aggressive and courtship displays. Therefore, it was easy to distinguish between territorial aggression and attempted predation. When adults attacked, juveniles were quickly lifted out of their reach to avoid injury. If, in the first 20 seconds, the focal adult moved farther than a meter away from its original position in the opposite direction of the juvenile, the trial was deemed invalid and another focal adult was found and the experiment was repeated. It is possible that adult lizards would not attack the juvenile because they were not hungry. To control for this possibility I did the following: in adult lizards that did not attack the juvenile lizard after three-minutes, I retrieved and untethered the juvenile and immediately replaced it with a caterpillar – a known food source of *P. pityusensis* (Dappen personal obs.). I then placed the caterpillar within one meter of the focal adult and allowed the lizard three-minutes to attack it. All trials were recorded with a video camera.

Video analysis was performed following all of the trials. A decision was made when analyzing the footage as to whether the resident adult was chasing the juvenile out of its territory or attempting to cannibalize. Focal adults that attacked the juvenile within the three-minute period were considered cannibals. If the focal adult did not attack the juvenile, but ate the caterpillar that was subsequently presented to it, the focal adult was considered a non-cannibal. If the lizard did not attempt to eat the juvenile or the caterpillar, I assumed the lizard was not hungry and these data were not included. After each successful trial, the focal adult was captured using a noose and I recorded its SVL, and mass before releasing it. Differences in juvenile size, color, and sex did not appear to affect the cannibalistic behaviors of focal adults in these trials, as all 14 juveniles used in the cannibalism trials were attacked at least once.

To investigate whether sex influences cannibalistic propensities in adult lizards, I compared the proportion of cannibalistic/non-cannibalistic males to the proportion of cannibalistic/non-cannibalistic females using a chi-squared test of independence. To investigate whether adult size influenced cannibalistic propensities, I compared the SVL and mass of cannibalistic males and females to non-cannibalistic males and females using ANOVA. Finally, I present raw data comparing the number of cannibals to non-cannibals to illustrate the propensity of cannibalistic behavior in males and females.

Clay Model Predation Experiments

To investigate whether predation pressure differs between open and vegetated habitats, I performed a clay model predation experiment. Using a silica mold formed from a preserved specimen of *P. pityusensis*, I crafted lizard replicas from pre-colored, non-toxic SCULPEY III® brand plasticine modeling clay (Polyform Products Co., Illinois). Plasticine modeling clay has been used in previous predation experiments because impressions from the teeth, beak or claws of predators will remain identifiable on the clay (Saporito et al. 2007). These marks allow investigators to estimate predation pressure on replicas that differ in color and to identify the predator types preying on these clay replicas.

I created a total of 300 clay-model lizard replicas; 100 replicas matched the spectral characteristics of conspicuously green lizards (Figure 4.5a); 100 models matched the spectral characteristics of conspicuously blue lizards (Figure 4.5b); and 100 matched the spectral characteristics of cryptic brown lizards (Figure 4.5c). All three color-forms can be found on Formentera. For details on how I matched clay color to actual lizard colors see Chapter 3.

I conducted three 24 h predation trials over six days at three different locations in the Cap de Barbaria. In each of these trials, I laid out models along three transects. In each transect, I walked until I found an open habitat. In that open habitat, I placed one replica of each color no closer than 1.5 m to another replica on the ground (models in each patch were never further than 5m from one another). I then continued walking the transect until I encountered a vegetated habitat, in which I again placed one replica of each color no less than 1.5 m apart on the ground below the vegetation. I continued walking the transect and laying replicas in alternating habitat types until all models were in the field. In the first and second trials predators destroyed some lizard replicas irreparably. Thus, I had less than 100 replicas to lay out in the second and third trials. After the three 24 h trials, 145 lizard replicas of each color had been placed in unique open habitats and 145 in unique vegetated habitats (N=290 of each replica color, N=145 of each replica color in each habitat type). After each 24-hour trial I collected the lizard replicas and inspected each one for evidence of predation. When a replica was attacked, I noted the color of the replica, the predator type (lizard, avian, or rodent) and the habitat where that replica was placed.

To test whether conspicuous lizard replicas are attacked more than cryptic replicas, I compared predation events on replicas of each color using a chi-squared test of independence. To test whether conspicuous lizards are attacked more in open habitats versus vegetated habitats and whether more attacks occur in open versus vegetated patches, I compared the number of attacks on each replica color between open versus vegetated habitats and the total number of attacks on all models between the two habitats using chi-squared tests of independence. To test whether predator types differed in open versus vegetated habitats I compared attack rates by each predator type between habitat types using a Chi-squared goodness of fit. Because adult lizards are unlikely to kill other adult lizards, but are likely to kill juveniles, lizard attacks on replicas represent increasd predation risks for juveniles only. On the other hand, predation events by avian predators represent predation risk on both adults and juveniles. Therefore, I also compare predation events between habitats by predator type using chi-squared tests of independence. All statistical analyses were done in JMP 9.0 (SAS).

Results

Habitat Surveys

In total, I captured 82 lizards in the 52 pitfall traps that I laid out in the open and vegetated habitats (104 trap-hours). I captured a total of 26 adult males, 48 adult females and 8 juveniles. There were significantly more adult females than adult males in vegetated (males=20, females=42, DF=1, χ^2=7.81; P=0.0052), but not in open habitats (males=6, females=6, DF=1, χ^2=0.00; P=1.0000). Open and vegetated habitats differed significantly in the number of adult males (males in vegetation=20, males in open=6; DF=1; χ^2=7.54; P=0.006), females (females in vegetation=42, females in open=6; DF=1; χ^2=27.00; P<0.0001), and juveniles (juveniles in vegetation=0, juveniles in open=8; DF=1; χ^2=8.00; P=0.0047; Figure 4.6).

Adult male lizards found in vegetated habitats had a significantly greater SVL (mean male SVL in open habitats (N=6)=72.50mm, SE±2.15; mean male SVL in vegetated habitats (N=20)=78.40mm, ±1.17; F=5.82, P=0.0238) and mass (mean male mass in open habitats (N=6) =9.13 g, ±1.04; mean male mass in vegetated habitats

(N=20) =12.23, ±0.57; F=6.88, P=0.0149) compared to adult male lizards in open habitat (Figure 4.7). However, this difference did not exist in females (mean female mass in open habitats (N=6) =7.25 g, ± 0.68, mean female mass in vegetated habitats (N=42) =7.07, ±0.26; F=0.06, P=0.807; mean female SVL in open habitats (N=6)=68.00mm, ± 2.01; mean female SVL in vegetated habitats (N=42)=68.24mm, ±0.76; F=0.012, P=0.912).

Cannibalism Trials

Aggression by adults on juveniles appears to be common. Of the 14 juveniles that I collected in the juvenile capture survey, every individual had signs of previous aggressive encounters with adults. All but one juvenile had bite-mark scars on their bodies or tails and the individual with no bite-mark scars was missing its tail. On average, juveniles had 1.36 (SE ±0.31) bite-mark scars on their body and 1.86 (SE ±0.48) bite-mark scars on their tail (Figure 4.8a). Eleven of the 14 lizards either had a new tail or were missing their tail (Figure 4.8b).

In total I performed cannibalism trials on 23 adult lizards—13 males and 10 females. In total 17 lizards attempted to cannibalize tethered juveniles, while only 6 were non-cannibals (did not attack the tethered juvenile, but did eat the tethered caterpillar; Figure 4.9). There was no significant difference in the cannibalistic propensities between the sexes (males: 8 cannibals versus 5 non-cannibals; females: 9 cannibals versus 1 non-cannibal; χ^2=2.38, P=0.123; Figure 4.10). Cannibalistic and non-cannibalistic females did not differ in SVL (average SVL cannibalistic female=66.56, ±1.38; average SVL non-cannibalistic female=65.00, ±4.13; F=0.128, P=0.7299) or mass (average mass cannibalistic female=7.64, ±0.35; average mass non-cannibalistic female=8.00, ±1.05;

F=0.106, P=0.754). However, cannibalistic males had a smaller average SVL than non-cannibalistic males (average SVL cannibalistic male=74.57, ±1.09; average SVL non-cannibalistic male=79.00, ±1.29; F=6.833, P=0.0259; Figure 4.11), while mass appeared to have no effect on this behavior in males (average mass cannibalistic male=11.21, ±0.52; average mass non-cannibalistic male=12.00, ±0.62; F=2.13, P=0.1751).

Clay Model Predation Experiments

I recovered 861 of the 870 replicas placed on different transects in the Cap de Barbaria. Models that were not found (N=9) are not included in these analyses. Of all the recovered replicas, 148 (16.44 % of all replicas used in study) were attacked; I attributed 62 attacks to avian predators (41.89% of attacks), 72 attacks to lizards (48.65% of attacks), and 14 to rodents (9.46 % of attacks). Replica forms were attacked at different rates when considering all predation events (blue=73, green=57, brown=20; DF=2, χ^2=29.56, P<0.0001; Figure 4.12a) and when considering predation events by only avian predators (blue=35, green=16, brown=11; DF=2, χ^2=15.52, P=0.0004; Figure 4.12b) and only lizards (blue=29, green=37, brown=6; DF=2, χ^2=21.58, P<0.0001; Figure 4.12c). However, rodents attacked replicas of all colors at similar rates (blue=7, green=4, brown=3; DF=2, χ^2=1.86, P=0.3591; Figure 4.12d). When considering predation events by all predators in open habitats replica color forms were attacked at different rates (blue=40, green 26, brown=12; DF=2, χ^2=15.08, P=0.0005). Blue replicas had a non-significant tendency to be attacked more than green models (blue=40, green=26, DF=1, χ^2=2.97, P=0.0848) and were attacked significantly more than brown replicas (blue=40, brown=12; DF=1, χ^2=15.08, P<0.0001), and green models were attacked significantly more than brown models (green=26, brown=12; DF=2, χ^2=5.16, P=0.0231). Predation events of replica color forms also differed in vegetated habitats when considering predation events by all predators in vegetated habitats (blue=33, green=31, brown=8; DF=2, χ^2=16.08, P=0.0003). In vegetated habitats, blue and green replicas were attacked at similar rates (blue=33, green=31, DF=2, χ^2=0.0625, P=0.8026) and both blue and green replicas were attacked significantly more than brown replicas (blue=33 versus brown=8; DF=1, χ^2=15.24, P<0.0001; green=33 versus brown=8; DF=1, χ^2=13.56, P=0.0002).

When considering predation events by all predatory types, there was no difference in the total number of predation events on lizard replicas in open versus vegetated habitats (open=84, vegetated=73; DF=1, χ^2=0.771, P=0.380; Figure 4.13). This result was consistent for all model colors (blue: open=40, vegetated=33, DF=1, χ^2=0.67, P=0.4126; green: open=26, vegetated=31, DF=1, χ^2=0.44, P=0.5078; brown: open=12, vegetated=8, DF=1, χ^2=0.80, P=0.3711). However, with the exception of predation events by rodents, predation events by predator type differed significantly between habitat types (Figure 4.14). Lizard replicas placed in open habitats were significantly more likely to be attacked by avian predators compared to replicas placed in vegetated habitats (open=53, vegetation=9, DF=1, χ^2=31.23, P<0.0001; Figure 4.14a). Conversely, lizard replicas placed in vegetated habitats were significantly more likely to be attacked by lizards than replicas placed in open habitats (open=21, vegetation=51, DF=1, χ^2=12.50, P=0.0004; Figure 4.14b). However, lizard replicas placed in open and vegetated habitats were equally likely to be attacked by rodents (open=5, vegetation=9, DF=1, χ^2=1.14, P=0.2850; Figure 4.14c).

Discussion

Traits that are shared among age groups may be subject to intralocus ontogenetic conflict due to age-specific natural and sexual selection. This antagonistic selection among age groups may strongly influence the evolution of display characters such as conspicuous coloration. In this study, I investigated factors that may result in antagonistic selection on conspicuous color expression among age groups to help understand the adaptive significance of ontogenetic color changes in *P. pityusensis*. Results from a habitat preference survey, a juvenile capture survey, cannibalism trials, and a clay model predation experiment suggest that lizards from different age groups may interact with the environment and with one another in unique ways. These age-specific interactions may result in antagonistic selection on color expression among age groups that could potentially influence the evolution of ontogenetic color change.

One way for selection to differ among age groups of the same species is for individuals of different ages to occupy unique habitats (Stamps 1983; Werner and Gilliam 1984). I performed a habitat preference survey to see whether differences in age class, size, or sex affected habitat settlement patterns in *P. pityusensis*. I found that adults and juveniles occupy different habitats. There were significantly more adult lizards in vegetated habitats and significantly more juveniles in open habitats. Ontogenetic habitat shift are common in reptiles (Andrews 1971; Bohlin 1977; Keren-Rotem et al. 2005; Scott et al. 1976; Stamps 1983) and are often attributed to changes in diet (Keren-Rotem et al. 2005; McCauley and Bjorndal 1999; Mushinsky et al. 1982). Dietary shift as a function of size is expected in most carnivorous reptiles, because as individuals increase in size they can consume larger prey (Schoener 1967; 1968; 1977; Sexton et al. 1972). Considering the large size difference between adult and juvenile *P. pityusensis*, diet may differ among age classes of this species as well, however, age-specific differences in diet are unlikely to fully explain ontogenetic habitat use in this species.

Intraspecific competition and aggression may also lead to spatial or temporal niche separation among age groups (Schall 1974; Stamps 1983). Most environments have high quality habitats interspersed throughout lower quality marginal habitats. When the ability to compete for these habitats depends on age and/or size, consistent differences in settlement patterns may occur among age groups. I found that adult male lizards in vegetated habitats had a larger SVL and mass compared to adult male lizards found in open habitats, suggesting that the largest adult males may competitively exclude smaller males from the high quality breeding sites. The high abundance of female *P. pityusensis* in vegetated habitats and the difference in size between males found in vegetative versus open habitats suggests that vegetated patches may represent valuable breeding sites that male lizards compete over.

Duckworth (2006) experimentally demonstrated that more aggressive male western bluebirds compete more effectively for high quality territories and, as a consequence, aggressive and non-aggressive males were sorted into distinct habitats with consistent differences in selection on morphology. Intraspecific competition in *P. pityusensis* may similarly sort individuals of different age groups into distinctly high and low quality habitats. Several authors have noted that delayed plumage maturation is more common in bird species that fiercely compete for limited breeding sites (Ficken and Ficken 1967; Orians 1961; Selander 1965). Perhaps the same is true for the occurrence of ontogenetic color change in reptiles. Conspicuous color in *P. pityusensis* (Chapter 2) and other lacertids (Anderholm et al. 2004; Olsson 1994) has been shown to honestly signal fighting ability. Aggressive encounters escalate to fights more commonly among well-matched individuals (Hofmann and Schildberger 2001). If smaller males fully express conspicuous color before they are able to compete with the largest males, they may elicit fights with large males and risk serious injury.

Another factor that may influence the differences in settlement patterns observed among age groups of *P. pityusensis* is cannibalism. I performed a juvenile capture survey and cannibalism trials to investigate the occurrence of cannibalism in *P. pityusensis*. I found that all juvenile lizards had bite-mark scars on their body and tail and/or were missing their tail or had regrown it. Further, the majority of adult lizards in the cannibalism trials attempted to cannibalize juveniles. These results, coupled with my observations of intraspecific predation in the field suggest that cannibalism may be common in *P. pityusensis*. Adults are abundant in vegetation and the risk of being cannibalized may drive juveniles to relatively adult-free open habitats. This explanation is consistent with the result that all juveniles captured in the habitat preference survey occurred in open habitats, where adults were scarce. Similar ontogentic habitat shifts that allow juveniles to minimize interactions with adults occur in arboreal *Anolis* lizards (Irschick et al. 2000; 2005; Moermond 1979; Schoener 1970). Keren-Rotem et al. (2005) found that juvenile and adult common chameleons occupied different habitats, that juveniles actively avoid the presences of adults, and that adults would readily attack and consume juveniles. They concluded that the risk of cannibalism towards juveniles was an important selective force behind the ontogenetic habitat shift observed in the common chameleon (Keren-Rotem et al. 2005). In the present study, the abundance of adult lizards in vegetated habitats, the presence of juveniles in only open habitats, the high number of bite-mark scars on juveniles, and the common occurrence of cannibalistic behavior among adult lizards suggest that the risk of cannibalism towards juveniles may also be an important selective force behind the ontogenetic habitat shift observed between adult and juvenile *P. pityusensis*.

It is currently unclear what factors influence cannibalistic behaviors in *P. pityusensis*. Research suggests that cannibalism is often influenced by age, size, sex, population density, food availability, habitat heterogeneity and other factors (Castilla and Van Damme 1996; Collins and Cheek 1983; Fox 1975; Gehlbach 1971; Heusser 1970; Pafilis et al. 2009; Polis 1981; Polis and Myers 1985). In this study I found no difference in the propensities of cannibalistic behaviors of males and females. I did, however, find a difference in the SVL, but not mass between cannibalistic and non-cannibalistic males. Unexpectedly, adult males with a smaller SVL were more likely to be cannibals. One explanation for this result may be that smaller adult males are frequently outcompeted by larger adult males for high quality vegetated habitats, forcing them into marginal habitats where juveniles are common. Because these smaller adults also lack the nutrition afforded to larger males in high quality habitats, they may incorporate juveniles into their diet more readily than larger males.

Predation plays a fundamental role in the evolution of colors and patterns in many species (Cooper 1999; Endler 1983a; Endler 1986; Hamilton and Zuk 1982; Morehouse and Rutowski 2010; Zahavi 1975; Zuk and Kolluru 1998). In a previous study, I demonstrated that conspicuously colored clay lizard replicas are attacked more frequently than cryptic lizard models (Chapter 3). My results from the present study are consistent with those results when considering predation events by all predator types and when comparing predation events by lizard and birds alone.

Differences in the intensity and form of predation between habitats that are occupied by different age classes may generate antagonistic selection on traits shared among age groups. For example, in the tropical python, neonates hatch either yellow or red and both change to green with age. In a rare demonstration of the adaptive significance of full-body ontogenetic color changes in reptiles, Wilson et al. (2007) demonstrated that yellow and green provides camouflage from visually oriented avian predators in the different habitats used by juveniles and adults. In the present study, predator types differed significantly between habitats. Lizard replicas were more likely to be attacked by avian predators in open habitats, while replicas in vegetated habitats were more likely to be attacked by real lizards. This result suggests that predation intensity on adult lizards is greater in open habitats than vegetated habitats because, while adult lizards may kill and eat juveniles, they are not likely to kill adult lizards. As such, increased predation events by lizards on replicas placed in vegetation suggests that adult lizards are more likely to be exposed to intraspecific aggression in vegetation while juveniles may experience an increased risk of cannibalism in vegetation. The lack of attacks by avian predators on lizard replicas placed in vegetation may imply that lizards large enough to not be cannibalized may reduce their risk of avian predation by occupying vegetated habitats.

Research on the adaptive significance of ontogenetic color changes in reptiles is scarce (Booth 1990; Cooper and Greenberg 1992), and of those that exist, few studies explicitly test adaptive hypotheses. Currently, the existing framework for understanding ontogenetic color changes in lizards focuses on color changes associated with 1) thermoregulation, 2) interspecific mimicry, 3) intraspecific mimicry (i.e. female mimicry), 4) crypsis, and 5) status signaling. Many populations of *P. pityusensis* become darker as they get older and larger and this change (presumably a result of increased melanin production) may be the result of a need to thermoregulate more effectively at larger sizes (Cirer and Martinez-Rica 1990; Martinez-Rica and Cirer 1982); however, this thermoregulation hypothesis is not likely to explain the change juveniles undergo from being cryptically brown to bright green or blue. The interspecific mimicry hypothesis is equally unlikely to explain ontogenetic color changes in *P. pityusensis* as these lizards do not resemble any other organisms in the Pityusic archipelago.

Some researchers have hypothesized that juveniles of various reptiles will mimic female coloration to reduce intraspecific aggression by adults (Carpenter 1995; Husak et al. 2004; Lemos-Espinal, et al. 1996; Montanucci 1978; Werner 1978). Female mimicry may be an alternative reproductive strategy among adult male lizards (Werner 1978; Whiting et al. 2009); however it does not appear to generally explain female-like coloration in pre-reproductive individuals. Juvenile *P. pityusensis* often resemble females with respect to color. However, the frequency of cannibalism on juveniles by adults makes female mimicry a risky strategy and is therefore also an unlikely explanation for ontogenetic color changes in this species.

In a review of ontogenetic color change Booth (1990) concluded that, while ontogenetic color changes occur under extremely diverse circumstances, background matching to avoid predation (crypsis hypothesis) and mate/competitor recognition (status signaling hypothesis) are the most commonly suggested adaptive functions of ontogenetic color changes in vertebrates. Similarly, in a review of delayed plumage maturation in birds, Hawkins et al. (2011) concluded that delayed plumage maturation is most often explained by the crypsis and/or status-signaling hypotheses.

In the present study, I demonstrated that adult and juvenile *P. pityusensis* are found in distinct habitats and that adult males found in vegetated habitats are larger than those found in open habitats. This size difference, however, does not occur among adult females. I also demonstrated that adult males and females are highly cannibalistic and that juveniles frequently suffer from this behavior. Finally, I showed that conspicuous lizard replicas are attacked more by predators than cryptic replicas and that risk of predation may be greater in open habitats compared to vegetated habitats, because predator types differ between these two habitats—clay lizard replicas are more likely to be attacked by lizards in the vegetation and avian predators in open habitats. These results support the hypothesis that intraspecific competition among adults for high quality habitats, and cannibalism by adults on juveniles, force smaller adults and juveniles, respectively, to occupy more exposed, lower quality open habitats, where the costs of being conspicuously colored (as a result of avian predation) may be higher. These results support the crypsis and status-signaling hypotheses as adaptive explanations for ontogenetic color change in *P. pityusensis*. Together with previous research suggesting that conspicuous color is favored in adult male *P. pityusensis* by sexual selection (Chapter 2) and the observation that different populations of *P. pityusensis* vary in their degree of ontogenetic color change, this research suggests that conspicuous color expression may be subject to antagonistic selection among age groups—it is favored in adult males by sexual selection yet it is disfavored in juveniles and small adults due to increased conspicuousness to predators and conspecifics. This antagonistic selection may drive intralocus ontogenetic conflict and may constrain the adaptive evolution of this display trait. Variation in the strength of intralocus ontogenetic conflcit among populations may broadly explain variation in ontogenetic color changes in many lizard species. Hormones are thought to mediate developmental changes in the expression of display trait in many species (Cooper 1984; Cooper and Crews 1987; Cooper and Greenberg 1992; Huyghe et al. 2009b; Lande 1980; Lande 1982a; Lande 1987; Sinervo and Calsbeek 2003; Tobler et al. 2011; Witschi 1961). Changes in hormone expression that regulate the expression of display traits may also affect other aspects of an organism's morphology, physiology and behavior (Adkins-Regan 2005; Sinervo and Calsbeek 2003).

Few studies have investigated the adaptive significance of ontogenetic color changes in lizards or how cannibalism might influence the evolution of display traits in this group (Rand and Andrews 1975). Given that cannibalism is common in many lizard species that live in variable habitats, the results from this study may help explain ontogenetic color changes in many lizards. Age-specfic selection on color can only drive intralocus ontogenetic conflict, if ontogenetic color change itself has a heritable basis (Westphal and Morgan 2010). Future research should focus on understanding the heritable basis for developmental color expression in this species. Further studies on the evolution of ontogenetic color change in *P. pityusensis* should investigate whether variation in habitat heterogeneity among different island populations influence variation in ontogenetic color changes in predictable ways. Finally, little is known about the effect of cannibalism on lizard ecology, behavior, morphology or physiology and less is known about the evolution of this behavior itself. Researchers should investigate the conditions that favor cannibalism, the heritable basis for this behavior, and the effects of this intraspecific predation on lizard ecology and evolution.

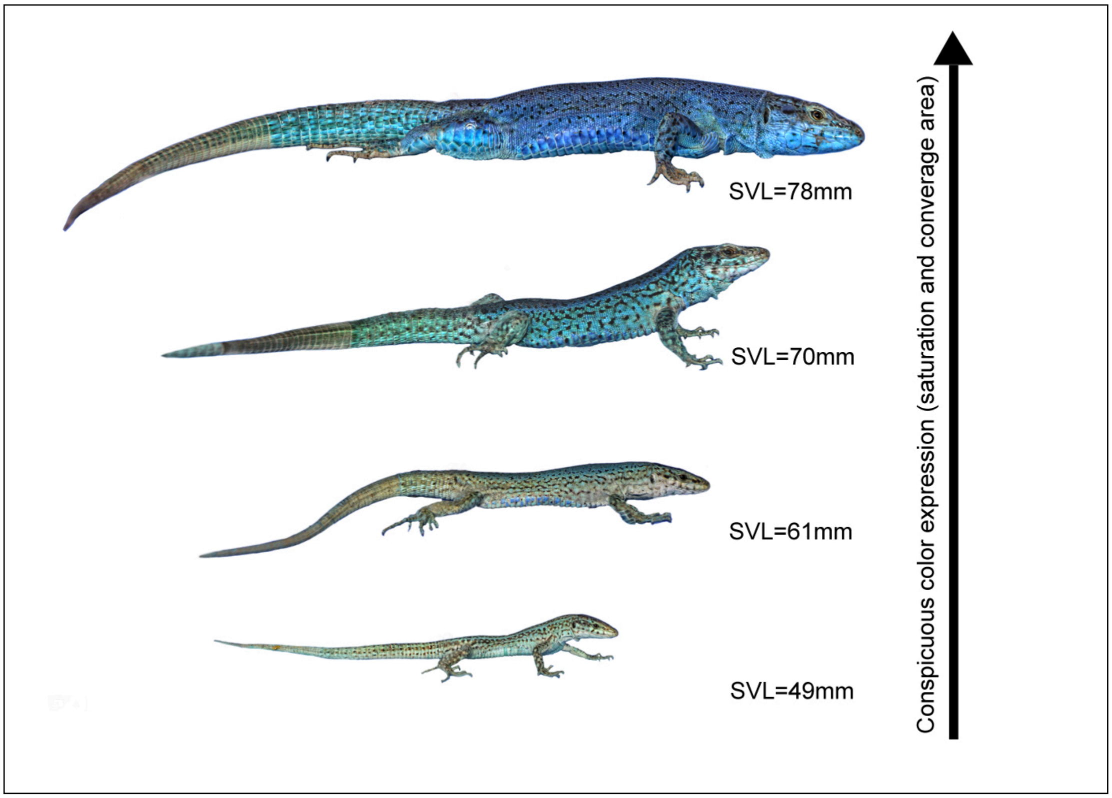

Figure 4.1 Examples of a male *P. pityusensis* that vary in age, size and color expression. Conspicuous green and blue colors increase in this species in both saturation and coverage area as lizards increase in size and age. As such, the largest lizards are generally the most conspicuously colored lizards.

Figure 4.2 An adult male *P. pityusensis* cannibalizing a juvenile on the island of Torreta. This adult has captured and killed a juvenile. Moments after this photograph was taken, the adult consumed the juvenile whole.

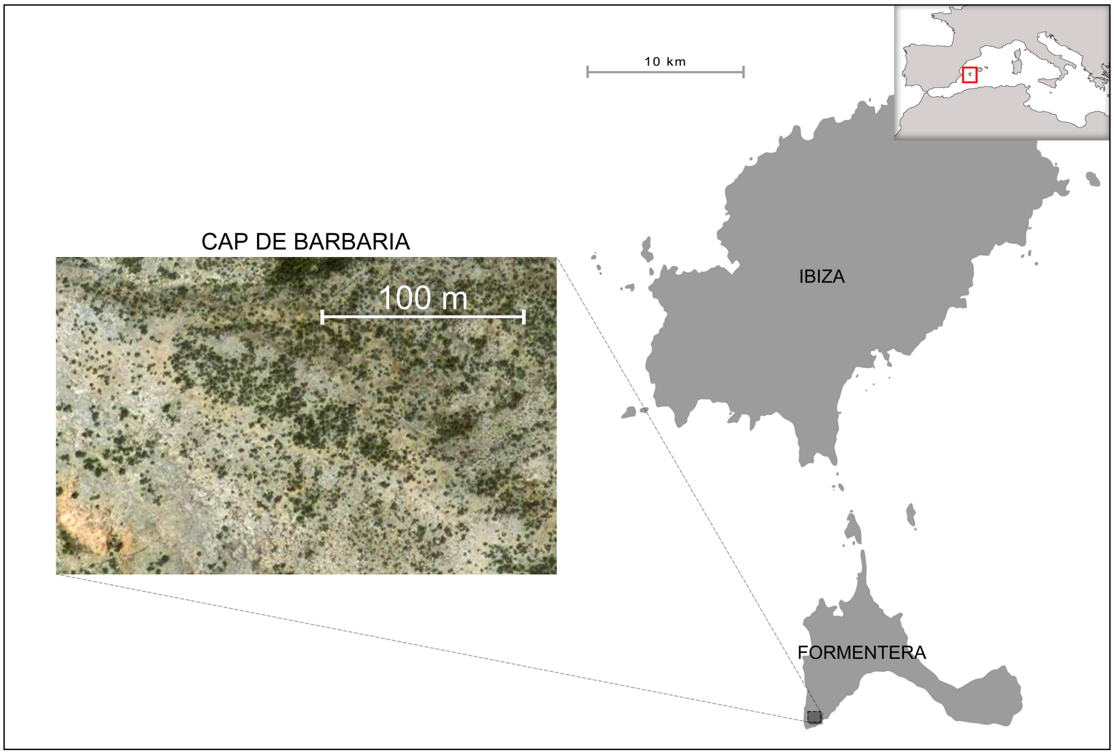

Figure 4.3 A map of the Pityusic Archipelago and an arial view of the Cap de Barbaria – the location on Formentera where this experiment was conducted.

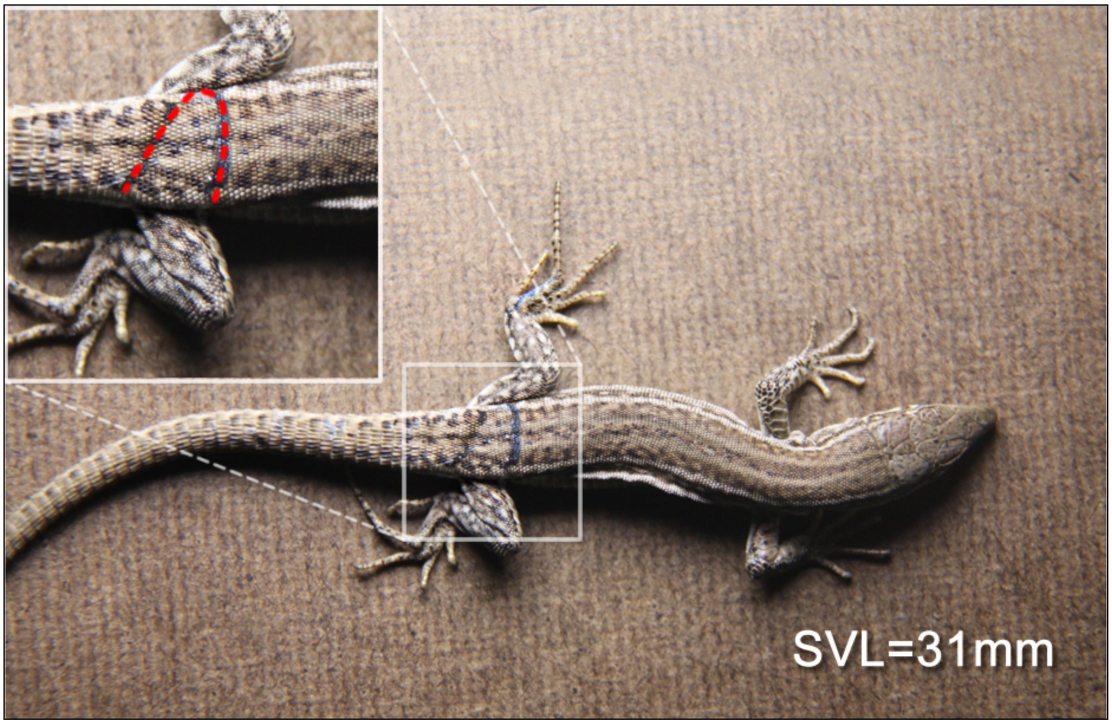

Figure 4.4 A juvenile *P. pityusensis* with a large bite-mark scar on its flank.

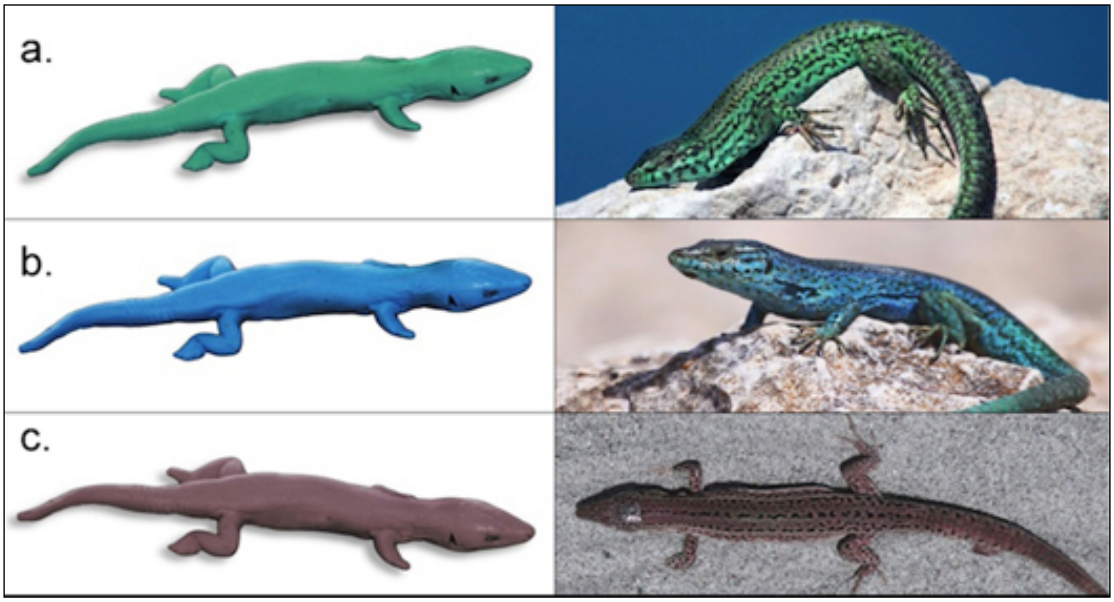

Figure 4.5 Clay model lizard replicas and their real-life counterparts from the island of Formentera. It is possible to find three distinct color forms of *P. pityusensis* on Formentera. I created 100 plasticine lizard replicas to resemble each these three color forms (N total=300).

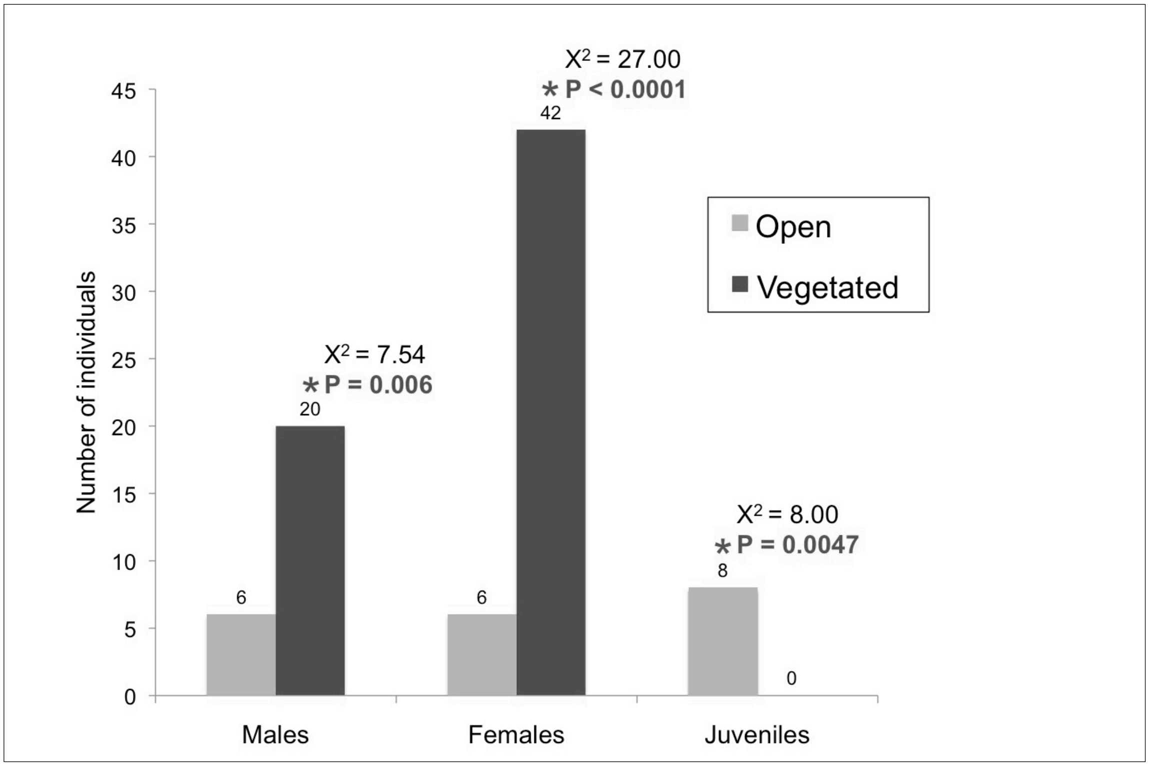

Figure 4.6 The effect of habitat type on the occurrence of males, females and juveniles.

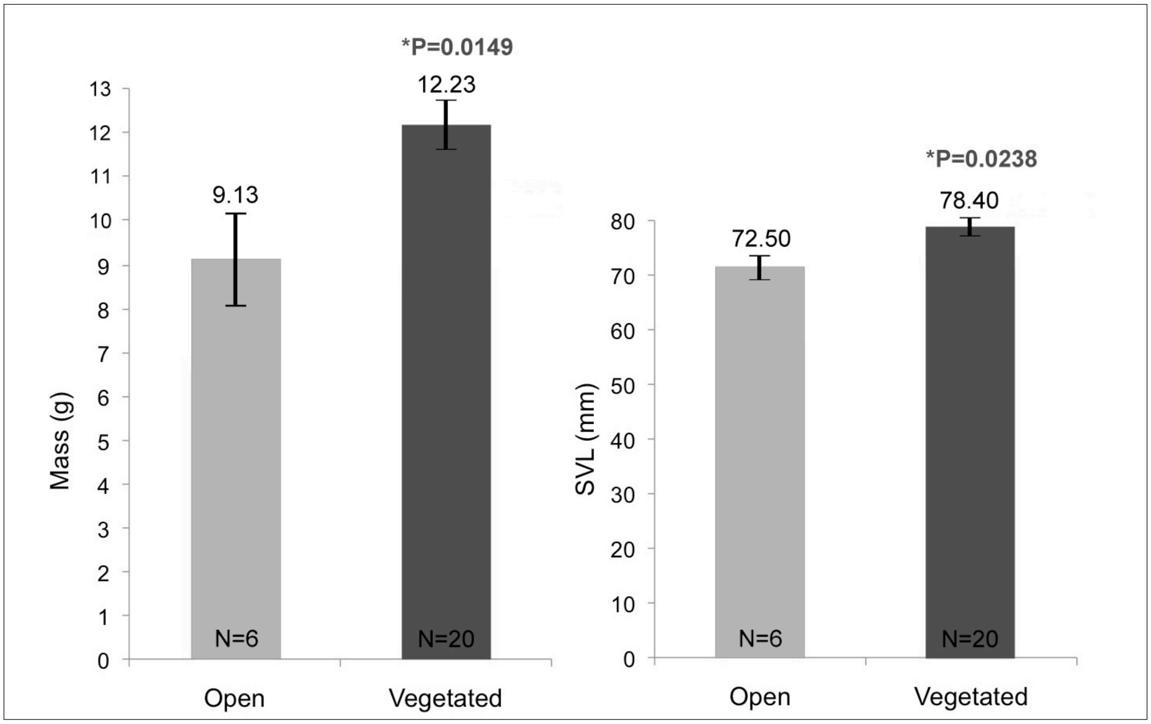

Figure 4.7 The mean mass and SVL of adult lizards in open and vegetated habitats.

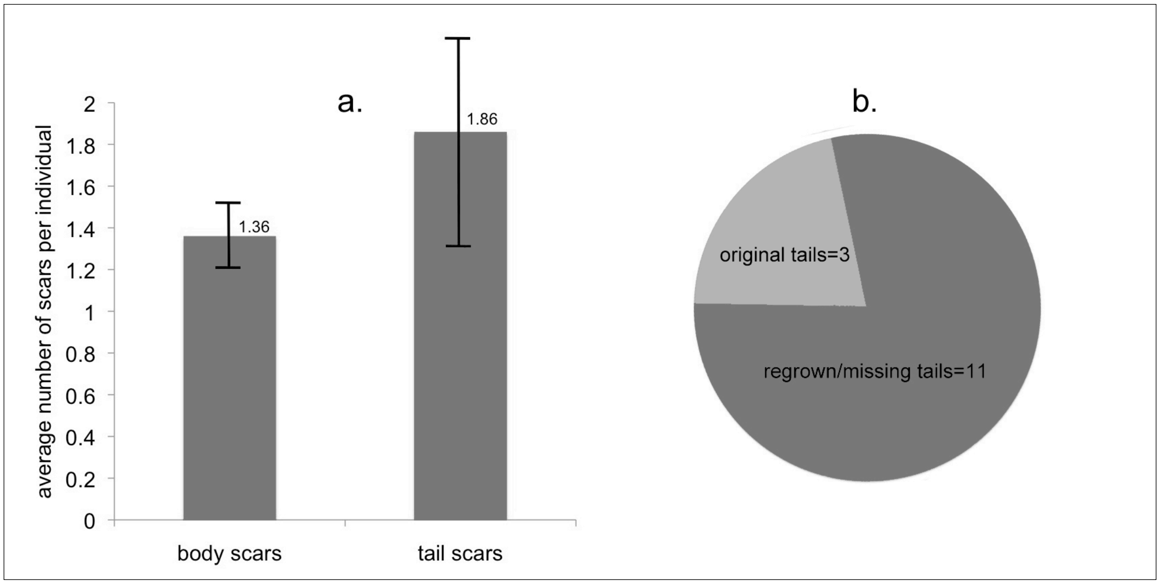

Figure 4.8 Results from the juvenile capture survey: showing a) the average number of bite-mark scars on captured juveniles' bodies and tails, and b) the number of juveniles captured with regrown or missing tails versus the number of juveniles with their original tails.

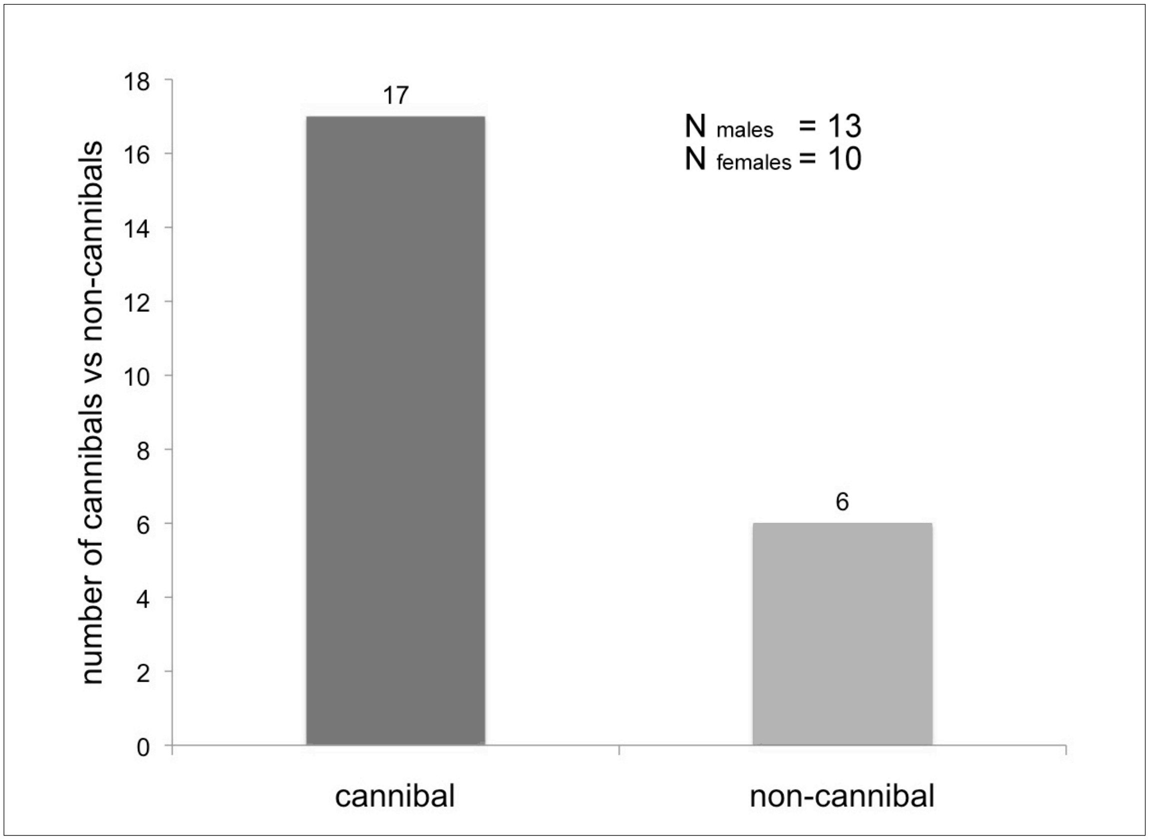

Figure 4.9 The cannibalistic propensities of Ibiza wall lizards: the total number of cannibals (lizards that attacked the tethered juveniles) versus the total number of non-cannibals (lizards that did not attack the tethered juvenile but attacked the teathered caterpillar).

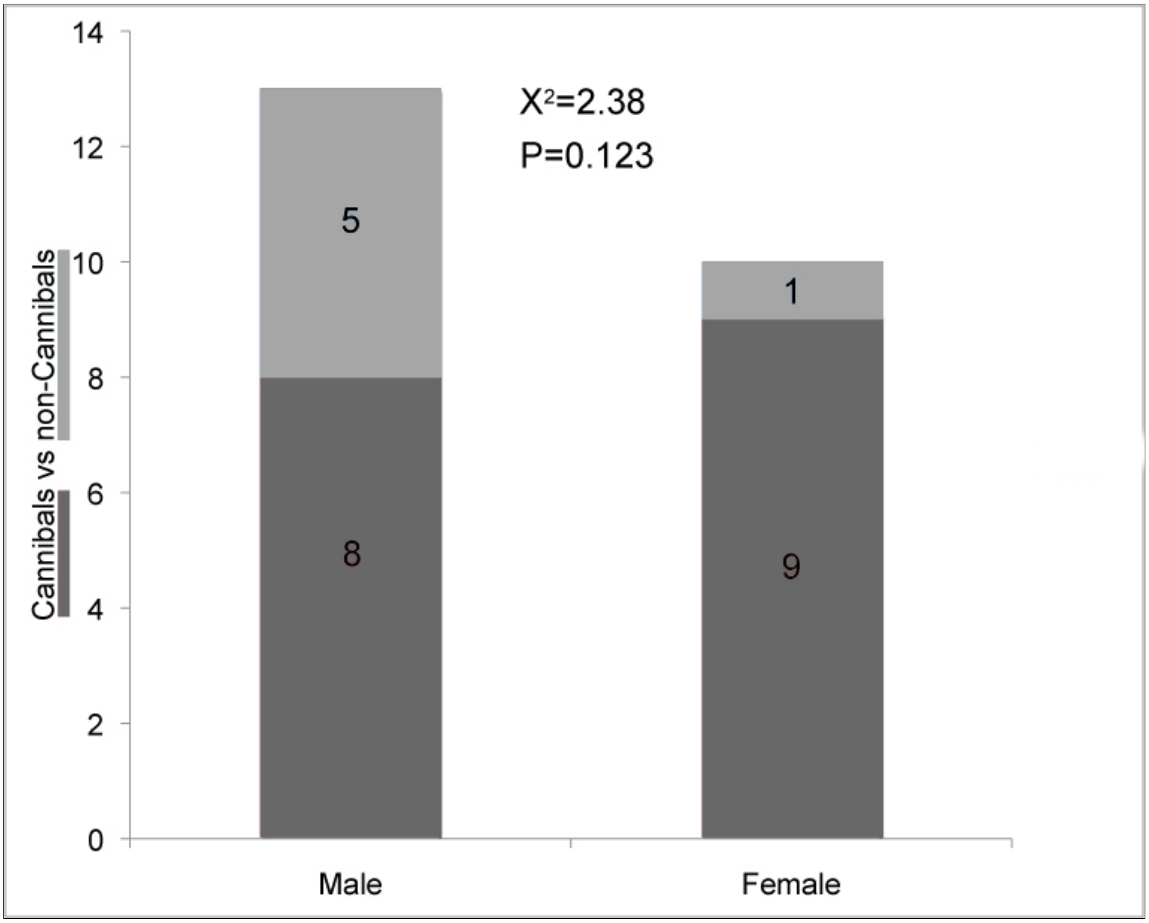

Figure 4.10 The proportion of cannibalistic versus non-cannibalistic males and females.

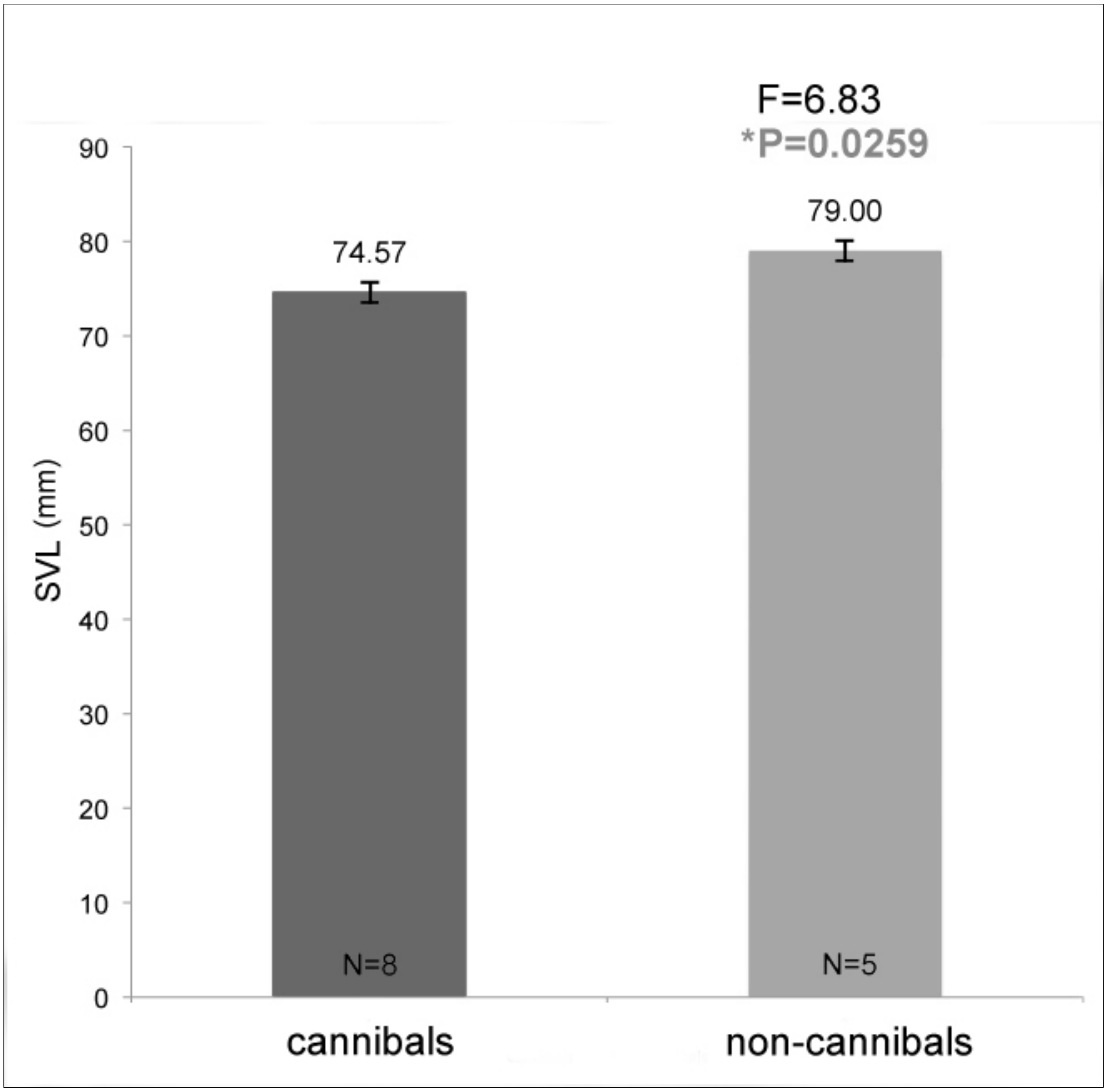

Figure 4.11 Average SVL of cannibalistic male lizards to non-cannibalistic male lizards.

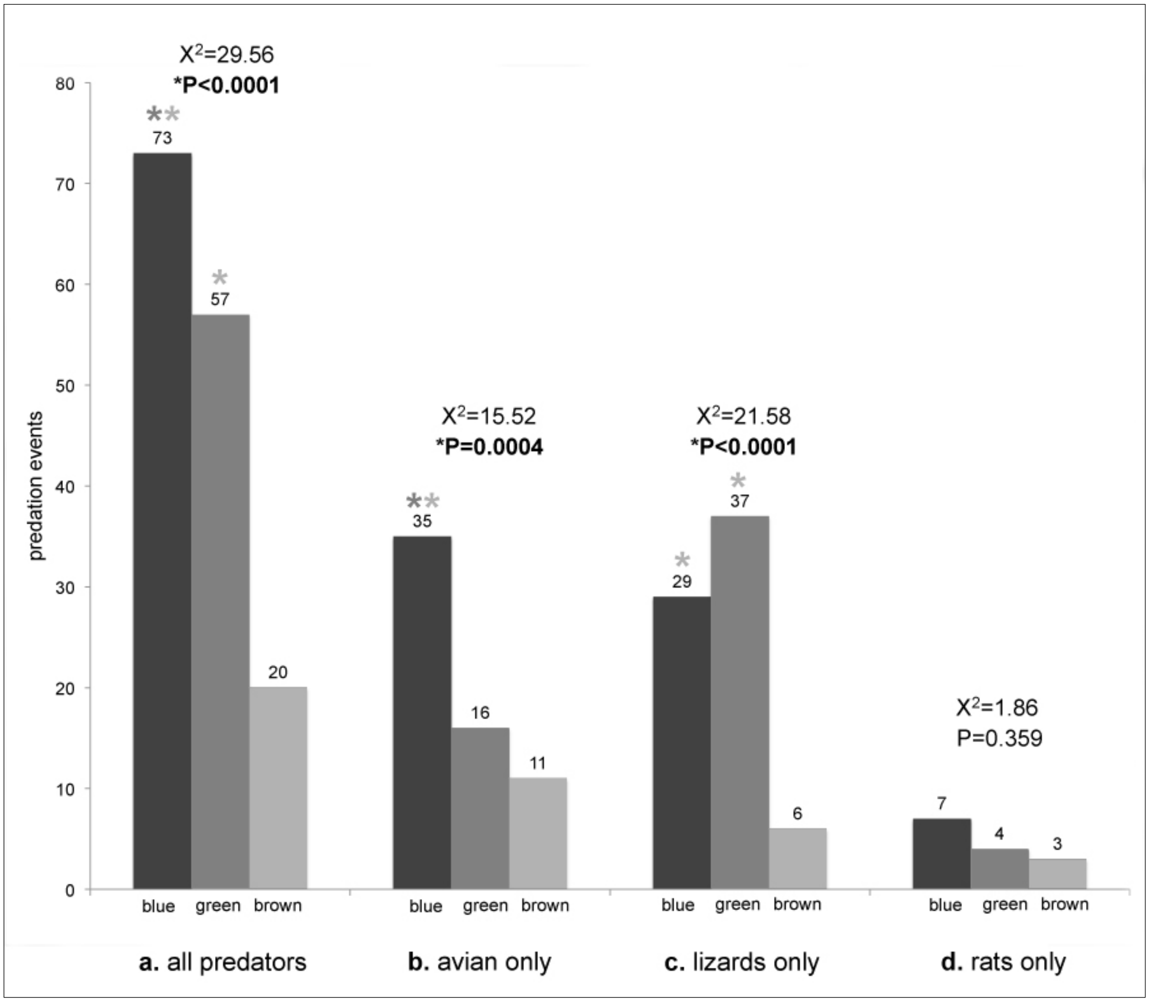

Figure 4.12 The effect of replica color on predation occurrence by predator type: (a) attacks on different colored models by all predators; (b) attacks on different model colors by avian predators only; (c) attacks on different model colors by lizards only; and (d) attacks on different model colors by rodents only.

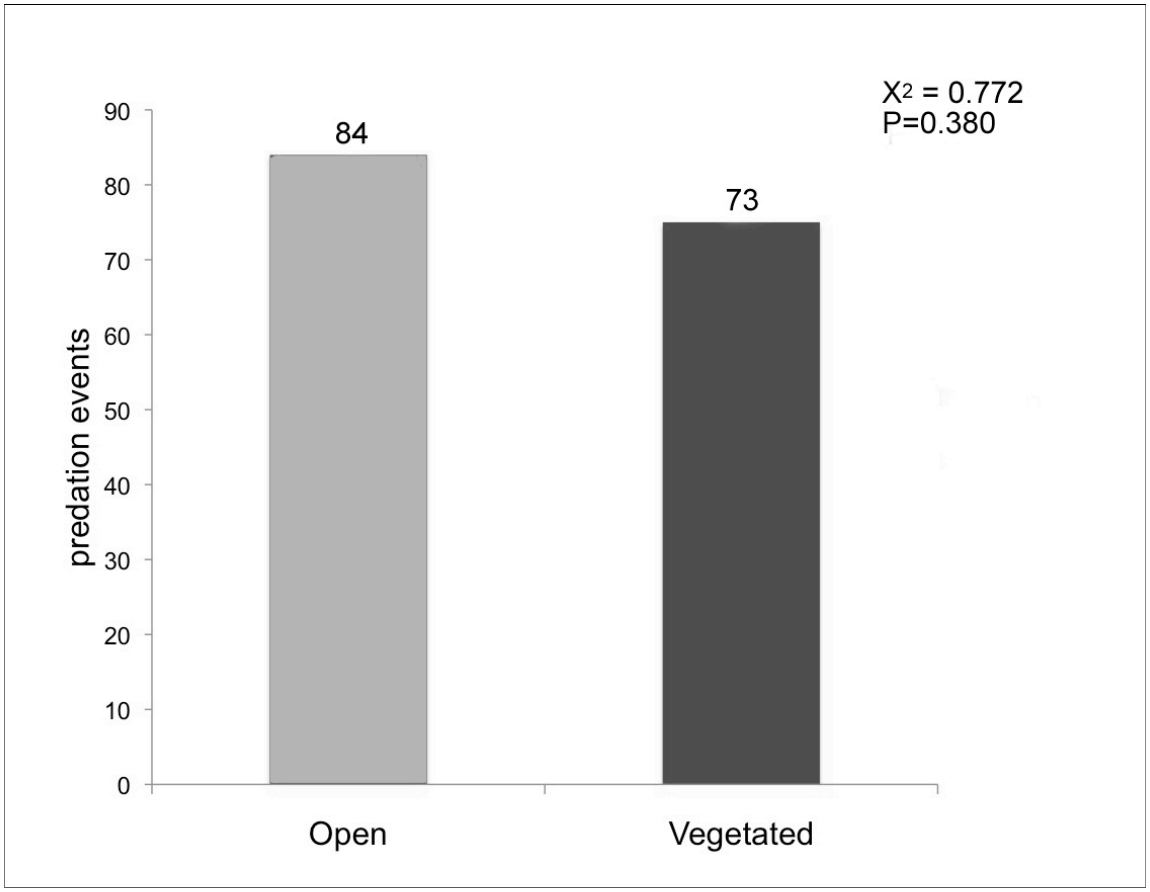

Figure 4.13 The effect of habitat type on predation occurrence.

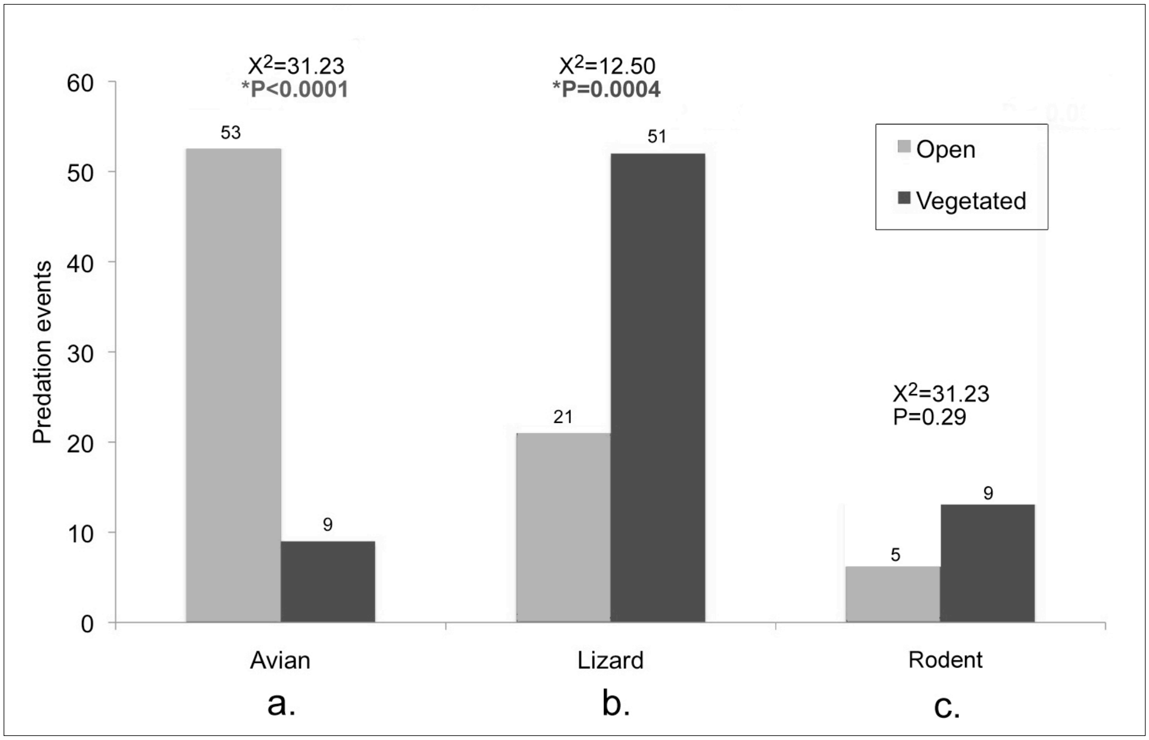

Figure 4.14 The effect of habitat type on predation occurrence by predator type: a) the number of avian predation events in open versus vegetated habitats; b) the number predation events by lizards in open versus vegetated habitats; and c) the number predation events by rodents in open versus vegetated habitats.

Chapter 5

Conclusions

In this dissertation, I investigated color evolution between the sexes and among age groups of the Ibiza wall lizard, *Podarcis pityusensis*. I first attempted to determine the adaptive significance of conspicuous color expression in male and female lizards by manipulating lizard color with tattoo ink and recording the effect of this manipulation on lizard social interactions. I found that conspicuous coloration might be favored by sexual selection in males as an honest signal of fighting ability in male-male contest competition. Female choice does not appear to influence color evolution in *P. pityusensis*. In females, male-typical color appears to serve no functional role. I suspect that, like many other species, female *P. pityusensis* express male-typical coloration due to a strong intersexual genetic correlation with males. That is, selection favoring the expression of conspicuous color in males has resulted in a correlated response on color expression in females.

Traits that evolve by sexual selection frequently evolve in opposition to other forms of natural selection such as predation (Endler 1980; Zahavi 1975). In the second part of my dissertation, I performed a clay model predation experiment using different colored plasticine clay lizard replicas to investigate how predation might influence the evolution of color in this species. I found that more conspicuously colored clay lizard replicas were attacked significantly more than cryptic models, suggesting that conspicuously colored lizards may also suffer higher predation rates than cryptically colored lizards. In light of my first experiment on the function of color in male and female lizards, these results suggest that conspicuous color expression may be subject to sexually antagonistic selection because conspicuous color seems to be favored in males by sexual selection as a signal for fighting ability, appears to play no functional role in females, and is disfavored in both sexes by predation.

My first two experiments focused on color evolution between the sexes. If color expression is controlled by similar genetic machinery in both sexes, the apparent sexually antagonistic selection that I found may drive intralocus sexual conflict over color expression. The logical next step would be to conduct a breeding experiment in order to determine the heritable basis for color expression in both sexes of this species. Also, while I was unable to identify a functional role for color expression in females, color may yet serve an adaptive purpose in females that was not relevant or detectable in the context of my experiment. For example, some researchers have found that female lacertids change color once pregnant and that this color change may result in less male harassment (Galan 2000). Perhaps the same is true in *P. pityusensis*. Future work should attempt to document potential changes in color expression at various reproductive stages in both males and females.

It seems unlikely that male-male contest competition, predation, and an intersexual genetic correlation can fully explain color evolution in this species. It is probable that other processes that influence color variation are also at work. Many researchers have suggested that color polymorphism in various lacertid species is maintained by alternative reproductive strategies in both males and females (Huyghe, et al. 2009a; Huyghe, et al. 2009b; Huyghe, et al. 2007; Svensson, et al. 2007; Vercken, et al. 2010). My research did not investigate the possibility of alternative reproductive strategies in *P. pityusensis*. However, within the population color diversity is often extraordinarily high in this species. The commonality of alternative reproductive strategies in lizards and the role of multiple-morph strategies in maintaining genetic diversity for color is intriguing. The possibility that alternative reproductive strategies might influence color evolution in *P. pityusensis* therefore begs further investigation.

Natural selection often differs among age groups of the same species due to the unique ways that individuals interact with the environment and one another during different stages of ontogeny (Anderson and King 1970). The last part of my dissertation therefore focused on color evolution among different age groups of *P. pityusensis*. Ibiza wall lizards undergo ontogenetic color changes as they transition from being hatchlings to fully mature reproductive adults. In general, juveniles tend to be cryptically colored, become more conspicuously colored as they approach reproductive maturity, and continue to increase in conspicuousness in adulthood. This change varies within and among populations. The last portion of my dissertation focused on identifying ways that selection on color might differ among age groups to help understand variation in ontogenetic color changes in the species.

I performed a habitat preference survey to determine whether adults and juveniles have different habitat settlement patterns; a juvenile capture survey and cannibalism trials to investigate the cannibalistic propensities of this species; and another clay model predation experiment to determine whether predation pressure differs between areas where adults and juveniles tended to settle. I found that adult and juvenile *P. pityusensis* may be subjected to unique selective pressures that could result in antagonistic selection on color among age groups. Adults and juveniles are found in different habitats—adults settle in vegetated habitats while juveniles settle in open habitats. Further, among adult males, larger individuals are found in vegetated habitats and smaller individuals in open habitats. I also found that adult lizards will readily kill and eat juveniles and that juveniles appear to have many bite-mark scars on their body, indicating that they are frequently attacked by adults. Further, predation on clay lizard replicas differed between the habitats where adults and juveniles are found. Replicas in vegetated habitats were attacked more by lizards, while replicas in open habitats were attacked more by birds.

The result from this last experiment support the hypothesis that intraspecific competition among adult *P. pityusensis* for high quality habitats, and cannibalism by adults on juveniles, force smaller adults and juveniles, respectively, to occupy more exposed, lower quality open habitats, where the costs of being conspicuously colored (as a result of avian predation) may be higher. Together with my results that suggest conspicuous color is favored in adult male *P. pityusensis* by sexual selection and the observation that different populations of *P. pityusensis* vary in their degree of ontogenetic color change, this research suggests that conspicuous color expression may be subject to antagonistic selection among age groups. Color appears to be favored in adult males by sexual selection yet it is disfavored in juveniles and small adults due to increased conspicuousness to predators and conspecifics. Other factors, such as age-specific male reproductive strategies (Whiting, et al. 2009) may influence ontogenetic color changes in *P. pityusensis*; however, the antagonistic selective pressures that I found among age groups are likely to contribute to the evolution of ontogenetic color changes in this species.

These findings are noteworthy because few studies have investigated the adaptive significance of ontogenetic color changes in lizards. In addition, to my knowledge, my study is the first study to tests how habitat heterogeneity and cannibalism might influence the evolution of display traits in reptiles. Given that cannibalism is common in many lizard species that live in variable habitats (Carretero, et al. 2010; Fox 1975; Keren-Rotem, et al. 2005; Pafilis, et al. 2009), the results from this study may help explain ontogenetic color changes in lizard species with similar life histories.

Much remains to be learned about color evolution in *P. pityusensis*. Most populations of this species are some shade or combination of blue, green and brown; however other populations express unique colors, and the adaptive significance of these colors are poorly understood. For instance, there are several melanistic populations of *P. pityusensis*. This black phenotype may be the result of mutations in melanocortin-1 receptor, agouti or other genes involved in the melanin-producing pathway (Uy, et al. 2009). Given the distribution of islands with black lizards, melanism may have evolved independently several times and undergone selective sweeps in different populations. Other islands have lizard populations that are orange, or almost red. This orange phenotype appears in different frequencies on many islands, and yet nothing is known about its adaptive significance. Further, little is know about the nature of these colors themselves. In most organisms, blue colors are the result of structural coloration while oranges, reds, and yellows are from carotenoids acquired through an organism’s diet. In birds, green feathers are often the result of blue structural colors mixed with yellow carotenoids. Similar mechanisms may be at work to produce the colors we observe in *P. pityusensis*; however, these studies have yet to be conducted. Color patterns also vary dramatically in these species. Some lizards have no dorsal patterning while others have black, green or blue patterning. To date, no studies have tested the adaptive significance of color pattern variation in this species.

In conclusion, my dissertation investigated the evolution of conspicuous color between the sexes and among age groups of *P. pityusensis*. The Ibiza wall lizard expresses an uncanny degree of color variation across its relatively small geographic range. My dissertation is the first body of work that empirically investigated color evolution in *P. pityusensis*; however, much research is needed to fully understand the evolution of color in this species. The study of animal coloration has been a powerful tool in our understanding many evolutionary processes (Hubbard, et al. 2010). The striking color variation expressed in *P. pityusensis* makes this species a model system for future work in ecology, evolution, and genetics.

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