A Study of the Biological Significance of a Male Color Polymorphism in the Lizard Sceloporus minor

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UNIVERSITY OF MIAMI

A STUDY OF THE BIOLOGICAL SIGNIFICANCE OF A MALE COLOR POLYMORPHISM IN THE LIZARD *SCELOPORUS MINOR*

By

Barry P. Stephenson

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
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the requirements for the degree of
Doctor of Philosophy

A STUDY OF THE BIOLOGICAL SIGNIFICANCE OF A MALE COLOR
POLYMORPHISM IN THE LIZARD *SCELOPORUS MINOR*

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Males of the Mexican lizard *Sceloporus minor* (Phrynosomatidae) exhibit striking variation in dorsal coloration, both within and among populations, which may have arisen by sexual selection. The possible significance of this trait was investigated through a combination of observational and experimental approaches. This research revealed that males in one population (La Manzana) in NW Hidalgo exhibit three discrete color morphs (blue, yellow, red) each characterized by morphological, physiological and behavioral differences. Furthermore, these morphs can be identified by an objective approach to color assessment (spectroradiometry). In addition, males in a second population (Escalerillas) from SE San Luis Potosí were also found to occur in at least two color morphs (yellow and red), suggesting that color polymorphism may be general in this species. The hypothesis of sensory exploitation by male contest competition was tested for *S. minor* from Escalerillas; however, no support for this hypothesis was found. Overall, results from this study are consistent with the hypothesis of alternative reproductive tactics in *S. minor*.
DEDICATION

To my parents Jim and Margaret

and my grandfather James

Thank you
ACKNOWLEDGEMENTS

This research would not have been possible without the support and encouragement of a great many people and organizations. First, I extend my sincerest thanks to the people of La Manzana, Hidalgo, who allowed me to live and work in such a beautiful and special place. The family of Alejandra Rosales-Salinas opened their house to my assistants and I for extended visits over some four years, and even tolerated my habit of bringing home lizards and other herpetological wonders of the area. Muchas gracias por todos. To my outstanding field assistants Jasmine Lopez, Pamela Podell, Erika Mendoza-Varela, and Christopher Jordan: thank you very much for all your hard work under challenging circumstances. Aurelio Ramírez-Bautista provided crucial logistical support throughout this project, including helping secure permits, and making laboratory space available to me during 2005. Fausto Méndez-de la Cruz also helped with permits and provided additional logistical assistance. Adrian Leyte-Manrique provided critical assistance during pilot work in 2004. SEMARNAT and the Government of Mexico generously provided permits; additional research approval and support was provided by the Presidencias Municipal of Zimapán, Hidalgo, and San Luis Potosí, San Luis Potosí. Barry Sinervo provided logistical and technical expertise, and helped generate new insights about this wonderful and mysterious animal. Lesley Lancaster provided invaluable technical assistance in the field. My advisor Richard Tokarz let me pursue my research goals, and kept me moving forward even when things got challenging; thank you for all your support. And finally, to my wife Nikolett Ihász—my most important discovery in Mexico—thank you for everything.
# TABLE OF CONTENTS

LIST OF FIGURES ........................................................................................................ vi

LIST OF TABLES ........................................................................................................... ix

Chapter

1 INTRODUCTION ........................................................................................................ 1

2 MALE COLOR POLYMORPHISM IN TWO POPULATIONS OF THE LIZARD *SCELOPORUS MINOR* ........................................................... 27

3 BODY SIZE, SHAPE, AND PERFORMANCE IN COLOR MORPHS OF THE LIZARD *SCELOPORUS MINOR* .................................................. 66

4 TERRITORIAL BEHAVIOR AND DEMOGRAPHICS IN THE POLYMORPHIC LIZARD *SCELOPORUS MINOR* ................................................. 114

5 A TEST OF THE SENSORY EXPLOITATION HYPOTHESIS IN THE LIZARD *SCELOPORUS MINOR* ............................................................ 148

References .................................................................................................................. 168
# LIST OF FIGURES

## CHAPTER 1

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Figure 1.1</td>
<td>19</td>
</tr>
<tr>
<td>Figure 1.2</td>
<td>20</td>
</tr>
<tr>
<td>Figure 1.3</td>
<td>21</td>
</tr>
<tr>
<td>Figure 1.4</td>
<td>22</td>
</tr>
<tr>
<td>Figure 1.5</td>
<td>23</td>
</tr>
<tr>
<td>Figure 1.6</td>
<td>24</td>
</tr>
<tr>
<td>Figure 1.7</td>
<td>25</td>
</tr>
<tr>
<td>Figure 1.8</td>
<td>26</td>
</tr>
</tbody>
</table>

## CHAPTER 2

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Figure 2.1</td>
<td>52</td>
</tr>
<tr>
<td>Figure 2.2</td>
<td>53</td>
</tr>
<tr>
<td>Figure 2.3</td>
<td>54</td>
</tr>
<tr>
<td>Figure 2.4</td>
<td>55</td>
</tr>
<tr>
<td>Figure 2.5</td>
<td>56</td>
</tr>
<tr>
<td>Figure 2.6</td>
<td>57</td>
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<tr>
<td>Figure 2.7</td>
<td>58</td>
</tr>
<tr>
<td>Figure 2.8</td>
<td>59</td>
</tr>
<tr>
<td>Figure 2.9</td>
<td>60</td>
</tr>
<tr>
<td>Figure 2.10</td>
<td>61</td>
</tr>
</tbody>
</table>
CHAPTER 3

Figure 3.1 ........................................................................................................ 94
Figure 3.2 ........................................................................................................ 95
Figure 3.3 ........................................................................................................ 96
Figure 3.4 ........................................................................................................ 97
Figure 3.5 ........................................................................................................ 98
Figure 3.6 ........................................................................................................ 99
Figure 3.7 ........................................................................................................ 100
Figure 3.8 ....................................................................................................... 101
Figure 3.9 ....................................................................................................... 102
Figure 3.10 .................................................................................................... 103
Figure 3.11 .................................................................................................... 104

CHAPTER 4

Figure 4.1 ....................................................................................................... 135
Figure 4.2 ....................................................................................................... 136
Figure 4.3 ....................................................................................................... 137
Figure 4.4 ....................................................................................................... 138
Figure 4.5 ....................................................................................................... 139
Figure 4.6 ....................................................................................................... 140
Figure 4.7 ....................................................................................................... 141

CHAPTER 5

Figure 5.1 ....................................................................................................... 162
Figure 5.2 ................................................................. 163
Figure 5.3 ................................................................. 164
Figure 5.4 ................................................................. 165
# LIST OF TABLES

## CHAPTER 2

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Table 2.1</td>
<td></td>
<td>62</td>
</tr>
<tr>
<td>Table 2.2</td>
<td></td>
<td>63</td>
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<tr>
<td>Table 2.3</td>
<td></td>
<td>64</td>
</tr>
<tr>
<td>Table 2.4</td>
<td></td>
<td>65</td>
</tr>
</tbody>
</table>

## CHAPTER 3

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<thead>
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<th>Table</th>
<th>Description</th>
<th>Page</th>
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<td>105</td>
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<td>Table 3.2</td>
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<td>106</td>
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<tr>
<td>Table 3.3</td>
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<td>107</td>
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<td>Table 3.4</td>
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<td>108</td>
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<td>Table 3.5</td>
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<td>109</td>
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<td>Table 3.6</td>
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<td>110</td>
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<td>Table 3.7</td>
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<td>111</td>
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<td>Table 3.8</td>
<td></td>
<td>112</td>
</tr>
<tr>
<td>Table 3.9</td>
<td></td>
<td>113</td>
</tr>
</tbody>
</table>

## CHAPTER 4

<table>
<thead>
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<th>Table</th>
<th>Description</th>
<th>Page</th>
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<tbody>
<tr>
<td>Table 4.1</td>
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<td>142</td>
</tr>
<tr>
<td>Table 4.2</td>
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<td>143</td>
</tr>
<tr>
<td>Table 4.3</td>
<td></td>
<td>144</td>
</tr>
<tr>
<td>Table 4.4</td>
<td></td>
<td>145</td>
</tr>
</tbody>
</table>
CHAPTER 1

Introduction

I. Intrsexual color polymorphisms and alternative reproductive tactics

Intrasexual color polymorphisms—the expression of multiple color forms among members of one sex—are a challenge to evolutionary theory. A single morph should become fixed in the population unless it has exactly equal fitness with other morphs or an advantage when rare (Shuster and Wade 2003), scenarios generally considered to be highly improbable (Gross 1996, but see Shuster and Wade 2003). Nevertheless, theory and empirical evidence indicates that within-sex polymorphisms can arise in several ways. One potential mechanism is apostatic selection, differential selection on prey types as a function of a predator search image. In this scenario, rare morphs experience relaxed selection since the search image is tuned to common morphs (Allen 1988). Dietary wariness, the avoidance of novel or unfamiliar prey types, has also been implicated in the evolution of large numbers of morphs (i.e., ‘exuberant’ polymorphisms: Oxford 2009, Franks and Oxford 2009), some of which may be sex-limited (Oxford and Gillespie 1996). In many cases, intrasexual color polymorphisms are linked to alternative reproductive tactics (ARTs: Taborsky et al. 2008). ARTs represent alternative pathways to reproductive success among members of a single sex, and represent the expression of multiple interrelated phenotypes working in concert to maximize fitness (Taborsky et al. 2008). ARTs have received substantial theoretical attention from researchers interested in their origin and maintenance (Gross 1996, Shuster and Wade 2003), fitness consequences (Sinervo and Svensson 2002), and evolution (Corl et al. 2010). ARTs are commonly investigated in the context of whether individuals can change tactics as a function of
prevailing social conditions (Moore 1991, Gross 1996, Tomkins and Hazel 2007). In this context a distinction has been made between genetically based phenotypes immune to environmental effects and phenotypes that are subject to plasticity in expression. This distinction is expected to have evolutionary consequences; tactics that are under strong genetic control are thought to be equal (Shuster and Wade 2003), whereas the mean fitnesses of morphs with plastic tactics are generally presumed to differ (Gross 1996, but see Shuster and Wade 2003 for a contrary view). Thus, ARTs represent a continuum of phenotypic plasticity, with developmentally or genetically fixed morphs or tactics on one end, to fully plastic tactics on the other end. In practice, most ARTs are likely to be subject to some phenotypic plasticity (Taborsky et al. 2008), and all must have a genetic component to respond to selection (Shuster and Wade 2003).

Lizards have proven to be popular subjects for investigations into the function of color. Many diurnal species are colorful, locally abundant and amenable to both field and laboratory studies. Investigations of color traits confirm that they can function as badges of status, potentially providing information about sexual identity (Cooper and Burns 1987), reproductive status (Rand 1990), fighting ability (Thompson and Moore 1991a, Olsson 1994, Stapley and Whiting 2006, Healey et al. 2007), and health (Ressel and Schall 1989). Crucially, variation in color has been linked to reproductive success (Zamudio and Sinervo 2000, Olsson et al. 2009). A number of studies have found evidence that male color polymorphisms are linked to ARTs, and that trait expression may be condition-dependent (Zucker 1989) or fixed (Moore et al. 1998), or involve complex combinations of fixed and plastic phenotypes (Sinervo and Lively 1996, Cote et al. 2008). Less is known about ARTs in females, partly because conspicuous color is less
common in female lizards than in males (e.g., Wiens 1999). In most species where females do express bright colors, color expression is transient and correlated with the vitellogenic cycle (e.g., Jessop et al. 2009), and so does not reflect alternative tactics. Nevertheless, bright female colors have been linked to ARTs in at least two species (e.g., Sinervo et al. 2000b).

Several ecological characteristics of lizards may favor the repeated evolution of ARTs. First, males of many species are strongly territorial (Stamps 1983). Females or other resources are often clumped in space; males that can exclude competitors from access to these resources increase mating skew and thus the intensity of sexual selection (Shuster and Wade 2003). Second, polygyny is common in lizards, further increasing variance in male mating success. Males that are relatively poor fighters may be at a strong disadvantage in one-on-one contests; thus, for these males, selection should favor traits that increase their mating opportunities in other ways. Third, overt female mate choice seems rare in lizards (Tokarz 1995) and male mating success seems to be more strongly predicted by male-male competition (e.g., Hews 1990). Whether female choice has not been reported in some lizards (e.g., Quinn 2001, Lailvaux and Irschick 2006) because it is indeed absent or merely hard to detect (e.g., Calsbeek and Sinervo 2004) is an area that needs further investigation. Nevertheless, male mating success in many lizards seems to be primarily determined by the outcome of male-male competition and territoriality, attributes that should tend to favor the evolution of ARTs (Shuster and Wade 2003).
II. Color polymorphisms and ARTs in lizards

A. Side-blotched lizard, *Uta stansburiana* (Phrynosomatidae)

The best-studied example of a polychromatic lizard with alternative reproductive tactics is the side-blotched lizard *Uta stansburiana*, a wide-ranging phrynosomatid native to the western United States and northern Mexico (Corl et al. 2010). In populations in coastal California males exhibit one of three throat color phenotypes (orange, yellow, and blue) each linked to a distinct reproductive strategy. Orange males are usurpers: they aggressively defend large territories containing multiple females, and expand their territories into those of neighboring blue males in search of additional females. Blue males defend smaller territories containing 1-2 females, and lose contests to orange males (Sinervo and Lively 1996). However, they buffer these losses by engaging in a cooperative tactic with neighboring (but unrelated) blue males that allows them to successfully prevent invasion of their individual territories from yellow males (Sinervo and Clobert 2003). Yellow males are sneakers, and strongly resemble females in both coloration and behavior. They exploit the usurping tactic of orange males through their complex mimicry, allowing them to mate with females undetected (Zamudio and Sinervo 2000). Thus, each morph successfully defeats one morph, but is in turn defeated by the other morph. Such a system is termed a rock-paper-scissors game for its resemblance to the eponymous children’s game (Sinervo and Lively 1996). Relative morph frequencies cycle over time as expected if maintained by negative frequency-dependent selection (i.e., rare morph advantage). The system never reaches equilibrium; instead the frequency of each morph oscillates across time as a function of the fitness of the other morphs (Sinervo and Lively 1996). The heritability for male morphs is very high, almost unity.
(Zamudio and Sinervo 2000), indicating that alternative tactics are under strong genetic control. Although the specific gene or genes responsible have not yet been isolated, a single locus (OBY) or possibly two tightly linked loci (Sinervo 2001) are thought to be largely responsible, exerting morph-specific effects on throat color (Sinervo et al. 2001), endocrinology (Miles et al. 2007a), physiology (Sinervo et al. 2000a), and behavior (Sinervo and Lively 1996).

Female *U. stansburiana* also exhibit alternative tactics, a density-dependent game linked to throat color (Sinervo et al. 2000b). Orange females produce many small offspring (*r*-strategists), whereas yellow females produce fewer larger offspring (*K*-strategists). At high densities immediately preceding a local population crash when resources tend to be scarce, yellow females are favored because offspring of orange females suffer disproportionate mortality relative to yellow females under these conditions. Conversely, orange females are favored at low to intermediate densities as their intrinsic rate of increase (*r*) is greater than that of yellow females (Sinervo et al. 2000b).

2. Tree lizard, *Urosaurus ornatus* (Phrynosomatidae)

Another phrynosomatid that exhibits color polymorphism linked to ARTs is the tree lizard *Urosaurus ornatus*. Like *Uta stansburiana*, males of *U. ornatus* are polymorphic for throat color (Hover 1985). Thompson and Moore (1991a, b, 1992) studied populations from Arizona, and found that males exhibited one of two main fixed phenotypes, orange and orange-blue. Orange-blue males are territorial and vigorously attempt to exclude rivals from neighboring females. Males with solid orange throats are
larger than orange-blue males, but do not defend territories; instead, they exhibit a condition-dependent plastic tactic linked to interannual patterns of rainfall. In rainy years, orange males reside on the periphery of the territories of orange-blue males (satellite strategy). Alternatively, during dry years orange males abandon territoriality completely and become wanderers (nomad strategy) (Moore et al. 1998). Orange males have reduced fighting ability relative to orange-blue males (Thompson and Moore 1991b) and court females less than orange-blue males (Thompson and Moore 1992). Although orange males are larger than orange-blue males, orange-blue males are more massive for a given body length (Hews and Moore 1994); orange-blue males are thus short and stocky, and orange males are long but skinny (Moore et al. 1998). Other studies have shown that orange males initiate flight from predators at greater distances, and remain in their refuge longer following flight relative to orange-blue males (Thaker et al. 2009). There is substantial variation in male throat color within and between populations: some populations are monomorphic and others exhibit as many as five different phenotypes (Thompson and Moore 1991a). At least nine different color variants have been described across the range of *U. ornatus* (Moore et al. 1998), some of which may also be linked to distinct behavioral phenotypes (e.g., Thaker et al. 2009).

Most studies of ARTs in *U. ornatus* have focused on polymorphic throat color; however, other color traits may also be linked to alternative tactics. In a population in New Mexico studied by Zucker (1989), males express only solid blue throats, but are polymorphic for dorsal color. Territorial males were black and defended territories that did not overlap with those of other black males. Floater males expressed the light brown dorsal color characteristic of males and females in most populations. Removal of a black
male resulted in the expression of black dorsal color in a single neighboring floater male. Thus, dorsal color may serve as a condition-dependent signal of dominance or fighting ability in this population (Zucker 1989), analogous to the fixed orange and orange-blue polymorphism of males from populations of *U. ornatus* in Arizona (Moore et al. 1998).

C. Red-lipped prairie lizard, *Sceloporus erythrocheilus* (Phrynosomatidae)

Rand (1988, 1990) found that males of *S. erythrocheilus* from Colorado exhibited one of three fixed chin color morphs: orange, yellow, and white. Orange males dominated yellow males in natural encounters, and courted females more frequently (Rand 1988), indicating that morph color is linked to ARTs. In this species, the intensity of morph color changes seasonally and is synchronous with changes in circulating testosterone (Rand 1990). Supplementation of testosterone following the breeding season induced bright chin color in males, however, males did not change morph class (i.e., switch from yellow to orange; Rand 1992). Thus, the underlying bases for morph expression are fixed (organized) in *S. erythrocheilus*, but subject to seasonal modification due to changes in circulating hormones (activated).

D. Painted rock dragon, *Ctenophorus pictus* (Agamidae)

In the Australian painted rock dragon *Ctenophorus pictus*, males are polymorphic for head color and occur in three discrete morphs (red, yellow, and orange; Olsson et al. 2008). Morphs do not differ in body size (Healey et al. 2007), or in the size of their natural territories (Olsson et al. 2008). However, red males are dominant to yellow males
in staged trials (Healey et al. 2007), whereas yellow males have proportionately larger testes than red males, and achieve higher success in sperm competition trials (Olsson et al. 2009). Despite these differences, multiple paternity is relatively low in natural populations (< 20% of clutches), and all morphs have approximately equal fitness within and across several years (Olsson et al. 2008), indicating that (successful) sneaking behavior is relatively uncommon under natural conditions. One factor that may predict the evolution and expression of ARTs is habitat heterogeneity (Forsman and Åberg 2008); habitats that are more complex should favor alternative tactics, perhaps due to reduced effectiveness of male vigilance (Olsson et al. 2008). Olsson et al. (2008) suggest that yellow males at their study site have abandoned sneaking and instead express the conventional territorial tactic of red males, perhaps because the absence of recent disturbance (such as fire) has rendered the habitat insufficiently complex to support alternative tactics.

E. Common lizard, *Lacerta vivipara* (Lacertidae)

Sinervo et al. (2007) studied populations of the European common lizard *L. vivipara* from southern France, where males occur in three main morphs (white, yellow, and orange). They found evidence that the complex rock-paper-scissors dynamic also occurs in *L. vivipara*, and that patterns of body color, performance, survival and offspring recruitment are strikingly similar to those seen in *Uta stansburiana*. For example, orange males exhibit greater stamina than other males, but also have lower interannual survival (Sinervo et al. 2007).
Color polymorphisms linked to alternative tactics in female *L. vivipara* have also been described. Females express yellow, orange or an intermediate color (‘mixed’) (Vercken et al. 2006). In staged contests, orange females were less aggressive than other morphs, indicating low fighting ability. Yellow and mixed females both exhibited high rates of aggression, but mixed females also had significantly higher rates of scratching (an index of stress) than other morphs (Vercken and Clobert 2008). Field studies of natural populations showed that yellow females laid smaller clutches than other females, whereas orange females could adjust their clutch sizes in response to female densities (Vercken et al. 2006). Experimental manipulations of morph densities showed that juvenile condition at hatching among all morphs was negatively related to the proportion of yellow morphs in a population perhaps as a function of stress induced by yellow female aggression (Vercken et al. 2010).

**F. Wall lizards, *Podarcis* spp. (Lacertidae)**

In populations of *Podarcis melisellensis* from Croatia, males express one of three discrete colors (orange, yellow, and white) expressed on the throat and abdomen. Orange males are larger, have proportionately larger heads and bite harder than yellow or white males (Huyghe et al. 2007, 2009a). Bite force appears to be linked to differences in muscle mass between morphs; orange males tend to have greater jaw adductor masses than yellow males (Huyghe et al. 2009a). Although morphs do not differ in levels of circulating testosterone (at least as adults), size-corrected bite force across all males was correlated with circulating testosterone (Huyghe et al. 2009b).

Males of the congener *Podarcis muralis* in northern Italy also exhibit three
discrete color morphs (white, yellow, and red; Sacchi et al. 2007a). Staged contests showed that male morphs did not differ in fighting ability (Sacchi et al. 2009). However, males do exhibit morph-specific variation in immune response: yellow morphs exhibited reduced swelling relative to white and red males following subcutaneous injection of phytohaemagglutinin (Sacchi et al. 2007b).

G. Iberian rock lizard, *Iberolacerta monticola* (Lacertidae)

Both male and female Iberian rock lizards exhibit variable dorsal coloration, and occur in two discrete color morphs: green and blue. Analysis of male femoral pore secretions showed that morphs differed in the relative proportions of major classes of compounds: blue males exhibited higher concentrations of steroids than green males in their femoral pore secretions, but lower concentrations of fatty acids (López et al. 2009). Intriguingly, further experiments showed that female *I. monticola* can discriminate between male morphs; they gave higher rates of tongue flicks towards secretions of males of their own color morph relative to males of the alternative morph. Males, however, did not differ in rates of tongue flicking towards the secretions of different morphs (López et al. 2009).

H. Summary

A growing body of research indicates that intrasexual color polymorphisms in lizards are linked to alternative tactics in both males and females (reviewed in Calsbeek and Sinervo 2008), though only a few studies have actually demonstrated a relationship between morph color and fitness (e.g., Zamudio and Sinervo 2000, Olsson et al. 2009). Color
polymorphisms linked to ARTs appear to be widely distributed evolutionarily, having been documented among representatives of at least three families (Vidal and Hedges 2005, Sinervo et al. 2007). The occurrence of ARTs in male lizards seems to be linked to territoriality, perhaps because the high mating skew of female- or resource-defense polygyny is thought to favor the evolution of alternative tactics (Shuster and Wade 2003). Notably, orange or red color morphs often have high fighting ability or are dominant to other morphs (e.g., Rand 1988, Sinervo and Lively 1996, Healey et al. 2007), a pattern observed in some other color polymorphic taxa (e.g., Gouldian finches: Pryke and Griffith 2006). Nevertheless, there are exceptions to this pattern among polymorphic lizards (e.g., *Urosaurus ornatus*: Moore et al. 1998), indicating that the relationship between color expression and behavioral phenotype may be labile, even among closely related species. Overall, research on color polymorphisms in lizards has generated significant insights into the relationship between color and alternative reproductive tactics. However, additional studies are needed to better determine the extent to which ARTs are the exception or the rule in polymorphic lizards, as well as the generality (or lack thereof) between color expression and particular tactic phenotypes.

III. Spiny lizards (*Sceloporus*)

The spiny lizards of the genus *Sceloporus* are a group of mostly small to medium-sized phrynosomatid lizards (Fitch 1978) ranging from southwestern Canada to Panama (Wiens and Reeder 1997). With more than 80 described species, *Sceloporus* represents the largest genus of reptiles endemic to North America (Wiens et al. 2010). The high diversity of the group, its broad distribution throughout North America, and general tractability to

Like most phrynosomatids, male spiny lizards are territorial (Ruby 1978) and aggressively attempt to exclude rivals from access to females found within their territories (Moore 1987). Males produce a species-specific headbob display during social
interactions, as well as other postural adjustments (e.g., Carpenter 1978). In escalated contests, males reveal conspicuous color patches (usually blue) on the abdomen and throat (Wiens 1999). Experimental studies indicate that males use these badges to assess opponent sex and reproductive status (Cooper and Burns 1987), and fighting ability (Quinn and Hews 2000). Although much less common, bright ventral color has evolved several times in females of *Sceloporus* (Wiens 1999), and studies have linked these badges to female-female aggression (Vinegar 1975) and reproductive status (Weiss 2002, Calisi and Hews 2007). Bright color in *Sceloporus* is usually restricted to the ventral surface, which may serve to simultaneously link signal expression to social context, and minimize detection by illegitimate receivers (Cooper and Greenberg 1992). Both sexes typically express dorsal coloration considered dull or cryptic to human observers (Fitch 1978), but bright dorsal color has been described in a number of species (e.g., Wiens et al. 1999). Males of the tropical *formosus* group typically express bright green dorsal color (Köhler and Heimes 2002), though the functional significance of such color is unknown.

Although most species of *Sceloporus* exhibit conspicuous color patches in one or both sexes (Wiens 1999), the extent to which these traits are polymorphic is largely unknown (but see below) and only a few studies have addressed the possible significance of intrasexual color polymorphism. Most research has focused on transient orange and red colors in females. In both *S. virgatus* (Weiss 2002) and *S. pyrocephalus* (Calisi and Hews 2007), female throat color is condition-dependent, with peak color saturation corresponding to the onset of ovulation. In *S. virgatus*, female orange color appears to stimulate male courtship (Weiss 2002). Calisi et al. (2008) also found that throat color in late-stage vitellogenic females of *S. pyrocephalus* negatively correlated with parasite
loads, indicating that red saturation could be a signal of female quality. Male color polymorphisms have also been described in *Sceloporus* (e.g., Rand 1990, Wiens et al. 1999). In *S. occidentalis*, abdominal color is condition-dependent; males with higher levels of a blood-borne pathogen (*Plasmodium*) expressed more black on their abdominal patches than uninfected controls (Ressel and Schall 1989). In addition, infected males exhibited reduced rates of displays relative to healthy males (Schall and Dearing 1987).

As described previously (see section II.C), at least one species of *Sceloporus* appears to exhibit ARTs linked to color morphs. Males of *S. erythrocheilus* express variable chin color that is fixed in adults for major color class (orange, yellow, and white), although subject to seasonal changes in saturation linked to circulating T levels (Rand 1990, 1992). Observations revealed that orange males tended to defeat yellow males in natural contests, and courted females more frequently than yellow males (Rand 1988).

More recent research indicates that color polymorphism may be characteristic of some other species of *Sceloporus* as well (Wiens et al. 1999, B. Sinervo et al., unpubl. data); however, the possible biological significance of such variation among members of this diverse group of lizards remains largely unexplored.

**IV. Study Species: Sceloporus minor**

**A. Species Distribution**

*S. minor* is a medium-sized (≤100 mm max SVL) spiny lizard restricted to saxicolous habitats in the southern Chihuahuan Desert and western slopes of the Sierra Madre Oriental in central Mexico above 1500 m (Chrapliwy 1964, Wiens et al. 1999, Martínez-Méndez and Méndez-de la Cruz 2007; Fig. 1.1). The largest population extends
throughout the central and western regions of the state of San Luis Potosí, west to extreme northeast and southeast Zacatecas, east to southwest Nuevo León and western Tamaulipas, and south to Guanajuato and extreme northeastern Jalisco. A second population occurs in the mountains of Querétaro and northern Hidalgo, and a third population is found in the upland forests of western Tamaulipas. The extent to which these disjunctions represent real discontinuities in the distribution of this species or a lack of sampling is not clear, and other authors interpret only one disjunction (Köhler and Heimes 2002) or none at all (Martínez-Méndez and Méndez-de la Cruz 2007). Although primarily associated with the arid and semi-arid interior of the southern Chihuahuan Desert, populations of *S. minor* extend into moist pine-oak forests near the margins of its range in the Sierra Gorda of northern Querétaro and NW Hidalgo (Smith 1936, Wiens et al. 1999). In SW Tamaulipas, *S. minor* is common in dry pine-oak forest and chaparral, but does not penetrate into tropical humid forests further east (Martin 1958).

B. Reproduction

Like all members of the *poinsettii* group, *S. minor* is viviparous (e.g., Méndez-de la Cruz et al. 1998). Gonadal analyses of *S. minor* from several populations indicate that mating occurs in the fall, with parturition the following spring (Ramírez-Bautista et al. 2002, 2008). This general phenology is characteristic of most live-bearing species of *Sceloporus* (Méndez-de la Cruz et al. 1998) as well as several unrelated viviparous taxa that occur at high altitudes in Mexico (Anguidae: Guillette and Casas-Andreu 1987; Scincidae: Ramírez-Bautista et al. 1998; Xenosauridae: Smith et al. 2000).
C. Sexual Dimorphism and Color Variation

Males are larger than females in *S. minor* (Ramírez-Bautista et al. 2008, B. Stephenson, unpubl. data), a pattern characteristic of many but not all species of *Sceloporus* (Fitch 1978). All mature males possess the blue throat and ventral patches (Wiens 1999) characteristic of the genus; females usually lack these patches entirely or express them only weakly (Chrapliwy 1964, B. Stephenson, pers. obs.). The most striking attribute of *S. minor* is the expression of conspicuous dorsal color that varies extensively within and among populations (Martin 1958, Grant and Smith 1959, Wiens et al. 1999). Males from populations in San Luis Potosí, Zacatecas and Nuevo León generally express a yellow, brown or orange color (Fig. 1.2) and to human observers tend to resemble females in this regard (Wiens et al. 1999; Fig. 1.3). Conversely, males in the two smaller, disjunct populations in western Tamaulipas, and Querétaro and Hidalgo are strongly sexually dimorphic (Wiens et al. 1999; Figs. 1.4-1.5). All males express bright blue color on the head, dorsum, legs and tail; other males possess paired yellow, orange or reddish dorsal patches, typically separated by a blue midline stripe (e.g., Martin 1958; Fig. 1.4). Historically, the (disjunct) Tamaulipas and Hidalgo populations were considered to belong to a single subspecies (*S. jarrovi immucronatus*: Chrapliwy 1964). However, phylogenetic data indicate that the distinctive blue dorsal color of these populations evolved at least twice from a common brown or orange ancestor in San Luis Potosí (Wiens et al. 1999), and no subspecies are currently recognized.
D. Study Sites

1. La Manzana

Sites were selected on the basis of available information about dorsal color in males, as well as their phylogenetic relationships relative to other populations sampled by Wiens et al. (1999). Most research was conducted at the principal study site near the community of La Manzana, Hidalgo (20° 52’ N, 99° 13’ W; 2.2 km from Population 5 in Wiens et al. 1999; Fig. 1.1) at various intervals between May and November from 2005-2008. This high elevation site (2500 m) is located in mixed oak-pine forest along a northwestern facing limestone escarpment on the western edge of the Sierra Madre Oriental (Figs. 1.6A, 1.7). Dominant trees in closed woodland areas included *Quercus crassipes*, *Pinus greggii*, and *P. patula*. In more exposed areas junipers (*Juniperus*) and agaves (*Agave*) were common, as well as various woody shrubs (Fig. 1.2a). Several species of *Salvia* were common terrestrial flowering plants. Mean temperature ranges from a low of 11°C in January to 17°C in May. Annual precipitation averages around 600 mm, and peaks from June-September (Anon. unpubl. pamphlet). Much of this precipitation appears to come in the form of fog (B. Stephenson, pers. obs.). During the summer and fall months, large cloud banks move up from the desert valley below and settle over the field site, blocking out direct sun for several hours each day and lowering air temperature substantially (B. Stephenson, unpubl. data).

2. Escalerillas

A second site was established near the community of Escalerillas, San Luis Potosí (22° 5’ N, 101° 4’ W; 3.0 km from Population 14 in Wiens et al. 1999; Fig. 1.1). Fieldwork at
this site was limited to two weeks in August-September of 2006 and eight weeks in October-November of 2007. Although work was conducted at several locations within about a 500-m radius, the main study site was located in an area dominated by large exposed granite boulders to the southwest of a newly built reservoir constructed at the base of a shallow river (Figs. 1.6B, 1.8). Vegetation was relatively sparse, and was mostly composed of grasses and other small herbaceous plants with occasional oak (*Quercus* spp.) and yucca (*Yucca* spp.). Data from the nearby city of San Luis Potosí (<10 km from Escalerillas) indicates that the area averages around 18°C annually, and receives about 300 mm per year of precipitation (Morafka 1977).

V. Study Objectives

I addressed four main questions regarding variation in male dorsal coloration, its possible social significance and evolution. In Chapter 2, I quantified the extent of male dorsal color variation at each of these two sites, and tested whether observed variation in each population is continuous or discontinuous. In Chapter 3, I tested whether hypotheses for color polymorphism in one population (La Manzana) characterized by extreme sexual dimorphism predict morphological and physiological differences that might be linked to ARTs. This question was extended in Chapter 4, as I investigated whether male dorsal color predicted patterns of social behavior, movement, and interannual persistence in a manner consistent with ARTs. Lastly, in Chapter 5 I tested whether the aggressive behavior of males from an ancestral population (Escalaerillas) is consistent with the hypothesis that deep blue dorsal color of males evolved in *S. minor* via sensory exploitation.
Figure 1.1 Distribution of *Sceloporus minor* in Mexico. 1 = La Manzana, 2 = Escalerillas, Z = Zacatecas, SLP = San Luis Potosí, NL = Nuevo León, T = Tamaulipas, H = Hidalgo, Q = Querétaro, G = Guanajuato. Modified from Wiens et al. (1999).

![Map of Mexico showing distribution of *Sceloporus minor*](http://www.d-maps.com/m/mexique/mexique08.gif)
Figure 1.2 Representative variation in dorsal color in adult male *Sceloporus minor* at Escalerillas, San Luis Potosí.
Figure 1.3 Representative variation in dorsal color in adult female *Sceloporus minor* at Escalerillas, San Luis Potosí.
Figure 1.4 Representative variation in dorsal color in adult male *Sceloporus minor* at La Manzana, Hidalgo.
Figure 1.5 Representative variation in dorsal color in adult female *Sceloporus minor* at La Manzana, Hidalgo.
Figure 1.6 Characteristic habitats of two populations of *Sceloporus minor*. A. La Manzana, Hidalgo. B. Escalerillas, San Luis Potosí.
Figure 1.7 Aerial view of five 50 x 50 m study plots erected at La Manzana, Hidalgo. Plot A = Green, Plot B = Red, Plot C = Magenta, Plot D = Yellow, Plot E = Turquoise.
Figure 1.8 Aerial view of study area at Escalerillas, San Luis Potosí. Plot F = Red. Bounded regions indicate capture localities for males used in intruder experiment (Chapter 5). A = Residents, B = Intruders.
CHAPTER 2

Male Color Polymorphism in Two Populations of the Lizard *Sceloporus minor*

I. Background

The existence of color polymorphisms is surprising, partly because theory predicts that one phenotype should become fixed via directional selection. Consequently, the persistence of color variation in natural populations has generated substantial interest regarding its evolution and maintenance (e.g., Glanville and Allen 1997, Forsman et al. 2008, Franks and Oxford 2009). Theory and empirical evidence indicate that sexual selection can drive the evolution of intraspecific color polymorphisms; when these polymorphisms become coupled to distinct behavioral and physiological phenotypes, alternative reproductive tactics (ARTs) can result (Taborsky et al. 2008). The existence of ARTs is often indicated by patterns of intraspecific color variation. However, human vision may both underestimate and overestimate the extent of biologically meaningful variation in color traits (Eaton 2005). In their seminal review of studies of animal color, Bennett et al. (1994) argued persuasively for the use of more objective approaches to color assessment. Their preferred approach, spectroradiometry, has gained wide acceptance among behavioral ecologists testing hypotheses for the function of color traits (e.g., Endler 1990, Cuthill et al. 1999, Montgomerie 2006). A major advantage to spectroradiometry is that color variation beyond the limits of human vision can be quantified. Many taxa at least have the potential to see UV light (Kelber et al. 2003, Osorio and Vorobyev 2008), and the observation that UV colors are often incorporated into male and female ornaments suggests these colors may be informative (e.g.,
butterflies: Wijnen et al. 2007; fish: Marshall et al. 2003, but see Losey et al. 2003; birds: Mullen and Pohland 2008). Recent experiments confirm that UV colors may act as reliable signals (Hunt et al. 1999, Stapley and Whiting 2006). Thus, failing to account for this variation may severely underestimate the biologically relevant color variation for a given trait. Spectroradiometry has the additional desirable property of describing color quantitatively, permitting the use of statistical techniques unavailable to more qualitative approaches (Cuthill et al. 1999). One prediction for ARTs is that discrete morphs should represent discontinuous clusters of correlated phenotypes in multivariate space (Sinervo and Svensson 2002). However, relatively few studies of polymorphic species have addressed whether variation in spectral traits actually corresponds to distinct color groups (e.g., Vercken et al. 2006, Sinervo et al. 2007). Complicating matters, different methods for quantifying color variation can lead to contradictory conclusions as to whether such variation is discrete or continuous (Cote et al. 2008, Vercken et al. 2008). Thus, the extent to which putative color morphs actually represent discrete color groups is largely unknown for most polymorphic species. This is surprising, since the quantitative form of data generated by spectroradiometry should permit color traits to be readily characterized as continuous or discontinuous (i.e., unimodal or multimodal). Partly to address this deficiency, I used spectrometry to test the hypothesis of alternative color morphs in a lizard (*Sceloporus minor*) that exhibits striking variation in male color both within and among populations.

Lizards are popular subjects for studies of color. Many species exhibit colorful badges that are displayed to rivals and mates in social interactions (Cooper and Burns 1987, Olsson 1994, Whiting et al. 2003) and spectroradiometry has become an important
tool for examining variation in these features within and across populations (e.g., McCoy et al. 1997, LeBas and Marshall 2000, Macedonia et al. 2002, Stuart-Fox et al. 2004, Molina-Borja et al. 2005, Whiting et al. 2006, Pérez i de Lanuza and Font 2008, Font et al. 2009). In addition, a number of studies have documented the existence of multiple discrete color morphs among individuals of the same population (e.g., Sinervo and Lively 1996, Moore et al. 1998, Huyghe et al. 2007), although the extent to which different morphs vary in spectral attributes has rarely been examined (for an important exception, see Vercken et al. 2006 and Cote et al. 2008).

The spiny lizards (Sceloporus) are a diverse group of New World lizards consisting of more than 80 species (Wiens et al. 2010). The genus is characterized by extensive sexual dimorphism of color traits; males in most species express bright blue color on the abdomen or throat (Wiens 1999), and these colors are revealed to conspecifics through displays (e.g., Cooper and Burns 1987). There is substantial variation in the intensity and placement of color both within and among species. For example, females of S. virgatus exhibit a seasonal transformation of throat color from blue to orange, which is correlated with the timing of ovulation (Weiss 2002); males retain exclusively blue throats across seasons. In the red-lipped prairie lizard S. erythrocheilus, males exhibit a polymorphism for chin color linked to ARTs (Rand 1988, 1990). A similar association of fixed male-biased color polymorphism is present in some other phrynosomatids (Urosaurus ornatus: Thompson and Moore 1992; Uta stansburiana: Sinervo and Lively 1996).

The minor lizard Sceloporus minor Cope is a common reptile of saxicolous habitats throughout the southern Chihuahuan Desert of central México and western
slopes of the Sierra Madre Oriental (Chrapliwy 1964). Like most spiny lizards, adult male *S. minor* express bright blue throats and abdominal patches that are usually absent or only weakly expressed in females (Smith 1936, Wiens 1999). In contrast, males exhibit exceptional variation in dorsal coloration within (Martin 1958, Grant and Smith 1959) and across populations (Chrapliwy 1964, Wiens et al. 1999). Geographic variation in dorsal color is sufficiently extensive that several earlier workers have used it as a marker for population-level taxonomy and systematics (Mertens 1950, Chrapliwy 1964, Wiens et al. 1999). However, little is known about the extent to which dorsal color varies within individual populations, and nothing is known about whether such polymorphism might be adaptive.

From 2005 to 2008, I studied aspects of the behavioral ecology of two populations of *S. minor* that represent the extremes of color variation known for this species. Males from La Manzana, Hidalgo, express bright blue dorsal color, often complemented by a pair of dorsal patches varying from green to red and separated by a blue midline stripe (Chrapliwy 1964, Wiens et al. 1999). Conversely, males near the community of Escalerillas, San Luis Potosí, typically possess a dull orange, brown, red or yellow dorsal color similar to that observed in most populations elsewhere in the north, central and western parts of its range (Wiens et al. 1999; Chapter 1).

I had two main objectives for this study. First, I sought to formally characterize dorsal color variation among males from La Manzana and Escalerillas using spectroradiometry. To my knowledge, there is only one published study describing spectral variation for any sexually dimorphic trait in *Sceloporus* (Stoehr and McGraw 2001) and none for any polymorphic species. Second, I tested whether color patterns in
males at each site were distributed according to expectations for the existence of multiple morphs at one or both sites. If color expression exhibits a continuous profile—grading from blue to red with only one frequency peak or none at all—this would be consistent with a condition-dependent basis for color. Alternatively, evidence of discontinuous color expression (e.g., a multimodal distribution) would be consistent with discrete color morphs. I addressed these issues using a combination of univariate and multivariate approaches (Grill and Rush 2000).

II. Materials and Methods

A. Field Methods

I captured free-ranging marked adult males exhibiting well-developed dorsal coloration in and around the communities of La Manzana, Hidalgo (May-October, 2006-2008) and Escalerillas, San Luis Potosí (August-November, 2006-2007). Collections coincided with periods of expected peak activity for each population (Ramírez-Bautista et al. 2008, B. Stephenson, unpubl. data). Lizards were captured by noose and taken to a local residence that served as a research station within a few hours. Spectral data were collected within 24 h of capture, and lizards were returned to their territories within 72 h. Males at each site undergo ontogenetic change in body color, probably at the onset of sexual maturity (B. Stephenson, unpubl. data). Therefore, I established minimum size thresholds for males in each population prior to selecting males to use in analyses (La Manzana: > 60 mm SVL; Escalerillas: > 80 mm SVL) to reduce the probability of including sexually immature males. It should be noted that adult males in Escalerillas on average are 18% larger than those at La Manzana (B. Stephenson, unpubl. data). In addition, males were
collected for use in a variety of different projects, some of which involved testing hypotheses for the function of color. Partly as a consequence, color variation in the collected males at La Manzana may not represent a completely random sample relative to the population.

B. Spectroradiometry

Prior to spectral measurements, each animal was placed in a tank (61 x 32 x 42 cm) heated to 25°C. Lizards were allowed to bask for 20 minutes; this was necessary since squamate skin may darken at low temperatures (e.g., Cooper and Greenberg 1992). Reflectance spectra were obtained with a USB4000 spectrophotometer connected to a pulsed xenon light source (PX-2). A bifurcated radiance probe was held at an angle of 45° from normal for all measurements; percent reflectance (in ~0.2 nm steps) was expressed relative to a 99% white standard. Readings were recorded from five separate locations on both the left and right sides of the dorsum; each reading was an average of 100 scans at a given location, collected over an integration time of 16 ms. Measurements were collected within a darkroom to minimize interference from external light; output was analyzed with Spectrasuite software (Ocean Optics: Dunedin, FL). Each spectrum was screened prior to analysis and I removed a spectrum if it: a) represented an exact copy of an immediately preceding spectrum in sequence, indicating a duplicate saved file; b) exhibited relative reflectance in excess of 100% at one or more wavelengths, a presumed impossibility under correct conditions; or c) was determined to be the result of placing the probe on an unintended location (e.g., reflectance <5% across all wavelengths, consistent with accidental measurement of the black nuchal collar).
A common approach to spectroradiometry of well-defined color badges is to collect multiple readings at different points in the same badge, and average across readings (e.g., Stuart-Fox et al. 2004). Initial observations of male *S. minor* revealed that individual dorsal scales sometimes express multiple hues (e.g., blue and yellow). One potential consequence of averaging readings that represent multiple hues is that a biologically meaningless ‘average’ color spectrum might result. To avoid this problem, I selected the single color spectrum associated with the reflectance peak (= hue: see below) of longest wavelength between 300 and 700 nm. This approach provided an estimate of the maximum “redness” of each subject. In the event that two or more spectra exhibited the same peak, one spectrum was selected at random.

I applied both univariate and multivariate approaches to the analysis of dorsal color of *S. minor* (Molina-Borja et al. 2005). For univariate analyses I calculated hue, chroma and brightness for each spectrum, using the following established definitions (Montgomerie 2006):

\[ \text{Hue} = \lambda_{R_{\text{max}}}, \text{ where } R_{\text{max}} = \text{maximum percent reflectance} \]

\[ \text{Chroma} = \frac{\lambda_{b} - \lambda_{700}}{\lambda_{b} - \lambda_{300}}, \text{ where } R_i = \text{percent reflectance at } i\text{th wavelength} \]

\[ \text{Brightness} = \int_{\lambda_{300}}^{\lambda_{700}} R_i = \text{mean reflectance from 300-700nm} \]

Although researchers have quantified these variables in other ways (see Montgomerie 2006), these definitions are widely used in the literature (e.g., Mennill et al. 2003, Stapley and Whiting 2006).
A common alternative approach in studies of color is principal components analysis (PCA). Raw color variables are typically highly correlated; PCA can convert these variables into a set of orthogonal variables that retain the original variation but are statistically independent (Cuthill et al. 1999). Although the interpretation of the PCs is not necessarily straightforward (Grill and Rush 2000), PC1 is typically correlated with spectral size (brightness) and PC2 and PC3 represent spectral shape (hue and chroma) (Cuthill et al. 1999, Montgomerie 2006). For PCA, I used the medians of 10-nm bins between 300-700 nm for each selected spectrum, generating 41 median values per spectrum.

C. Morphometrics

Male dorsal color variation may be linked to the physical size of dorsal color patches rather than or in addition to spectral properties alone. Thus, I also calculated patch area on the right side of the dorsum (i.e., right dorsal patch; hereafter, dorsal patch) for males from La Manzana. (Patch area was not measured for males from Escalerillas because most males from this population lack a distinct dorsal patch.) Dorsal patch width was the viewer perceived maximum linear distance of continuous dorsal color expression distinct from the (blue) background dorsal color recorded along the axis perpendicular to the long axis of the body. Patch length was the perceived maximum distance of continuous dorsal color distinct from the blue background measured parallel to the long axis of the male. In the most extreme cases, the patch would extend from the anterior edge of the nuchal collar to the posterior tip of the last caudal scale exhibiting non-blue color distinct from the blue of the tail. Patch area adjusted for body size (PA) was calculated as:
Patch area = $\sqrt{(L_{\text{Max}} \times W_{\text{Max}})}$, where $L_{\text{Max}}, W_{\text{Max}} =$ maximum patch length, width

Males were anesthetized prior to measurement of patch area with a small dose (0.05-0.10 cc) of 2\% lidocaine administered subcutaneously to the base of the lower left dorsum. Although local color expression occasionally appeared to darken following injection, color change did not extend to the right dorsal patch, and normal color expression on the left side returned completely within 20-30 min. Spectral data were always collected prior to administration of lidocaine to avoid any effects of anesthetization on skin reflectance measures.

D. Statistics

Analyses of color were restricted to 300-700 nm, a range likely to enclose the limits of visual sensitivity in this species (E. R. Loew, pers. comm.). For each population, I constructed frequency histograms of raw color variables to locate possible discontinuities in dorsal color expression that might indicate the presence of morphs. $k$-means cluster analysis was used to determine whether morphs might be assembled on the basis of raw spectral variables (hue, chroma, and brightness). Spectral variables were tested separately and in combination with all other color variable pairings. I constructed both two- and three-morph models, since examples of each have been documented in different populations of another phrynosomatid (Uta stansburiana: Corl et al. 2010). Outcomes with raw spectral variables were compared to those generated by principal components analysis. I used the broken-stick model (Jackson 1993) to determine the number of PCs.
retained for analysis. Nonparametric tests were used for hypothesis testing, with $\alpha = 0.05$ (two-tailed) adjusted by Bonferroni correction for multiple tests (Rice 1989). All statistics were performed using SYSTAT 12 (SYSTAT Software, Inc. 2007).

III. Results

A. La Manzana

A total of 119 adult males were collected for spectral analysis spanning the known range of color variation in this population as perceived by human observers (see Chapter 1: Fig. 1.4). Two males were not measured for patch area inadvertently. In total, 1185 separate spectra were collected; of these, only 17 spectra (1.4%) from 11 males were rejected prior to analyses ($\bar{X} = 9.8$ accepted spectra/male; range = 5-10 accepted spectra/male).

Frequency distribution histograms were constructed for each of the three spectral color variables and patch area (Fig. 2.1). Visual inspection revealed multimodal patterns consistent with multiple morphs. Hue (Fig. 2.1A) exhibited a trimodal distribution, with frequency peaks at 460-480 nm, 580-630 nm, and 690-700 nm. Red Chroma (Fig. 2.1B) also showed a multimodal pattern with peaks at 15-17.5%, 25-35%, and 50-52.5%.

Brightness and Patch Area (Fig. 2.1C-D) were less clearly multimodal. Brightness exhibited a strong peak at 8-9%, with possible additional peaks at 13-14% and 18-19%. Patch Area showed at least one peak (possibly two) centered around 2.8-3.4 area units.

Cluster Analysis

I used $k$-means cluster analysis to determine the extent to which spectral variables predicted putative morph assembly. Each spectral variable (hue, chroma, brightness) was
tested alone and in combination with all other spectral variables under two and three-morph models. Patch Area was also included as an input variable in a combined analysis with all other variables. In all models where it was entered as an input variable, hue consistently explained most of the variation between clusters (Tables 2.1-2.2). In both two and three-morph models, males with short wavelength hues (blue males) separated consistently from all other males (“orange” males) (Fig. 2.2). In a three-morph model, the “orange” group was further partitioned into two clusters (yellow and red: Fig. 2.2B). Collectively, these three groups overlapped perfectly with the three peaks observed in the distribution of hue.

To characterize morph coloration more generally, I calculated mean reflectance spectra for each of the three morphs identified by cluster analysis (Fig. 2.3). Blue males exhibited a rapid rise from 400-450 nm, followed by a peak around 470 nm. Reflectance declined gradually between 500 and 700 nm. Yellow males exhibited a sharp rise between 400 and 440 nm leveling off until around 500 nm, where it rose sharply again. It peaked around 600 nm, and then declined smoothly to 700 nm. Red males did not exhibit the step pattern of yellow males; instead, reflectance was low until 520 nm where it began to rise steeply. At 590 nm the rate of change slowed but reflectance continued to rise steadily to 700 nm. Blue, yellow, and red males strongly differed in hue (Kruskal-Wallis $H = 100.4$, $P < 0.001$), red chroma (Kruskal-Wallis $H = 77.3$, $P < 0.001$), and patch area (Kruskal-Wallis $H = 67.3$, $P < 0.001$; Table 2.4). Blue males exhibited shorter peak wavelengths, reduced red saturation, and smaller dorsal patches relative to both yellow (hue: Mann-Whitney $U = 0$, $P < 0.001$; chroma: Mann-Whitney $U = 29$, $P < 0.001$; patch area: Mann-Whitney $U = 67$, $P < 0.001$) and red males (hue: Mann-Whitney
Similarly, yellow males had shorter peak wavelengths (Mann-Whitney \( U = 1798, P < 0.001 \)), reduced red saturation (Mann-Whitney \( U = 1471, P < 0.001 \)), and patch area (Mann-Whitney \( U = 1367, P < 0.001 \)) relative to red males.

However, morphs did not differ in brightness (Kruskal-Wallis \( H = 3.4, P < 0.18 \)).

**Principal Components Analysis**

The first three PCs explained 46.7%, 29.4%, and 18.5% of variation in dorsal coloration respectively (Fig. 2.4). As expected, PC1 was strongly correlated with brightness \( (r^2 = 0.89; F_{1,117} = 999.7, P < 0.001) \). PC2 explained variation in the relative amount of long wavelengths to middle-to-short wavelengths and was strongly correlated with both hue \( (r^2 = 0.53; F_{1,117} = 131.7, P < 0.001) \) and red chroma \( (r^2 = 0.78; F_{1,117} = 421.3, P < 0.001) \).

PC3 described variation in the ratio of very short wavelengths to middle-to-long wavelengths and was correlated with UV chroma \( (r^2 = 0.39; F_{1,117} = 75.1, P < 0.001) \).

Frequency distribution histograms were constructed for each of the first three principal components (Fig. 2.5). PC1 and PC3 were unimodal, but PC2 was bimodal (Fig. 2.5B).

Consistent with Fig. 2.4, males with shorter hues and lower red chromas (i.e., blue males) tended to have negative PC scores, whereas red males tended to have positive PC scores. Yellow males had both positive and negative PC scores.

Morphs assembled under cluster analyses were tested for differences in their PC scores. In a two-morph model of blue and orange males, blue males had higher PC1 scores than orange males (Mann-Whitney \( U = 1795, P = 0.005 \)) but lower PC2 scores (Mann-Whitney \( U = 71, P < 0.001 \)). Blue and orange males did not differ in their PC3 scores.
scores (Mann-Whitney \(U = 1221, P = 0.48\)). A three-morph model of blue, yellow, and red males showed that morphs differed overall in PC1 (Kruskal-Wallis \(H = 11.8, P = 0.003\)) and PC2 (Kruskal-Wallis \(H = 63.8, P < 0.001\)), but not PC3 (Kruskal-Wallis \(H = 3.4, P = 0.18\)). Blue males had higher PC1 scores than red males (Mann-Whitney \(U = 704, P < 0.001\)) but not yellow males (Mann-Whitney \(U = 1091, P = 0.052\)). Blue males did have lower PC2 scores than both red males (PC2: Mann-Whitney \(U = 13, P < 0.001\)) and yellow males (Mann-Whitney \(U = 58, P < 0.001\)). Yellow males tended to have higher PC1 scores relative to red males (Mann-Whitney \(U = 670.5, P = 0.049\)) but this was not significant following Bonferroni correction. However, yellow males did have lower PC2 scores than red males (Mann-Whitney \(U = 1197.5, P = 0.010\)).

**B. Escalerillas (San Luis Potosí)**

A total of 69 males were collected for spectral analysis of dorsal color in 2006 and 2007 (see Chapter 1: Fig. 1.2). Of 730 total spectra, 13 (1.7\%) were removed prior to analysis (\(\bar{X} = 9.8\) spectra/male; range = 7-10 spectra/male). In addition, one of the 69 males exhibited an unusual uniform pale blue dorsal phenotype (see Chapter 1: Fig. 1.2A) not seen in any other male. Thus, cluster models with and without this individual were run to examine effects on hypotheses for putative morphs. Frequency histograms were constructed for each of the three spectral color variables (Fig. 2.6). Of the three spectral variables, only the frequency distribution for Hue (Fig. 2.6A-B) indicated multimodality, with peaks at 620-630 nm, 640-650 nm, 670-680 nm and 690-700 nm. In addition, the single uniform pale blue male (\(\lambda_{\text{max}} = 486\) nm) was widely separated from the main cluster(s), possibly indicating another frequency peak around 480-490 nm. Red Chroma
and Brightness appeared to be unimodal. For Red Chroma (Fig. 2.6C), a strong peak was found at 40-42.5%, and a much smaller one at 50-52.5%. Brightness (Fig. 2.6D) showed a primary peak at 17.5-20%, with two smaller peaks at 7.5-10%, and 35-37.5%.

Cluster Analysis
Models were run with and without the single blue male for comparison of effects on clustering. Hue explained most of the variation among models where it was included as an input variable; however, the output from only one model is presented for brevity (Table 2.3). A two-morph model without the blue male (Table 2.3) revealed a yellow and red dichotomy similar to that observed in La Manzana (Fig. 2.7A). A three-morph model resulted in substantial morph reassignment, classifying two males with unusually high brightness (mean reflectance = 57.9% and 43.1% respectively) as a third cluster. In a two-morph model with the blue male included, this individual clustered as its own group with all others contained within a single “orange” (= yellow + red) phenotype class. A three-morph model revealed a blue/yellow/red complex (Fig. 2.7B).

Mean reflectance spectra for morphs from Escalerillas are shown in Fig. 2.8. Yellow males exhibited a sharp rise between 400 and 450 nm. Reflectance increased at a slower rate until around 520 nm, where it rose sharply again, peaking around 640 nm, declining smoothly to 700 nm. The reflectance curve for red males was similar to that of yellow males, except that overall reflectance was lower than for yellow males, and peak reflectance was shifted to 670 nm. In addition, the reflectance spectrum for the single blue male is shown. A rapid rise from 400 to 470 nm was followed by a peak around 490 nm, with a gradual decline from 500 to 700 nm. Mann-Whitney tests confirmed that
yellow and red morphs differed in hue (Mann-Whitney $U = 1107$, $P < 0.001$), red chroma (Mann-Whitney $U = 771$, $P < 0.006$), and brightness (Mann-Whitney $U = 288$, $P < 0.001$). Yellow males had a shorter peak wavelength and reduced red chroma relative to red males, but were also brighter than red males (Table 2.4).

Principal Components Analysis

The single blue male from Escalerillas was excluded from PCA. The first two principal components explained 78.6% and 12.3% of the remaining variation in dorsal color (Fig. 2.9). PC1 was strongly correlated with brightness ($r^2 = 0.97$, $F_{1,66} = 2258.4$, $P < 0.001$; Fig. 2.9). Alternatively, PC2 explained variation in the ratio of very short to medium-to-long wavelengths (Fig. 2.9). PC2 was not correlated with hue ($r^2 = 0.53$, $F_{1,117} = 131.7$, $P = 0.07$) or red chroma ($r^2 = 0.01$, $F_{1,66} = 0.9$, $P = 0.32$), but was strongly correlated with UV chroma ($r^2 = 0.38$, $F_{1,66} = 40.0$, $P < 0.001$). Yellow males (from cluster analysis) had higher PC1 scores than red males (Mann-Whitney $U = 302$, $P = 0.002$), but these two groups did not differ in PC2 scores (Mann-Whitney $U = 703$, $P = 0.06$). Frequency distribution histograms of PC1 and PC2 revealed unimodal patterns for each (Fig. 2.10).

C. Population Comparison

All population comparisons excluded the single blue individual from Escalerillas. Mean reflectance of males differed between the two populations: males from La Manzana were darker than those from Escalerillas overall (Mann-Whitney $U = 6121$, $P < 0.001$). Excluding the blue males from La Manzana did not change the pattern (Mann-Whitney $U$
= 4631, \( P < 0.001 \)). Comparing similar morph pairs showed that yellow males from Escalerillas were brighter than yellow males from La Manzana (Mann-Whitney \( U = 2048, P < 0.001 \)). However, there was no difference in brightness of red males between the two sites (Mann-Whitney \( U = 528, P = 0.09 \)). Population comparisons of hue and red chroma that included all males made little sense and were not performed. However, pairs of similar color morphs were compared with respect to hue and chroma. Yellow males from La Manzana had smaller peak wavelengths (hue: Mann-Whitney \( U = 2203.5, P < 0.001 \)) and reduced red saturation (red chroma: Mann-Whitney \( U = 1709, P < 0.001 \)) relative to males from Escalerillas. Red males from La Manzana had longer peak wavelengths (hue: Mann-Whitney \( U = 581, P < 0.001 \)) than males from Escalerillas, but did not differ in red chroma (Mann-Whitney \( U = 384, P = 0.59 \)).

**IV. Discussion**

Studies of color polymorphisms in lizards have provided major insights into the function and evolution of intrasexual color variation, both within (Sinervo and Lively 1996, Stuart-Fox et al. 2004, Stapely and Whiting 2006) and among populations (Corl et al. 2010). Variation in color has been linked to extent of aggression (Vinegar 1975), dominance status (Sinervo and Lively 1996), fighting ability (Thompson and Moore 1991a, Olsson 1994), degree of female receptivity (Cooper 1984, Weiss 2002, Calisi and Hews 2007), health (Ressel and Schall 1989, Calisi et al. 2008), female mate choice (Bleay and Sinervo 2007), male mate choice (LeBas and Marshall 2000), and alternative reproductive tactics, both in males (Zucker 1989, Thompson and Moore 1991a, Sinervo and Lively 1996, Zamudio and Sinervo 2000, Huyghe et al. 2007, Sinervo et al. 2007,
Olsson et al. 2009) and females (Sinervo et al. 2000b, Vercken et al. 2006). Nevertheless, few studies have directly tested whether proposed color morphs can actually be assorted into spectrally discrete color groups. Males of the lizard *Sceloporus minor* exhibit extensive variation in a sexually dimorphic trait (dorsal color) both within and among populations (Wiens et al. 1999). I quantified differences in dorsal color for males and tested whether color variation at La Manzana and Escalerillas was more consistent with a condition-dependent (plastic) or discrete (fixed) morph model.

**A. La Manzana**

In agreement with previous workers (Smith 1936, Chrapliwy 1964, Wiens et al. 1999) dorsal color variation was extensive among males at La Manzana (see Chapter 1: Fig. 1.4) The distribution of hue and chroma (but not brightness or patch area) revealed patterns consistent with multimodality (Fig. 2.1) and the existence of as many as three color morphs (blue, yellow, and red). Cluster models indicated that hue explained most of the variation among putative groups (Tables 2.1-2.2). When hue was included in any cluster model as an input variable, my morph assignment perfectly matched the frequency distribution of Hue (Fig. 2.2). In addition, male cluster assignment was unchanged in any model where hue was entered as an input variable. Cluster models did not correspond well to the distributions of Red Chroma, Brightness, or Patch Area regardless of the combination of variables entered (data not shown). Principal components analysis (PCA) also supported the hypothesis of multiple morphs. PC1 and PC3 appeared to be unimodal, but PC2 was bimodal (Fig. 2.5). PC2 described variation in short to medium-to-long wavelengths (Fig. 2.4), and was correlated with both hue and
red chroma. Thus, a bimodal distribution in PC2 appears to correspond to a blue and “orange” two-morph complex.

**B. Escalerillas**

Observed color variation (see Chapter 1: Fig. 1.2) was generally consistent with that reported by Wiens et al. (1999), with most males expressing a red, brown, or yellow phenotype. One notable exception was the discovery of a single uniform blue male (Chapter 1: Fig. 1.2A). This observation is congruent with a Grant and Smith (1959) report, in that these investigators collected several male *S. minor* with a pale blue phenotype near the city of San Luis Potosí. Thus, blue males may be more common at Escalerillas than suggested by my data, a finding supported by observations of other males with distinct yellow or red dorsal patches on a light blue background (Chapter 1: Fig. 1.2D).

Excluding the single uniform blue male from cluster analysis with two groups revealed yellow and red clusters separated at $\lambda_{\text{max}}$ of 660 nm (Fig. 2.7A). This is very similar to that observed between yellow and red males in La Manzana ($\lambda_{\text{max}} = 650$ nm). A three-morph model of the data reshuffled male assignment substantially, placing two (red) males of high brightness into their own group. Including the single blue male in a two-morph model resulted in a blue group composed of one male, and another group containing all other lizards (i.e., an “orange” group). A three-morph model split the single large cluster back into yellow and red groups, with morph assignment matching that generated under a two-morph model without the blue male (Fig. 2.7B). Principal components analysis did not find support for multiple morphs in males collected at
Escala
erillas (Fig. 2.10). In addition, PCA indicated that neither hue nor red chroma contributed substantially to the observed variation across males. PC2, which described variation in spectral shape rather than size (i.e., brightness), was not correlated with either variable, but was correlated with UV chroma.

C. Color variation within populations

Alternative strategies linked to color polymorphism within populations have been described in a wide range of taxa (Calsbeek and Sinervo 2008). Typically such species are territorial and strongly diurnal, traits that are likely to favor the evolutionary coupling of behavioral and color polymorphisms (e.g., Shuster and Wade 2003). Nevertheless, the extent to which polymorphic taxa actually exhibit spectral variation in color traits in accordance with that perceived by humans is rarely tested. An interesting exception is provided by studies of the lacertid lizard, *Lacerta vivipara*. In this species, female ventral color varies from pale yellow to bright orange (Vercken et al. 2006). Ventral color is heritable, and has been linked to alternative mating tactics (Vercken et al. 2006, Vercken and Clobert 2008). Nevertheless, ventral color was found to grade continuously rather than forming discrete groups (Vercken et al. 2006), consistent with evidence of substantial plasticity in this trait (Cote et al. 2008).

In this study I used cluster analysis and PCA to characterize spectral variation of dorsal color in each of two populations of *S. minor*. However, results obtained from each method were generally not congruent. Cluster analysis of male color in La Manzana indicated that dorsal color occurred in three groups, whereas PCA supported a two-morph model. In Escalerillas, cluster analysis found support for a two-morph model, but PCA
provided no evidence for multiple morphs. Disparities in results obtained using these two approaches have been reported in some other studies (Molina-Borja et al. 2005). Grill and Rush (2000) compared estimates of hue, chroma, and brightness generated by PCA and by Endler’s (1990) segment classification (SC) method to known values of these variables from Munsell color standards. Spectral variables were calculated separately for each of four major Munsell color groups (red/orange, yellow/green, green/blue and blue/purple), and for all four color groups combined. (This latter analysis is broadly similar to that described in the present study, in which I compared males within and among populations that exhibit multiple hues.) Grill and Rush (2000) found that PCA and SC each accurately predicted hue and brightness, but neither method characterized chroma well. Concerns were also raised about the reliability of PCA when data sets are highly variable (Grill and Rush 2000). Thus, characterization of color variation from PCA in the present study might be expected to be less reliable than that generated by cluster analysis of the untransformed spectral variables. In this context, a three-morph model of blue, yellow, and red appears to be the best-supported hypothesis for male color at La Manzana, and a two-morph model of yellow and red is supported for males from Escalerillas.

D. Color variation between populations

Males from La Manzana had greater mean reflectance (i.e., were brighter) than those from Escalerillas. However, this appeared to be mainly attributable to differences between putative yellow morph pairs, as there was no difference in brightness between red males from the two populations. Yellow males from La Manzana had shorter peak
wavelengths (Table 2.4) and reduced red saturation relative to yellow males from Escalerillas. Red males from La Manzana had longer hues than those from Escalerillas but did not differ in red chroma (Table 2.4). The possible adaptive basis (if any) for this variation is unknown, but several non-mutually exclusive hypotheses could explain these observed differences. One possibility is that color represents an adaptation to the specific lighting environments characteristic of each population. La Manzana is dominated by dense stands of oak-pine (*Quercus-Pinus*) forest with exposed limestone outcroppings distributed throughout the surrounding forest matrix. During the summer and fall months, large cloud banks rapidly swell up from the valley floor, enclosing the study site in heavy fog for up to several hours a day, and limiting opportunities for lizards to bask and engage in various social behaviors (B. Stephenson, pers. obs.). Conversely, the study site at Escalerillas contains outcroppings of large boulders of volcanic origin (Aranda-Gómez et al. 2007) surrounded mostly by low-growing grasses and bushes; oaks (*Quercus*), juniper (*Juniperus*), and yucca (*Yucca*) are only thinly distributed around the main study area. If dorsal color serves as a signal to conspecifics, all else being equal it should be adapted to effectively exploit the available light characteristic of the habitats of the intended receivers (Endler 1992, Leal and Fleishman 2004). The lighting environment for displaying adult males in La Manzana appears to conform to the ‘woodland shade’, ‘large gaps’ or ‘cloudy’ environments described by Endler (1992). ‘Woodland shade’ is characterized by bluish-grey light, which should increase the conspicuousness of blue color patches, since these would tend to reflect the largest proportion of available wavelengths. ‘Large gaps’ and ‘cloudy’ exhibit essentially the same light (white), which should render all colors relatively conspicuous against the background. Thus, saturated
blue colors might be a common component of dorsal coloration in *S. minor* from La Manzana in part because it is relatively conspicuous against most lighting environments.

Another possibility is that mean predation risk across all morphs differs between the two sites. Males at Escalerillas are generally less conspicuous to human observers relative to those at La Manzana (Wiens et al. 1999, B. Stephenson, pers. obs.). One possibility is that males at this locality are under stronger selection for crypsis than males at La Manzana. If true, we might expect the abundance and/or diversity of visually oriented predators to be greater at Escalerillas. In support of this idea, several known predators of small lizards were found at Escalerillas including whipsnakes (*Masticophis*), patch-nosed snakes (*Salvadora*), Mexican pine snakes (*Pituophis deppei*), and collared lizards (*Crotaphytus*); a small diurnal rattlesnake (*Crotalus aquilus*) was also present. However, only two of these species were found in La Manzana. Whipsnakes were present but rare (B. Stephenson, pers. obs.); conversely, *C. aquilus* was highly abundant, and was seen consuming *S. minor* on several occasions (B. Stephenson, pers. obs.). Like other crotaline vipers, *C. aquilus* probably uses infrared cues in capturing prey. Although rattlesnakes evidently have good vision (Haverly and Kardong 1996), the extent to which they might also use color as a cue for prey is unknown. Taken together, my data are at least consistent with the idea that males at Escalerillas experience a different selection regime than males at La Manzana, though the possible role of mammalian or avian predators on selection for lizard color should also be considered (e.g., Stuart-Fox et al. 2003).

A third possibility is that dorsal color is linked to thermoregulation. Many squamates darken in response to cold temperatures, which appears to facilitate rapid
heating during basking (Norris 1967). One possibility is that low brightness of lizards in La Manzana allows males to rapidly warm up following intermittent and unpredictable breaks in fog during the summer and fall months. Alternatively, low reflectance may be disadvantageous for males in Escalerillas, which are subject to higher mean temperatures than La Manzana. Interestingly, one study of a polymorphic lacertid (*Podarcis melisellensis*) found evidence of a morph-specific difference in activity and temperature; yellow males were active under warmer air temperatures than white or orange males, though no difference in mean body temperature was found among morphs (Huyghe et al. 2007).

E. UV reflectance

Ultraviolet (UV) colors are widespread in animals (Shi and Yokoyama 2003) and may play an important role in mate choice (Hunt et al. 1999, Smith et al. 2002) or male-male competition (Stapley and Whiting 2006). Many reptiles can see UV (turtles: Loew and Govardovskii 2001; geckos: Loew 1994, Ellingson et al. 1995, Loew et al. 1996; collared lizards: Macedonia et al. 2009; anoles: Loew et al. 2002; garter snakes: Sillman et al. 1997; pythons: Sillman et al. 1999, Davies et al. 2009; rainbow snakes: Davies et al. 2009), and many species express ornaments that strongly reflect in the UV (see Fleishman et al. 1993, Molina-Borja et al. 2005, Steffen and McGraw 2007). Crucially, there is evidence that variation in UV may predict the outcome of social interactions (LeBas and Marshall 2000, Whiting et al. 2006). Strong evidence for a function of UV in lizards was found by Stapley and Whiting (2006) in their study of male flat lizards (*Platysaurus broadleyi*). They observed that males with throats experimentally
manipulated to reflect less UV were challenged more frequently by opponents than controls, indicating that UV reflectance is a signal of fighting ability. Several population-level studies indicate that variation in UV may even predict evolutionary trajectories (Thorpe and Richard 2001, Leal and Fleishman 2004). In *Sceloporus minor*, UV reflectance of the dorsum was low among all putative morphs in both populations (Tables 2.2-2.3). This suggests that any potential signaling function of dorsal coloration in either population of *S. minor* is not linked directly to variation in UV expression.

The absence of strong UV reflectance in the dorsum also offers clues as to the proximate basis of skin color in *S. minor*. With rare exceptions, blue color in vertebrates is structural in origin (Bagnara et al. 2007), but yellows and reds often have a pigmentary component (e.g., Steffen and McGraw 2007). In *Sceloporus*, blue abdominal and throat color has been attributed to the combined effect of iridophores and melanophores (Cooper and Greenberg 1992). Alternatively, orange and yellow tissues have been linked to the expression of additional pigments (pteridines: Morrison et al. 1995). For example, in *S. erythrocheilus* males occur in three morphs characterized by differences in chin color (yellow, orange, and gray; Rand 1988). An iridophore layer is present in all morphs, but in yellow and orange males an additional xanthophore layer occurs above the iridophore layer. The xanthophores contain pteridine pigments that selectively reflect longer wavelengths, although differences in iridophore size and arrangement probably play a role in color expression as well (e.g., Sherbrooke and Frost 1989, Morrison et al. 1995). Although the proximal basis of dorsal color in *S. minor* is unknown, reflectance spectra of male morphs are not consistent with expectations for the presence of carotenoids. These pigments (perceived as yellow to red in normal human vision) are
often incorporated in the colorful ornaments of vertebrates, including squamates (anoles: Macedonia et al. 2000, Steffen and McGraw 2007; chuckwallas: Kwiatkowski and Sullivan 2002). In addition, carotenoids can provide important benefits to immune system functioning, and diversion of these pigments into ornaments renders them unavailable for immune system repair. Unlike pteridines, carotenoids cannot be synthesized de novo in animals and are often limiting in the diet. Consequently, variation in carotenoid-based ornaments may reliably signal a number of important qualities to potential mates or rivals, including health and immunocompetence, foraging ability, territory quality, and predator avoidance capability (Olson and Owens 1998). However, carotenoids probably do not contribute substantially to male dorsal color in *S. minor*, as these pigments typically exhibit a secondary peak in the UV (Bleiweiss 2005), a peak that was not detected in the reflectance spectrum of any male morph (Figs. 2.6, 2.11).
Figure 2.1 Frequency distribution of dorsal color variables from males at La Manzana. A: Hue. B: Red Chroma. C: Brightness. D: Patch Area.
Figure 2.2 Frequency distribution of Hue for males from La Manzana modified to indicate assignment by cluster analysis. A: Two-morph model (blue/orange). B: Three-morph model (blue/yellow/red).
Figure 2.3 Mean reflectance (± SE) of the dorsum for the three putative color morphs of male *S. minor* at La Manzana, Hidalgo. Curves represent smoothed averages in 10 nm increments between 300 and 700 nm. Standard error bars plotted at 20 nm increments for clarity. Blue: *N* = 30; Yellow: *N* = 58; Red: *N* = 31.
Figure 2.4 Plot of the first three principal components generated from reflectance spectra of the dorsum from *S. minor* in La Manzana.
Figure 2.5 Frequency distribution of each of first three principal components derived from reflectance spectra from males at La Manzana. A: PC1, correlated with Brightness. B: PC2, correlated with Red Chroma and Hue. C: PC3, correlated with UV Chroma.
Figure 2.6 Frequency distribution of dorsal color variables from males at Escalerillas. A: Hue (all). B: Hue (600-700 nm only). C: Red Chroma. D: Brightness.
Figure 2.7 Frequency distribution of Hue for males from Escalerillas modified to indicate assignment by cluster analysis to a two-morph model (yellow/red). A: Distribution of yellow and red male morphs only (600-700 nm). B: Distribution extended to include single observed blue individual (400-700 nm).
Figure 2.8 Mean reflectance (± SE) of the dorsum for putative color morphs of male *S. minor* at Escalerillas, San Luis Potosí. Curves represent smoothed averages in 10 nm increments between 300 and 700 nm. Standard error bars plotted at 20 nm increments for clarity. Blue: *N* = 1; Yellow: *N* = 41; Red: *N* = 27.
Figure 2.9 Plot of the first two principal components generated from reflectance spectra of the dorsum from *S. minor* in Escalerillas.
Figure 2.10 Frequency distribution of the first two principal components derived from reflectance spectra from males at Escalerillas. A: PC1, correlated with Brightness. B: PC2, correlated with UV Chroma.
Table 2.1 Summary table from two-morph cluster analyses of male dorsal color in La Manzana. $N = 119$ for all models except *, where $N = 117$.

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Table 2.2 Summary table from three-morph cluster analysis of male dorsal color in La Manzana. $N = 119$ for all models except *, where $N = 117$.

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Table 2.3 Summary table from two-morph cluster analysis of male dorsal color in Escalerillas with blue male excluded. \( N = 68 \) for all models.

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<td>Brightness</td>
<td>539.5</td>
<td>6226.9</td>
<td>5.7</td>
</tr>
</tbody>
</table>
Table 2.4 Descriptive statistics of the dorsum for morphs of male *S. minor* from La Manzana and Escalerillas assembled by cluster analysis. (* = not included in cluster models)

<table>
<thead>
<tr>
<th>Trait</th>
<th>La Manzana</th>
<th>Escalerillas</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Blue</td>
<td>Yellow</td>
</tr>
<tr>
<td>Hue (nm)</td>
<td>477.18</td>
<td>3.87</td>
</tr>
<tr>
<td>Red Chroma (%)</td>
<td>23.12</td>
<td>0.78</td>
</tr>
<tr>
<td>UV Chroma (%)*</td>
<td>11.9</td>
<td>0.86</td>
</tr>
<tr>
<td>Brightness (%)</td>
<td>4.10</td>
<td>0.17</td>
</tr>
<tr>
<td>Patch Area (units)</td>
<td>1.92</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>26.22</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>2.67</td>
<td>--</td>
</tr>
</tbody>
</table>
CHAPTER 3

Body Size, Shape and Performance in Color Morphs of the Lizard *Sceloporus minor*

I. Background

The existence of intrasexual polymorphisms—the expression of two or more forms of a phenotype among members of one sex—is a challenge to evolutionary theory. A single morph should become fixed in the population unless it has exactly equal fitness with other morphs or an advantage when rare (Gross 1996, Shuster and Wade 2003). Nevertheless, within-sex polymorphisms can arise and be maintained in several different ways. For example, apostatic selection is differential selection on prey types as a function of a predator search image; since the search image should be tuned to common prey phenotypes, rare morphs should experience relaxed selection. Another possibility is that color morphs reflect alternative reproductive tactics (ARTs). ARTs represent alternative pathways to reproductive success among members of a single sex, and represent the expression of multiple interrelated phenotypes working in concert to maximize fitness (Taborsky et al. 2008). ARTs have received substantial theoretical attention (e.g., Gross 1996, Shuster and Wade 2003, Tomkins and Hazel 2007), especially regarding the extent to which individuals may be able to shift between tactics (Moore 1991, Gross 1996), either in response to short-term changes in the social environment (natterjack toads: Arak 1988), or as a function of seasonal changes in age or body size, or local territory occupancy (collared lizards: Baird and Timanus 1998). This has lead to debate regarding the distinction between genetically based phenotypes immune to environmental effects.
and phenotypes that are subject to plasticity in expression. This distinction is non-trivial from an evolutionary standpoint, because the mean fitness of morphs of plastic tactics are generally presumed to differ (i.e., best of a bad job: Gross 1996), whereas tactics that are under strong genetic control are thought to be equal (Shuster and Wade 2003). However, most ARTs are likely to exhibit some phenotypic plasticity (Taborsky et al 2008), even in systems where heritability of traits linked to tactics is quite high (Vercken et al 2006). As part of related research in a lizard that exhibits variable sexually dimorphic color in males (S. minor), I tested the hypothesis of alternative reproductive tactics in the context of both condition-dependent and discrete color polymorphisms.

Lizards have been popular subjects of studies that investigate the relationship of color polymorphisms to ARTs (Calsbeek and Sinervo 2008). Many species are locally abundant and easy to catch, and amenable to both field and laboratory-based studies. Such studies have included investigations of the various component phenotypes (Hover 1985, Thompson and Moore 1991a, Healey et al. 2007, Huyghe et al. 2007, Sacchi et al. 2007a, b), the hormonal underpinnings of morph expression (Hews et al. 1994, Olsson et al. 2007a, Miles et al. 2007b, Mills et al. 2008), the relationship of morph phenotypes to male fitness (Sinervo and Lively 1996, Sinervo et al. 2007, Olsson et al. 2007b), and the mechanisms favoring the long-term stability and evolution of ARTs using phylogeny-based (Corl et al. 2010) or modeling approaches (Sinervo 2001, Calsbeek et al. 2002). One of the model systems for the study of alternative tactics is the side-blotched lizard (Uta stansburiana). In populations in coastal California males exhibit a complex three-morph system of ARTs linked to throat color (orange, yellow, and blue). This system exhibits population dynamics similar to the children’s game of rock-paper-scissors, in
that each morph defeats one morph, but in turn is defeated by another morph (Sinervo and Lively 1996). Orange males aggressively defend large territories, and usurp the territories of neighboring blue males, which defend smaller territories. Yellow males are sneakers, and strongly resemble females in both coloration and behavior; they invade the large territories of orange males, and sneak matings with females surreptitiously (Zamudio and Sinervo 2000). However, yellow males are readily detected and chased away by pairs of cooperating blue males, collectively preventing invasion of sneaking female mimics into their respective territories (Sinervo and Clobert 2003). Multi-year field studies confirm that morph frequencies cycle over time and that a rare morph advantage driven by negative frequency-dependent selection leads to a perpetual oscillation in morph frequency (Sinervo and Lively 1996). Morph heritability is very high (Zamudio and Sinervo 2000) and it is thought that a single locus (OBY) or possibly two tightly linked loci exert pleiotropic effects on throat color, endocrinology, physiology, and behavior (Sinervo et al. 2000a, Mills et al. 2008, Corl et al. 2010). The rock-paper-scissors dynamic has been recently described in another species, the European common lizard *Lacerta vivipara* (Lacertidae) (Sinervo et al. 2007). In populations in France, males exhibit patterns of body color, performance, survival, and offspring recruitment that are remarkably similar to those seen in the side-blotched lizard. For example, males occur in three morphs, orange, yellow, and white (instead of blue); orange males exhibit greater stamina than the two other male morphs, but also have lower interannual survival (Sinervo et al. 2007).

In some other lizards male morphs differ in morphological, physiological, and behavioral traits in a manner consistent with ARTs, although data on offspring
recruitment and survival in the wild are unavailable. In the tree lizard *Urosaurus ornatus*, males with solid orange throats have reduced fighting ability relative to males with blue throat spots against an orange background (orange-blue males) (Hover 1985, Thompson and Moore 1991a). Orange-blue males vigorously defend territories, and spend more time interacting with females than orange males (Thompson and Moore 1992). Orange males are larger than orange-blue males, but do not defend permanent territories. Instead, they exhibit a condition-dependent plastic tactic mediated by environmentally induced stress: they reside on the periphery of orange-blue males during rainy years (satellite strategy), but abandon territoriality completely during drought years (nomad strategy) (Moore et al. 1998). Orange males also initiate flight from predators at greater distances and remain in their refuge for a longer period of time following flight relative to orange-blue males (Thaker et al. 2009). In the Dalmatian wall lizard *Podarcis melisellensis* (Lacertidae) males with orange throat and abdominal color attain larger body size, have proportionately larger heads, and bite harder than yellow or white males (Huyghe et al. 2007). Males of a close relative, the congener *P. muralis*, exhibit morph-specific variation in immune response: yellow morphs exhibit reduced swelling relative to white and red males following subcutaneous injection of phytohaemagglutinin (Sacchi et al. 2007a). Collectively, these studies indicate that male-biased ARTs (and their color correlates) are widespread in non-ophidian squamates (Vidal and Hedges 2005).

**Study Species**

The genus *Sceloporus* is a large group (> 80 spp.) of New World lizards ranging from Canada to Panama (Wiens and Reeder 1997). Males of most species express sexually
dimorphic colors (often blue) on the abdomen and throat, features that are revealed to conspecifics in courtship and aggressive encounters. Although a number of reports have documented color variation in *Sceloporus*, few studies have addressed the possible social significance of this trait. An important exception is the work of Rand (1988, 1990) who found evidence in *S. erythrocheilus* that male color morphs (orange, yellow, and white) were linked to ARTs. These findings are of additional importance in light of more recent research, which indicates that color polymorphism is widespread in the genus (Sinervo et al. unpubl.).

*Sceloporus minor* is a common and conspicuous diurnal lizard of both xeric and mesic habitats associated with the southern terminus of the Chihuahuan Desert in central Mexico (Chrapliwy 1964). Males from populations near the community of La Manzana (20° 52′ N, 99° 13′ W) in NW Hidalgo state exhibit striking color variation of the dorsal surface (Fig. 3.1), consistent with earlier reports of this species from nearby localities (Smith 1936, Sutton 1961, Wiens et al. 1999). Analyses of dorsal color indicate that three discrete color morphs exist (blue, yellow, and red), distinguished primarily by differences in hue (Fig. 3.2). Adults do not switch color class within or between years, indicating that morph differences are fixed by the onset of sexual maturity (B. Stephenson, unpubl. data) Notably, the pattern of color variation in *S. minor* broadly parallels that reported in several other close relatives (e.g., *S. erythrocheilus*: Rand 1990; *Urosaurus*: Thompson and Moore 1991b; *Uta*: Sinervo and Lively 1996).

Although models for male color in *S. minor* are most consistent with a three-morph system, it is conceivable that the scarcity of males of intermediate color (Fig. 3.2) is a product of sampling design, and thus may only reflect biases in capture rate of males.
with these phenotypes. If so, male coloration may be more evenly distributed among the population than currently recognized. A unimodal distribution of color variables would be expected if dorsal color is a condition-dependent trait in *S. minor*. Many colorful traits in animals are condition-dependent, with brighter or more colorful ornaments produced by individuals in better condition (e.g., fence lizards: Ressel and Schall 1989; house finches: Hill 1990). For example, an important source of yellow, orange, and red colors in animal tissues are carotenoids, long-wavelength pigments that cannot be synthesized de novo in animals, and so must be acquired in the diet where they are often limiting (Olson and Owens 1998). Carotenoids provide a variety of benefits to animals, and are especially well known for their role in immune system functioning (Olson and Owens 1998). Since diversion of carotenoids into ornaments renders them unavailable in health maintenance, color traits that covary with carotenoid density may reliably reveal male quality, as only healthy, vigorous males can afford to produce the color signal without incurring the cost of a compromised immune system (Lozano 1994). Carotenoid-based traits may reliably indicate other attributes linked to mating success, such as foraging ability or predator avoidance (Olson and Owens 1998). Whether carotenoids contribute to the yellow and reddish colors seen in *S. minor* is unknown, but they are known to occur in the colorful tissues of other iguanid lizards (chuckwallas: Kwiatkowski and Sullivan 2002; anoles: Steffen and McGraw 2007).

In *S. minor*, the apparent distinction of any two putative color morphs (e.g. yellow and red) may only reflect poor sampling of males with intermediate phenotypes, rather than indicate true scarcity. Constraining male assignment to two groups rather than three using cluster analysis (Chapter 2) indicated that an orange morph representing a
combined yellow and red group might exist, in combination with a blue group (Fig. 3.1). An orange morph is characteristic of several phrynosomatid lizards (e.g., *S. erythrocheilus*, Rand 1990; *Uta stansburiana*, Sinervo and Lively 1996; *Urosaurus ornatus*, Meyers et al. 2006). In addition, some *S. minor* males have dorsal patches that appear orange, but spectrally fall within the observed distribution of yellow males (Fig. 3.2). Thus, putative yellow and red morphs could conceivably represent a single morph (‘orange’) characterized by extensive variation in hue.

I tested for differences in morphometrics and performance in male *S. minor*, using each of three models for color (condition-dependent, two-morph, and three-morph). If color is exclusively or largely a condition-dependent trait, I predicted that body size, condition, and performance would be linearly correlated with spectral variables. If dorsal color corresponds to a two-morph system of blue and orange males, or to a three-morph system of blue, yellow, and red males, I predicted that morphs would differ in these variables but made no prediction as to the direction of outcome. Strong support of a three-morph model over the other models would be found if males of the yellow class—the spectrally intermediate group—were consistently larger or smaller in size, or exhibited greater or lesser performance in endurance trials relative to blue and red males.

II. Materials and Methods

A. Morphometrics

Males were collected in and around the community of La Manzana between July 2005 and November 2008. Lizards were caught by noose while they were basking on boulders
or hiding in crevices, and taken to a local residence for data collection. All linear measures were recorded with dial calipers (Mitutuyo: accuracy ± 0.025 mm). Mass was measured on a portable electronic balance (Scout: accuracy ± 0.1 g). Following Hews (1990), I measured each trait three times with the condition that all three measurements must fall within a pre-established error range. If the third measurement fell outside this range, an additional measurement was taken until three consecutive measurements met this condition. Means of these three measurements were then subjected to statistical analysis.

Each of the following measurements was constrained to an error range of ± 1 mm. Snout-vent length (SVL) was measured from the tip of the snout to the posterior edge of the anal scale. Intact tail length (ITL) was measured from the anterior end of the post-anal scales to the posterior edge of the last scale underlain by caudal vertebrae. Total tail length (TTL) was measured from the anterior end of the enlarged post-anal scales to the terminal tip of the tail, whether regrown or intact. On occasion, lizards were found with forked tails, a phenomenon that arises when a tail is fractured without complete autotomy. In these cases, total tail length was determined by measuring from the post-anal scale to the distal edge of the longest existing tail branch, whether intact or regrown. Forelimb length (FL) was computed as the sum of the upper arm length, lower arm length and midhand length (Vanhooydonck et al. 2001). Upper arm length was the distance from the shoulder joint to the elbow. Lower arm length was the distance from the elbow to the wrist. Forefoot length was the distance from the wrist to the third digit of the hand. Hindlimb length (HL) was measured as the sum of femur length, tibia length and midfoot length (Vanhooydonck et al. 2001). Femur length was the distance from the pelvic joint
to the knee. Tibia length was the distance from the knee joint to the ankle. Hindfoot length was the distance from the ankle joint to the base of the third digit. Forelimb to hindlimb ratio (FHR) was calculated as FL/HL. All limb measurements were taken exclusively on the left limbs.

Several other traits were measured to a more narrow range (± 0.2 mm). Jaw length (JL) was the distance from the tip of the rostral scale to the posterior edge of the last labial scale on the upper jaw. Head width (HW) was measured as the maximal distance between scales on the first scale rows immediately anterior to each ear opening. Head depth (HD) was the distance between the top of the supraciliary scale row at the level of the pupil to the base of the labial scale on the upper jaw (Hews 1990). Jaw length and head depth were both measured exclusively along the right side of the head.

Body mass was measured to an error range of ± 0.1 g. I calculated an index of male body condition (BCI) as [mass$^{1/3}$/SVL] (Olsson 1994). With the exception of mass, all morphometric data were collected following administration of a small dose (0.05-0.10 cc) of 2% lidocaine, which helped to minimize lizard movement during data collection. Lizards were released as soon as possible, usually between 24 and 72 h after collection.

B. Stamina

Performance capacity was measured in adult males collected in and around the community of La Manzana from 4 September to 3 October 2008. This timeframe corresponds to the period of peak mating behavior in this species (Ramírez-Bautista et al. 2008; B. Stephenson, unpubl. data). Performance trials were conducted at the same
locality as morphometric work. Most males ($N = 29$) were measured for color using spectroradiometry, and assignment to putative morph determined by cluster analysis (see Chapter 2) following data collection. For these males, color data were always collected the day before each performance trial, to allow lizards time to recover from the stress resulting from the capture and spectroradiometry prior to endurance testing. The remaining males ($N = 22$) were scored for color by photographic inspection (see III. Color Morph Assignment for details) after the conclusion of experiments.

For all males, endurance was measured one day after capture. To facilitate comparison among studies I followed the general protocols described in Sinervo and Huey (1990) and Sinervo et al. (2000a). About 30 min prior to stamina testing, lizards were weighed on a portable digital scale ($\pm 0.1$ g). Each was then placed in a separate glass terrarium (61 x 32 x 42 cm) containing a bed of wood chips and a small pile of rocks under a red heat lamp and allowed to bask while visually isolated from other lizards. The optimal activity temperature range has not been determined for any population of $S.\, minor$; however, lizards were presumed to be at or near their thermal optimum when warm to touch. The treadmill measured approximately 30 x 40 cm and was bounded on three sides by partitions. The forward partition was composed of clear plastic permitting forward viewing by the lizard; the two sides were composed of opaque cardboard. The treadmill rotated at a speed of 0.5 km/h, an ecologically relevant speed for other small terrestrial lizards (Sinervo et al. 2000a). A red heat lamp placed over the center of the treadmill served to maintain a similar temperature ($33^\circ C$) to that in each warming terrarium. Lizards were placed in the middle of the treadmill and allowed to run until exhaustion. To encourage forward movement, subjects were gently prodded on the
legs or the base of the tail. Exhaustion was determined by failure to maintain the righting response (Miles et al. 2007a), assessed by picking up the tested lizard and flipping it onto its back. If the lizard was able to right itself within three seconds, the trial was continued; if not, the trial was terminated. When testing the righting response, trial time was paused and resumed only if the tested animal was returned to the treadmill. All trials were concluded following a third check for exhaustion, even if the tested lizard retained the righting response.

In addition to stamina, I scored several other behavioral measures during each trial. Jumps are vertical leaps of at least 50% of the height of the treadmill walls. Reversals are 180° rotations of the body, so that the torso and limbs of the lizard are oriented in the same direction as the current of the treadmill. Handedness is a bias in the general directionality of the lizard on the treadmill, and was scored as a subjective assessment of the side (left or right) to which the lizard preferred to run. In trials where males either ran straight ahead or ran to the left and right equally, males were interpreted as exhibiting no bias, and so a score of “none” was assigned.

After completion of endurance tests, lizards were returned to their individual collection bags and allowed to rest undisturbed. Following a minimum 1-h recovery period, lizards were measured or scored for several other morphometric variables as described previously. All were released at their site of capture within 72 h of collection.

C. Color Morph Assignment

Most males were measured for color using spectroradiometry, and the details of the acquisition and analysis of spectral data are described elsewhere (Chapter 2). Previously I
generated two- and three-morph models, indicating either a blue/orange assortment or a blue/yellow/red assortment (male assignment to the blue morph category did not change under two- and three-morph models). All total, 118 males classified using cluster analysis were made available for morphometric analyses.

Due to logistical complications a spectroradiometer was not available during all phases of work. In addition, a large number of captured males ($N = 87$) were unavailable for spectral analysis. Rather than remove these subjects from the analysis, I asked whether human visual inspection could accurately assign males to putative morphs generated by cluster analyses. If so, males missing spectral data might be reliably assigned to putative color class by comparing their photos to those of males of known morph under two-morph (blue/orange) and three-morph (blue/yellow/red) models. Thus, photographs of lizards classified to morph by cluster analysis were examined by the author to gain experience with the extent of variation perceived within each respective morph class. I then scored males lacking spectral data by comparing their photos to those of males of known morph. Although the use of subjective approaches to color classification requires caution and is best avoided whenever possible (Bennett et al. 1994), I have no indications that any errors in classification were directionally biased (i.e., repeatedly scoring true yellow males as red males). I then tested morph hypotheses for body size and shape using the cluster morph- (i.e., spectral) and photograph- (i.e., non-spectral) based data sets separately, and together in a combined analysis. For the test of endurance capacity sample sizes of males with and without spectral data were separately low, so only a single analysis was performed for each morph model.
D. Statistics

For all tests involving measures of body size (SVL, mass, body condition) or tail length (ITL, TTL), I used untransformed values of the raw data in hypothesis testing. For variables linked to head size (JL, HW, HD) and limb length (FL, HL), I first calculated the residuals from regressions of each transformed trait against SVL. For the three head measures only, I then used principal components analysis (PCA) to transform the residuals of each of the head variables into a single composite orthogonal variable (Head Size), which was then subjected to analysis. PCA was performed separately for each unique data set (Grill and Rush 2000).

To test for linear relationships of color with body size and shape I ran multiple regressions of three spectral variables (hue, chroma, and brightness) against each morphometric trait. I used nonparametric Mann-Whitney and Kruskal-Wallis tests to test for differences among putative morphs in morphometric and behavioral variables that failed to meet conditions of normality and homogeneity of variance when partitioned into multiple groups. When a significant Kruskal-Wallis test was found, I ran separate Mann-Whitney tests between group pairs, with adjustment of alpha for multiple comparisons. For analyses of morph performance I used the analysis of variance (ANOVA). Significant outcomes were examined with analysis of covariance (ANCOVA) to test for an effect of capture date or body size on performance. Statistics were computed using SYSTAT 12 (SYSTAT Software, Inc. 2007). Means are reported ± SE. For all tests, I set $\alpha = 0.05$ with Bonferroni correction for multiple tests (Rice 1989) when appropriate.
III. Results

A. Morphometrics

1. Single Morph/Condition-Dependent Model

I used multiple regression to test for correlations of raw spectral variables with eight morphometric traits linked to body size and condition (Table 3.1). The regression model revealed a trend towards a significant relationship between red chroma and the forelimb to hindlimb ratio; redder males tended to have slightly longer hindlimbs relative to their forelimbs. However, the overall model was not significant ($r^2 = 0.24$, $P = 0.17$). Overall, I found little support for a linear correlation of dorsal color with any morphological trait examined.

2. Two Morphs (B/O)

Cluster Model

Blue males tended to be larger than orange males in body length (Mann-Whitney $U = 1713.5$, $P = 0.008$; Table 3.2), but this difference was not quite significant. No other differences among morphs were found.

Photographs

Blue males were larger than orange males (Mann-Whitney $U = 793.5$, $P = 0.004$; Fig. 3.3, Table 3). In addition, orange males tended to have proportionately longer forelimbs
than blue males (Mann-Whitney $U = 69, P = 0.008$; Table 3.3) but this was not significant following Bonferroni correction.

**Combined Analysis**

Blue males were larger than orange males (Mann-Whitney $U = 4848.5, P < 0.001$; Fig. 3.4, Tables 3.4-3.5). Blue males also tended to have larger heads (Mann-Whitney $U = 4291, P = 0.031$; Table 3.4) than orange males and proportionately shorter forelimbs (Mann-Whitney $U = 208, P = 0.023$; Table 3.4), but neither difference was significant following Bonferroni adjustment.

3. Three Morphs (B/Y/R)

**Cluster Model**

Mean SVL differed significantly among color morphs (Kruskal-Wallis $H = 18.98, P < 0.001$; Fig. 3.5, Table 3.2). Yellow males were smaller than both blue and red males (B > Y: Mann-Whitney $U = 1221, P < 0.001$; R > Y: Mann-Whitney $U = 1327, P < 0.001$), whereas blue and red males were not different in size (Mann-Whitney $U = 492.5, P = 0.52$).

**Photographs**

Blue males tended to be larger than other morphs (Kruskal-Wallis $H = 9.78, P = 0.007$) and have shorter forelimbs relative to their body size (Kruskal-Wallis $H = 6.97, P =$
0.031). In addition, yellow males tended to have smaller heads than other males (Kruskal-Wallis $H = 6.94, P = 0.031$). However, none of these differences was significant following Bonferroni correction.

### Combined Analysis

Morphs differed in size (Kruskal-Wallis $H = 24.63, P < 0.001$; Fig. 3.6, Tables 3.4, 3.6). Both blue and red males were larger than yellow males (B > Y: Mann-Whitney $U = 3607.5, P < 0.001$; R > Y: Mann-Whitney $U = 3628, P < 0.001$), whereas blue and red males did not differ (Mann-Whitney $U = 1241, P = 0.15$). Head size also differed significantly among morphs (Kruskal-Wallis $H = 13.15, P = 0.001$; Fig. 3.7, Table 3.4); specifically, yellow males had proportionately smaller heads than both blue and red males (B > Y: Mann-Whitney $U = 3256, P = 0.003$; R > Y: Mann-Whitney $U = 3474, P = 0.005$), whereas blue and red males did not differ (Mann-Whitney $U = 1035, P = 0.87$).

Following Huyghe et al. (2007), I asked whether relative head size changed with body size differently among morphs. First, I conducted a principal components analysis with each original head size variable and not the residuals, thereby retaining variation due to body size in each PC. The first principal component (PC1) explained 68.0% of variation in (unadjusted) head size and each original head variable loaded positively onto it (eigenvalues: JL = 0.50, HW = 0.65, HD = 0.57); thus, an increase in PC1 corresponds to an increase in unadjusted head size. PC1 was regressed against SVL (Fig. 3.8). As expected, the overall model was significant (ANCOVA: $F_{5, 199} = 71.22, P < 0.001$), and there was a significant main effect of both color ($F_{2, 199} = 7.73, P < 0.001$) and SVL ($F_{1, 199}$,
199 = 201.07, \( P < 0.001 \)), but not the interaction term (Color x SVL interaction: \( F_{2, 199} = 1.3, \ P = 0.27 \)) indicating relative head size does not change differently between morphs.

B. Stamina

Endurance was measured in 51 males, representing the known range of major color variation at this population. Mean (+ SE) endurance time for all males was 96.7 ± 4.8 s (range: 26.9-186.3 s).

1. Single Morph/Condition-Dependent Model

Only a subset of males (29/51) used in the endurance experiments was measured for spectral color, and thus available for use in testing the condition-dependent model of color. To test for a relationship of color to performance, I used multiple regression of the three spectral variables for color (Table 3.7). No significant relationship was found between any color variable examined and male stamina (Fig. 3.9), jumps or reversals.

2. Two-Morph Model (B/O)

Stamina did not differ between male morphs (\(|t_{49}| = 1.66, \ P = 0.10\); Fig. 3.10, Table 3.8). Morphs also did not differ in the number of jumps (Mann-Whitney \( U = 69.5, \ P = 0.99 \)) or reversals (Mann-Whitney \( U = 306, \ P = 0.41 \)) performed during endurance trials. Neither behavior was correlated with endurance time overall (Jumps: \( r^2 = 0.02, \ F_{1, 49} = 0.80, \ P = 0.37 \); Reversals: \( r^2 = 0.00, \ F_{1, 49} = 0.01, \ P = 0.92 \)). Running direction (handedness) did
differ from an expectation of neutral ($\chi^2 = 3.10, P = 0.0015$). Lizards ran mostly towards the right side of the treadmill more often than expected by chance relative to running mostly towards the left side, or to the left and right sides of the treadmill equally. However, no difference in handedness was found between morphs ($\chi^2 = 3.55, P = 0.17$).

There was a significant difference in the median capture date of morphs (Mann-Whitney $U = 382.5, P = 0.02$); blue males were caught later in the experimental period than orange males. However, there was no effect of capture date on endurance overall ($r^2 = 0.02, F_{1,50} = 0.83, P = 0.37$). A full factorial ANCOVA of morph color and stamina with capture date as a covariate was also not significant ($F_{3, 47} = 1.78, P = 0.16$). Mean SVL differed among morphs (Mann-Whitney $U = 384.5, P = 0.02$); orange males were smaller than blue males (Table 3.8). However, there was no relationship between SVL and stamina overall ($r^2 = 0.01, F_{1, 49} = 0.55, P = 0.46$), and a full factorial ANCOVA of morph color and stamina with SVL as a covariate was also not significant ($F_{3, 47} = 0.96, P = 0.42$). There was a significant positive relationship between body condition (= mass$^{1/3}$/SVL) and stamina ($r^2 = 0.08; F_{1, 49} = 4.10, P = 0.05$). However, body condition did not differ between morphs (Mann-Whitney $U = 225, P = 0.35$). A full factorial ANCOVA with body condition as a covariate of male morph against stamina was also not significant ($F_{3, 47} = 2.18, P = 0.10$). Blue and orange morphs did not differ in total tail length (Mann-Whitney $U = 219, P = 0.29$; Table 3.9), and tail length was not correlated with endurance ($r^2 = -0.02, F_{1, 49} = 0.80, P = 0.96$). Stamina was related to tail status: males with freshly broken tails had lower performance than males with non-freshly broken tails (i.e., intact or regrown tails: Mann-Whitney $U = 242, P = 0.02$). However,
blue and orange males did not differ in their frequency of broken tails (Fisher’s Exact Test, \( P = 0.66 \)).

3. Three-Morph Model (B/Y/R)

Endurance differed among morphs (ANOVA: \( F_{2, 48} = 3.51, P = 0.038 \); Fig. 3.11, Table 3.9). Yellow males exhibited greater stamina overall than blue and red males, although no individual comparison attained statistical significance (Tukey’s HSD: Y vs. B: \( P = 0.06 \); Y vs. R: \( P = 0.11 \); B vs. R: \( P = 0.99 \)). Morphs did not differ in the number of jumps (Kruskal-Wallis \( H = 4.64, P = 0.10 \)) or reversals (Kruskal-Wallis \( H = 0.69, P = 0.71 \)) during endurance trials, and no difference in handedness was found between morphs (\( \chi^2 = 5.82, P = 0.21 \)).

Median capture date differed between morphs (Kruskal-Wallis \( H = 6.77, P = 0.03 \)); specifically, blue males were caught later than yellow males (B > Y: Mann-Whitney \( U = 294, P = 0.016 \)). In an ANCOVA of endurance with capture date as a covariate (\( F_{5, 45} = 2.73, P = 0.031 \)), only the main effect of morph color was significant (morph: \( P = 0.012 \); capture date: \( P = 0.27 \); morph x capture date: \( P = 0.27 \)). Mean SVL differed among morphs (Kruskal-Wallis \( H = 16.1, P < 0.001 \); Table 3.9). Both blue and red males were larger than yellow males (B > Y: Mann-Whitney \( U = 324, P = 0.001 \); R > Y: Mann-Whitney \( U = 211, P = 0.001 \)), whereas blue and red males did not differ (Mann-Whitney \( U = 60.5, P = 0.68 \)). A full factorial ANCOVA of morph against stamina with SVL as a covariate was not significant (\( F_{5, 45} = 1.87, P = 0.12 \)). A model without the interactive term was also not significant (\( F_{3, 47} = 2.38, P = 0.08 \)). Body condition did not differ between morphs (Kruskal-Wallis \( H = 1.06, P = 0.59 \)). A full factorial ANCOVA
with body condition as a covariate of male morph against stamina was significant overall (ANCOVA: $F_{5,45} = 2.74$, $P = 0.03$) but no main effect or interactive term was significant (morph: $P = 0.06$; body condition: $P = 0.30$; morph x body condition: $P = 0.26$).

Similarly, a model without the interactive term was significant overall (ANCOVA: $F_{3,47} = 3.58$; $P = 0.02$) but neither main effect was significant (morph: $P = 0.052$; body condition: $P = 0.07$). Morphs also did not differ in total tail length (Kruskal-Wallis $H = 1.11$, $P = 0.57$; Table 3.9), or in their frequency of broken tails ($\chi^2 = 3.71$, $P = 0.16$).

**IV. Discussion**

Color polymorphisms are widespread in animals, and in some species have been linked to alternative reproductive tactics (ARTs: Taborsky et al. 2008). Conclusively demonstrating the existence of ARTs usually requires long-term observational and experimental data on morph survival and reproduction within and across years (Roulin 2004). As a first approach, however, exploratory studies can offer insights on the extent to which ARTs are likely to be operating (e.g., Huyghe et al. 2007). Previous research (Chapter 2) on *Sceloporus minor* indicated that three discrete male color morphs—blue, yellow, and red—exist, each primarily distinguished by major differences in hue (Figs. 3.1-3.2). However, the distribution of the male color phenotypes among samples analyzed in this study might have deviated from that generated by random sampling (see Chapter 2). Although it is unlikely that sampling was so skewed as to render this model uninformative, it is nevertheless conceivable that the observed trimodal pattern in dorsal color may not accurately characterize color diversity in this population. Alternatively, variation in dorsal color might be unimodal, exhibiting a continuous range of phenotypes,
an expectation if color is largely condition-dependent. Dorsal color might also be bimodal rather than trimodal, due to a false distinction of two putative morphs (i.e., yellow and red) that actually comprise a single phenotype.

I tested three hypotheses for a relationship between dorsal coloration and ARTs. If dorsal coloration is a unimodal, condition-dependent trait rather than multimodal, I expected to find a linear relationship of male body size and performance with spectral variables. Alternatively if male dorsal color conforms to a three-morph model of blue, yellow, and red, I expected that morphs would differ significantly in body size and shape, and performance. Similarly, if a two-morph model of blue and orange males better characterizes color variation, I expected to see morph differences in these traits as a function of collapsing the yellow and red groups into an orange class.

A. Male morphs, body size and performance

1. Single-morph/condition-dependent model

I found no correlation between any dorsal color variable and male body size, condition, or performance in *S. minor* (Fig. 3.7-3.9, Table 3.1). However, there were at least two reasons to suspect that dorsal color could be a condition-dependent trait in this species. First, there is evidence that color badges in some other lizards are condition-dependent, including those of some close relatives (*S. occidentalis*: Ressel and Schall 1989; *S. pyrocephalus*: Calisi et al. 2008). Second, yellow, orange, and red colors such as those in *S. minor* can be produced by carotenoids, long-wavelength pigments of special importance in the condition-dependence of traits and honest signaling (Olson and Owens
1998). For example, in some populations of the common lizard (*Lacerta vivipara*) females occur in three morphs: orange, yellow, and mixed; morph hue is correlated with carotenoid deposition in the skin (Vercken et al 2006, Cote et al 2008).

Although these results do not support the hypothesis that dorsal color is a condition-dependent trait, additional tests are needed to conclusively rule out this possibility. For example, high performance liquid chromatography (HPLC) can determine what pigments contribute to skin color, and dietary manipulation studies can reveal whether supplementation of carotenoids affects dorsal color expression. One clue regarding the possible presence (or absence) of carotenoids in *S. minor* is afforded by inspection of dorsal reflectance spectra. Carotenoids commonly exhibit a characteristic two-peaked reflectance spectrum: a major peak from 500-700 nm corresponding to yellow, orange, and red in human vision, and a smaller peak between 320-400 nm in the ultraviolet (UV) region (e.g., Bleiweiss 2005). Analysis of reflectance spectra reveals no evidence of a secondary UV peak in *S. minor* (Chapter 2).

2. Two-Morph Model (B/O)

Males used in hypothesis testing in both two- and three-morph models were assigned to morph in one of two different ways, either from cluster analysis of spectral data or by visual inspection of photographs. I analyzed each group of males separately, and together in a combined analysis. Cluster analysis of spectral data constrained to two morphs showed a major separation between blue males ($\lambda_{\text{max}} \leq 530$ nm) and all other males. As with the condition-dependent model, it is conceivable that putative yellow and red males actually represent extremes along a continuous distribution of color in a single morph.
From a human visual perspective, color variation in this second group ($\lambda_{\text{max}} > 530$ nm) ranged from yellow to orange to dark red. Blue and orange morphs have been described in several species of phrynosomatines (Cal-production and Sinervo 2008), and so might be expected to occur in *S. minor* as well.

Overall, there was little support for a blue/orange model of color with respect to ARTs. Analyses of males scored by photographs only and all males combined did show that blue males were larger (greater SVL) than orange males (Tables 3.3-3.4, Figs. 3.3-3.4); analysis of males scored by spectral properties alone also found that blue morphs tended to be larger than orange morphs (Table 3.2). These findings are opposite to that observed in two polymorphic relatives, where orange males were larger than blue males (*U. stansburiana*: Sinervo et al. 2000a) or blue-orange males (*U. ornatus*: Thompson and Moore 1991a). Orange males also tended to have proportionately longer forelimbs than blue males (Tables 3.3-3.4), whereas blue males tended to have larger heads than orange males (Table 3.4), but these differences were not significant. Stamina also did not differ between blue and orange morphs.

3. Three-morph model (B/Y/R)

I found good support for a three-morph, blue/yellow/red model of color in males of *S. minor*. Analyses of males scored by spectral data alone and all males combined found that yellow males were smaller than blue and red males (Tables 3.2, 3.4, Figs. 3.5-3.6). A trend towards the same pattern (B > R > Y) was found in an analysis of males scored from photographs only, but these differences were not significant following correction for multiple tests (Table 3.3). Males also differed in head size, with yellow males having
portionately smaller heads than blue and red males (Table 3.4, Fig. 3.7), although a statistical difference in this trait was only found in a combined analysis of all males. These differences are in broad concordance with those found in some other polymorphic lizards. For example, yellow males are smaller than orange males (but not blue males) in *Uta stansburiana* (Sinervo et al. 2000a). In the lacertid *Podarcis melisellensis* yellow males are smaller than orange and white males, and have proportionately smaller heads (Huyghe et al. 2007). In *P. melisellensis*, orange males had larger heads on average than other morphs at sexual maturity, but because head size increased more slowly relative to other morphs, very large males among all morphs should have similar-sized heads.

Conversely, in *S. minor* head growth trajectories did not differ between morphs (Fig. 3.8) indicating that yellow males have smaller heads relative to their body size across all adult age classes.

Stamina also differed significantly among the three morphs of *S. minor*: yellow males had higher mean endurance capacity than blue or red males (Fig. 3.11), though no pairwise comparison attained statistical significance. Nevertheless, yellow males exhibited almost 30% greater stamina on average than blue and red males (Table 3.9). This pattern contrasts with that seen in *Uta stansburiana*, where orange males had high endurance, and blue and yellow males had low endurance (Sinervo et al. 2000a). One possibility is that observed differences in performance reflect temporal biases in morph sampling. Most studies measuring endurance capacity in lizards test individuals from a single population within a few days, in part to control for possible seasonal effects on performance (e.g., Sinervo et al. 2000a, Sinervo et al. 2007). Endurance in lizards is at least partly under hormonal control (Sinervo et al. 2000a, Miles et al. 2007a, Mills et al.)
2008), and strong seasonal differences in circulating testosterone have been documented in some close relatives (*S. jarrovi*: Moore 1986). Thus, differences in stamina might be an artifact of unbalanced morph sampling during a period coinciding with major changes in circulating androgens. In this study, morph sampling was uneven; blue males tended to be caught later in the experimental period than yellow males. However, there was no effect of capture date on endurance, either within individual morphs or across all males, indicating that any seasonal effects on performance were small.

Another possible explanation for the observed difference in morph performance is that the sample of yellow males was biased towards individuals that were exceptionally vigorous. Such an interpretation is not necessarily incompatible with a hypothesis for alternative morphs (e.g., Moore et al. 1998), but also might represent an artifact of biased sampling. In this study, body size (SVL) differed among morphs but was not correlated with stamina. Conversely, body condition was positively correlated with stamina, but morphs did not differ in body condition. Thus, morph-specific differences appear to be independent of male size and condition, but might reflect other morphological or physiological traits, such as muscle density or structure (Huyghe et al. 2009a), limb length (Bonine and Garland 1999), or differences in levels of circulating androgens (Sinervo et al. 2000a). In this regard, it is notable that morphs did not differ in measures of limb length or limb ratio (Table 3.6). Theoretical and experimental evidence indicate that stamina and maximum sprint speed trade off (Vanhooydonck et al. 2001), a phenomenon conspicuously evident in the differing body profiles of elite human sprinters and marathoners (Weyand and Davis 2005). Limb length has been shown to predict sprint speed in phrynosomatid lizards (Bonine and Garland 1999), and sprint speed and stamina
were negatively correlated in a cross-species study of lacertids (Vanhooydonck et al. 2001). Therefore, if stamina is linked to ARTs, we might predict that a) morphs differ in sprint speed in an opposite fashion to stamina, and b) morphs differ in limb length consistent with morph-specific differences in endurance. The first prediction remains to be tested; however, no support was found for the second prediction in this study.

**B. Color polymorphism and alternatives to ARTs**

Although the observed dorsal color patterns (Figs. 3.1-3.2) and correlated differences in body size and performance are consistent with the existence of ARTs in *S. minor*, other mechanisms may be involved. One possibility is apostatic selection, which arises when predators develop a search image for polymorphic prey; since the most common morph receives disproportionate predation, selection is relaxed against rare morphs (Allen 1988, Glanville and Allen 1997; but see Franks and Oxford 2009). If prey color contributes to the search image, stronger selection should be exerted on color traits exposed to predators, relative to those that are hidden (Huyghe et al. 2007). *S. minor* is unusual among congeners in expressing conspicuous colors on the dorsum; these features are usually restricted to the throat or abdomen in this genus (Wiens 1999). Elsewhere in its range male dorsal color is less strongly sexually dimorphic and less conspicuous to human observers (Wiens et al. 1999, Chapters 1-2). If human-perceived conspicuousness indicates the strength of apostatic selection acting on dorsal color, then populations near La Manzana might be expected to be under only weak apostatic selection. The only confirmed predator of adult *S. minor* in the La Manzana area is a small rattlesnake (*Crotalus aquilus*), a locally abundant viper commonly encountered during the day in
habitats frequented by several species of small lizards (B. Stephenson, unpubl. data). Given that crotaline vipers supplement visual cues with access to infrared channels (Haverly and Kardong 1996), and often exhibit crepuscular or nocturnal activity, at least on a seasonal basis (Campbell and Lamar 2004), this particular predator class might be expected to exert only weak selection on color. However, hypotheses for the relative conspicuousness of phenotypes should be tested directly (Leal and Fleishman 2004), especially given that the visual systems of predators (and prey) are expected to differ substantially from our own (Bennett et al. 1994). One approach is to place models of variously colored prey out in habitats used by the polymorphic species; the frequency of damage or removal of models can be used as an index of attacks on morphs in the wild (e.g., Stuart-Fox et al. 2003). Other methods include determining the visual sensitivity of individual predator species, then modeling prey discrimination based on predator visual properties, prey color and the lighting environment (Endler 1990).

**Summary and Future Directions**

I tested whether male color morphs exhibited differences in body size, condition and performance consistent with alternative reproductive tactics. I found no support for a condition-dependent model of dorsal color, and only weak support for a two-morph model. However, I found good support for a three-morph model consistent with that predicted by spectral analysis (Chapter 2). Blue and red males were larger than yellow males, and had proportionately larger heads. Yellow males also had greater performance than blue and red males. An important question, therefore, is why? One possibility is that yellow males represent a sneaker phenotype. Sneaking tactics have been identified in
Figure 3.1 Representatives of each of the three putative male morphs of *Sceloporus minor* at La Manzana.

Blue  Yellow  Red
Figure 3.2 Frequency distribution of hue (λ_{max}) for sample of 119 males of *S. minor* collected near La Manzana from 2006-2008. Male morph classification reflects assignment by cluster analysis model with hue, chroma and brightness as input variables.
**Figure 3.3** Differences in body size (SVL) among putative blue/orange color morphs of male *S. minor* at La Manzana. Data set includes only males assigned by visual inspection of photographs (*N* = 87).

Mann-Whitney *U* = 793.5, *P* = 0.004
Figure 3.4 Differences in body size (SVL) among putative blue/orange color morphs of male *S. minor* at La Manzana. Data set includes all males assigned by cluster analysis (*N* = 118) and visual inspection of photographs (*N* = 87).

Mann-Whitney *U* = 4848.5, *P* < 0.001
Figure 3.5 Differences in body size (SVL) among putative blue/yellow/red color morphs of male *S. minor* at La Manzana. Data set includes only males assigned by cluster analysis (*N* = 118).

Kruskal-Wallis $H = 18.98, P < 0.001$
Figure 3.6 Differences in body size (SVL) among putative blue/yellow/red color morphs of male *S. minor* at La Manzana. Data set includes all males assigned by cluster analysis (*N* = 118) and visual inspection of photographs (*N* = 87).

Kruskal-Wallis *H* = 24.63, *P* < 0.001
Figure 3.7 Differences in relative head size between blue/yellow/red color morphs of male *S. minor* at La Manzana. Data set includes all males assigned by cluster analysis (*N* = 118) and visual inspection of photographs (*N* = 87).

Kruskal-Wallis $H = 13.15$, $P = 0.001$
Figure 3.8 Relationship of head size to body size between blue/yellow/red morphs of male *S. minor*. Circles = Blue (B), Triangles = Yellow (Y), Squares = Red (R). Data set includes all males assigned by cluster analysis (*N* = 118) and visual inspection of photographs (*N* = 87).

![Graph showing relationship between head size (PC1) and body size (SVL) for different morphs of male *S. minor*. The graph includes data points for blue (B), yellow (Y), and red (R) morphs. The x-axis represents SVL (mm), ranging from 60 to 90, and the y-axis represents PC1 (Head Size), ranging from -6 to 4. ]
Figure 3.9 Male stamina plotted against dorsal color. A: Hue ($\lambda_{\text{max}}$). B: Red chroma. C: Brightness.
Figure 3.10 Differences in endurance capacity (stamina) between blue/orange color morphs of male *S. minor* at La Manzana. Stamina recorded as latency to exhaustion on treadmill rotating at 0.5 km/h.

$$|t_{49}| = 1.66; P = 0.10$$
Figure 3.11 Differences in endurance capacity (stamina) between blue/yellow/red color morphs of male *S. minor* at La Manzana. Stamina recorded as latency to exhaustion on treadmill rotating at 0.5 km/h.

\[ F_{2,48} = 3.51, P = 0.038 \]
Table 3.1 Multivariate regressions of dorsal color variables and morphological traits of male *S. minor* at La Manzana.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Overall Model</th>
<th>Color Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r^2$</td>
<td>$F$</td>
</tr>
<tr>
<td>SVL</td>
<td>0.01</td>
<td>0.21</td>
</tr>
<tr>
<td>Body Condition</td>
<td>0.02</td>
<td>0.90</td>
</tr>
<tr>
<td>Head Size</td>
<td>0.01</td>
<td>0.43</td>
</tr>
<tr>
<td>Intact Tail Length</td>
<td>0.05</td>
<td>2.16</td>
</tr>
<tr>
<td>Total Tail Length</td>
<td>0.02</td>
<td>0.91</td>
</tr>
<tr>
<td>Residuals Forelimb Length</td>
<td>0.14</td>
<td>0.95</td>
</tr>
<tr>
<td>Residuals Hindlimb Length</td>
<td>0.02</td>
<td>0.13</td>
</tr>
<tr>
<td>Ratio FL/HL</td>
<td>0.24</td>
<td>1.87</td>
</tr>
</tbody>
</table>
Table 3.2 Mann-Whitney $U$ tests and Kruskal-Wallis $H$ tests of differences in morphological traits among putative blue/orange and blue/yellow/red male morphs. Morph assignment determined from cluster analysis of spectral variables ($N = 118$).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Two-Morph (B/O)</th>
<th>Three-Morph (B/Y/R)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$U$</td>
<td>df</td>
</tr>
<tr>
<td>SVL</td>
<td>1713.5</td>
<td>1</td>
</tr>
<tr>
<td>Body Condition</td>
<td>1335</td>
<td>1</td>
</tr>
<tr>
<td>Head Shape</td>
<td>1423</td>
<td>1</td>
</tr>
<tr>
<td>Intact Tail Length</td>
<td>1180</td>
<td>1</td>
</tr>
<tr>
<td>Total Tail Length</td>
<td>1265</td>
<td>1</td>
</tr>
<tr>
<td>Resid. Forelimb Length†</td>
<td>32</td>
<td>1</td>
</tr>
<tr>
<td>Resid. Hindlimb Length†</td>
<td>27</td>
<td>1</td>
</tr>
<tr>
<td>Ratio FL/HL†</td>
<td>35</td>
<td>1</td>
</tr>
</tbody>
</table>

B (29), O (89) B (29), Y (58), R (31)
†B (4), O (18) †B (4), Y (15), R (3)

* indicates significant at adjusted $\alpha = 0.05/8 = 0.0062$
Table 3.3 Mann-Whitney $U$ tests and Kruskal-Wallis $H$ tests of differences in morphological traits between putative blue/orange and blue/yellow/red male morphs of *S. minor* at La Manzana. Morph assignment determined from visual inspection of photographs ($N = 87$ males).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Two Morphs (B/O)</th>
<th>Three Morphs (B/Y/R)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$U$</td>
<td>df</td>
</tr>
<tr>
<td>SVL</td>
<td>793.5</td>
<td>1</td>
</tr>
<tr>
<td>Body Condition</td>
<td>588.5</td>
<td>1</td>
</tr>
<tr>
<td>Head Shape</td>
<td>698</td>
<td>1</td>
</tr>
<tr>
<td>Intact Tail Length</td>
<td>488</td>
<td>1</td>
</tr>
<tr>
<td>Total Tail Length</td>
<td>533.5</td>
<td>1</td>
</tr>
<tr>
<td>Resid. Forelimb Length</td>
<td>69</td>
<td>1</td>
</tr>
<tr>
<td>Resid. Hindlimb Length</td>
<td>117</td>
<td>1</td>
</tr>
<tr>
<td>Ratio FL/HL†</td>
<td>126.5</td>
<td>1</td>
</tr>
</tbody>
</table>

B (15), O (72) B (15), Y (55), R (17)

†B (9), O (36) B (9), Y (27), R (9)

* indicates significant at adjusted $\alpha = 0.05/8 = 0.0062$
Table 3.4 Mann-Whitney $U$ tests and Kruskal-Wallis $H$ tests of differences in morphological traits between putative male morphs. Data set includes all males assigned by cluster analysis ($N = 118$) and visual inspection of photographs ($N = 87$).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Two Morphs (B/O)</th>
<th>Three Morphs (B/Y/R)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$U$</td>
<td>df</td>
</tr>
<tr>
<td>SVL</td>
<td>4848.5</td>
<td>1</td>
</tr>
<tr>
<td>Body Condition</td>
<td>3851.5</td>
<td>1</td>
</tr>
<tr>
<td>Head Size</td>
<td>4291</td>
<td>1</td>
</tr>
<tr>
<td>Intact Tail Length</td>
<td>3175</td>
<td>1</td>
</tr>
<tr>
<td>Total Tail Length</td>
<td>3445</td>
<td>1</td>
</tr>
<tr>
<td>Resid. Forelimb Length†</td>
<td>208</td>
<td>1</td>
</tr>
<tr>
<td>Resid. Hindlimb Length†</td>
<td>269</td>
<td>1</td>
</tr>
<tr>
<td>Ratio FL/HL†</td>
<td>315.5</td>
<td>1</td>
</tr>
</tbody>
</table>

B (44), O (161) B (44), Y (113), R (48)
†B (13), O (54) †B (13), Y (42), R (12)

* indicates significant at adjusted $\alpha = 0.05/8 = 0.0062$
Table 3.5 Descriptive statistics for male morphometric traits of putative blue and orange morphs from La Manzana. Data set includes all males assigned by cluster analysis ($N = 118$) and visual inspection of photographs ($N = 87$).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Blue</th>
<th>Orange</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{x}$</td>
<td>SE</td>
</tr>
<tr>
<td>SVL</td>
<td>75.98</td>
<td>0.44</td>
</tr>
<tr>
<td>Mass</td>
<td>15.53</td>
<td>0.32</td>
</tr>
<tr>
<td>Jaw Length (mm)</td>
<td>9.96</td>
<td>0.12</td>
</tr>
<tr>
<td>Head Width (mm)</td>
<td>18.24</td>
<td>0.13</td>
</tr>
<tr>
<td>Head Depth (mm)</td>
<td>6.10</td>
<td>0.07</td>
</tr>
<tr>
<td>Intact Tail Length (mm)</td>
<td>70.37</td>
<td>6.12</td>
</tr>
<tr>
<td>Total Tail Length (mm)</td>
<td>98.57</td>
<td>2.95</td>
</tr>
<tr>
<td>Forelimb Length (mm)</td>
<td>26.99</td>
<td>0.30</td>
</tr>
<tr>
<td>Hindlimb Length (mm)</td>
<td>36.29</td>
<td>0.48</td>
</tr>
</tbody>
</table>
Table 3.6 Descriptive statistics of morphometric traits among putative blue/yellow/red morphs of male *S. minor* from La Manzana. Data set includes all males assigned by cluster analysis (*N* = 118) and visual inspection of photographs (*N* = 87).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Blue</th>
<th></th>
<th></th>
<th>Yellow</th>
<th></th>
<th></th>
<th>Red</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
<td>SE</td>
<td>N</td>
<td>$\bar{X}$</td>
<td>SE</td>
<td>N</td>
<td>$\bar{X}$</td>
<td>SE</td>
</tr>
<tr>
<td>SVL</td>
<td>75.98</td>
<td>0.44</td>
<td>44</td>
<td>73.18</td>
<td>0.36</td>
<td>113</td>
<td>75.28</td>
<td>0.58</td>
</tr>
<tr>
<td>Mass</td>
<td>15.53</td>
<td>0.32</td>
<td>44</td>
<td>13.69</td>
<td>0.22</td>
<td>113</td>
<td>15.22</td>
<td>0.42</td>
</tr>
<tr>
<td>Jaw Length (mm)</td>
<td>9.96</td>
<td>0.12</td>
<td>44</td>
<td>9.35</td>
<td>0.06</td>
<td>113</td>
<td>9.80</td>
<td>0.10</td>
</tr>
<tr>
<td>Head Width (mm)</td>
<td>18.24</td>
<td>0.13</td>
<td>44</td>
<td>17.32</td>
<td>0.09</td>
<td>113</td>
<td>18.11</td>
<td>0.15</td>
</tr>
<tr>
<td>Head Depth (mm)</td>
<td>6.10</td>
<td>0.07</td>
<td>44</td>
<td>5.83</td>
<td>0.04</td>
<td>113</td>
<td>6.06</td>
<td>0.08</td>
</tr>
<tr>
<td>Intact Tail Length (mm)</td>
<td>70.37</td>
<td>6.12</td>
<td>44</td>
<td>79.22</td>
<td>3.34</td>
<td>113</td>
<td>76.35</td>
<td>5.09</td>
</tr>
<tr>
<td>Total Tail Length (mm)</td>
<td>98.57</td>
<td>2.95</td>
<td>44</td>
<td>98.19</td>
<td>1.85</td>
<td>113</td>
<td>96.90</td>
<td>3.68</td>
</tr>
<tr>
<td>Forelimb Length (mm)</td>
<td>26.99</td>
<td>0.30</td>
<td>13</td>
<td>26.88</td>
<td>0.27</td>
<td>42</td>
<td>28.03</td>
<td>0.55</td>
</tr>
<tr>
<td>Hindlimb Length (mm)</td>
<td>36.29</td>
<td>0.48</td>
<td>13</td>
<td>35.72</td>
<td>0.20</td>
<td>42</td>
<td>37.25</td>
<td>0.52</td>
</tr>
</tbody>
</table>
Table 3.7 Multivariate regressions of dorsal color variables and performance traits of male *S. minor* at La Manzana.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Overall Model</th>
<th>Color Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r^2$</td>
<td>$F$</td>
</tr>
<tr>
<td>Endurance</td>
<td>0.23</td>
<td>2.51</td>
</tr>
<tr>
<td>Jumps</td>
<td>0.12</td>
<td>1.14</td>
</tr>
<tr>
<td>Reversals</td>
<td>0.16</td>
<td>1.58</td>
</tr>
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</table>
Table 3.8 Descriptive statistics for putative blue/orange color morphs used in performance trials in 2008.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Blue (N = 15)</th>
<th>Orange (N = 36)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
<td>SE</td>
</tr>
<tr>
<td>SVL (mm)</td>
<td>75.6</td>
<td>0.7</td>
</tr>
<tr>
<td>Tail Length (mm)</td>
<td>93.5</td>
<td>5.8</td>
</tr>
<tr>
<td>Endurance (sec)</td>
<td>84.5</td>
<td>7.1</td>
</tr>
<tr>
<td>Jumps</td>
<td>1.4</td>
<td>0.4</td>
</tr>
<tr>
<td>Reversals</td>
<td>0.8</td>
<td>0.2</td>
</tr>
</tbody>
</table>
Table 3.9 Descriptive statistics for putative blue/yellow/red color morphs used in performance trials in 2008.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Blue ($N = 15$)</th>
<th>Yellow ($N = 27$)</th>
<th>Red ($N = 9$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
<td>SE</td>
<td>range</td>
</tr>
<tr>
<td>SVL (mm)</td>
<td>75.6</td>
<td>0.7</td>
<td>70.2 – 79.3</td>
</tr>
<tr>
<td>Tail Length (mm)</td>
<td>93.5</td>
<td>5.8</td>
<td>36.0 – 126.6</td>
</tr>
<tr>
<td>Endurance (sec)</td>
<td>84.5</td>
<td>7.1</td>
<td>26.9 – 119.5</td>
</tr>
<tr>
<td>Jumps</td>
<td>1.4</td>
<td>0.4</td>
<td>0 – 6</td>
</tr>
<tr>
<td>Reversals</td>
<td>0.8</td>
<td>0.2</td>
<td>0 – 2</td>
</tr>
</tbody>
</table>
CHAPTER 4
Territorial Behavior and Demographics in the Polymorphic Lizard *Sceloporus minor*

I. Background
Territoriality is often linked to alternative reproductive tactics (ARTs: Taborsky et al. 2008). The high mating skew associated with resource-defense or female-defense polygyny is thought to favor the evolution of ARTs, and models suggest that the greater the concentration defended by males, the easier it is for an alternative tactic such as a ‘sneaker’ to invade (Shuster and Wade 2003). Territoriality is common in lizards, and is often accompanied by high mating skew (Stamps 1983). Thus, the potential for territorial, polygynous lizards to evolve ARTs would seem to be high. In support, a number of studies have documented ARTs in territorial lizards (see review in Calsbeek and Sinervo 2008). One of the best-studied examples is that of the side-blotched lizard (*Uta stansburiana*). In this species, males express one of three throat colors, each linked to a distinct tactic. Males with orange throats defend large territories that encompass the home ranges of many females (Sinervo and Lively 1996). Blue males defend smaller territories that contain fewer females; unrelated males commonly form dyads, and blue male pairs cooperatively defend the separate territories of each individual blue male (Sinervo and Clobert 2003). Yellow males are non-territorial and exhibit a sneaking strategy defined by mimicking female morphology and behavior (Sinervo and Lively 1996). Orange males usurp the territories of neighboring blue males, and obtain high fitness at the expense of blue males. However, blue males vigorously defend their territories from sneaking yellow males. Sneaking yellow males are able to exploit mating opportunities made available by
the larger territories of orange males that contain many females. Thus, each morph successfully defeats one morph but is in turn defeated by another morph. Morph expression is heritable and fixed in most males (Sinervo et al. 2001). However, at least some yellow males (by heterozygotes for the OBY locus) can switch to a blue throat phenotype later in the reproductive season when orange males become less common and local territories become available (Sinervo et al. 2000a). Overall, a substantial body of work indicates that color polymorphisms are often linked to ARTs in lizards (see Chapter 1), and that the fitness consequences of male tactics are likely to be related to the ability of males to locate and defend access to multiple females.

**Study Species**

The phrynosomatid lizard *Sceloporus minor* is a colorful reptile of rock outcroppings and boulders in the southern Chihuahuan Desert of central Mexico (Chrapliwy 1964; see Chapter 1). Like most congeners, male *S. minor* express sexually dimorphic throat and abdominal colors that are revealed to conspecifics in social interactions (B. Stephenson, pers. obs.). However, males also express sexually dimorphic dorsal color, and exhibit extensive variation in this trait within and among populations (Wiens et al. 1999). Previous work showed that male *S. minor* near the community of La Manzana in NW Hidalgo express an extreme form of dorsal dichromatism that may be linked to ARTs (Chapters 2-3). At La Manzana, males occur in one of three fixed color morphs (blue, yellow, and red). Blue males express a uniform blue dorsum, whereas both yellow and red males express paired dorsal patches usually separated by a blue midline stripe (Chapter 3: Fig. 3.1). Blue and red males are larger than yellow males, and have
proportionately larger heads. However, yellow males have higher endurance than blue and red males. Thus, yellow males are both morphologically and physiologically distinct relative to blue and red males, consistent with the hypothesis of alternative tactics. However, a defining property of ARTs is the expression of unique behavioral phenotypes linked to each morph (Taborsky et al. 2008). In other polymorphic lizards, male morphs commonly differ from each other in aspects of space use and movement (Sinervo and Lively 1996, Moore et al. 1998), access to females and proximity to other males (Sinervo and Clobert 2003), relative aggressive behavior (Thompson and Moore 1991a, 1992) and survival or persistence within and among years (Sinervo et al. 2007). Thus, I tested whether differences in home range, access to females, persistence, and display behavior of marked males on plots across years were consistent with the existence of ARTs in this species. I also present data on female movement and behavior for comparison with males. In addition, many species exhibit alternative tactics involving mimicry of female morphology and behavior (Gross 1991, Shuster and Wade 1991, Sinervo and Lively 1996); thus, evidence of similar behavior patterns between females and some males might indicate the adoption of female-like behavior among certain morphs.

II. Methods

Size Classes

Males were considered adults if SVL was greater than 60 mm (see Chapter 2); adult females were greater than 57 mm SVL. In the absence of data on gonadal development, determining the lower size limit for sexual maturity can be difficult in lizards. This problem is made more challenging when obvious morphological or behavioral cues to
reproductive maturity are lacking. Neonates of both sexes of *S. minor* express a phenotype distinct from adult males and most adult females: they have bright yellow heads and a light grey dorsum with black spots. However, many adult females retain this phenotype into adulthood and so distinguishing small adults from subadults with certainty may be impossible. In other populations of *S. minor*, gonadal inspection indicates that females may become sexually mature in individuals as small as 50 mm SVL (Ramírez-Bautista, unpubl. data). Although I cannot rule out the possibility that some females less than 57 mm SVL were also sexually mature, capture data from the breeding season (September-November) indicates that most females at or around this size are at least 1.5 yr old, and thus likely to be sexually mature. It should be noted that putative female adults at La Manzana are 15% smaller on average than adult males, and attain smaller maximum size (B. Stephenson, unpubl. data).

**Marking**

Lizards were captured by noose, and transferred by canvas bag to a local field house for measurements and surgical procedures. All lizards > 45 mm SVL were marked with a sequence of colored beads following the protocols of Fisher and Muth (1989). A small drop of non-toxic Krazy Glue was applied to help bind beads to the skin and minimize snagging (Zucker 1989). Sutures with beads were naturally removed over time but usually remained in place for 6-12 months. Beginning in 2006, all captured lizards regardless of size were also toe-clipped and tissues preserved in 95% ethanol (Simmons 2002). Since clipping of multiple toes may reduce clinging ability in climbing lizards (Bloch and Irschick 2004), I excised only the terminal phalange on each clipped toe, and
only clipped one toe per hand. Prior to all surgical procedures, lizards were anesthetized with a small dose (0.01-0.1 cc) of 2% lidocaine injected subcutaneously to the lower left dorsum (Klukowski and Nelson 2001). Lizards were allowed to rest for several hours before release following restoration of normal locomotory behavior.

**Study Plots**

I measured home range and movement patterns of adult males and females of *S. minor*. Plots were visited at different times in different years (Table 4.1), but were surveyed regularly in September and October during each of three years: 2005, 2006 and 2008. Hence, estimates of lizard densities during these time periods should be most directly comparable across years. This period is also biologically relevant as *S. minor* exhibits fall breeding (Ramírez-Bautista et al. 2008, B. Stephenson, unpubl. data.). Three 50 x 50 m plots (Plots A, B and C) laid out in 5 m transects were constructed in 2005; two more plots (D and E) were added in 2008 (Chapter 1: Fig. 1.7). Each year, attempts were made to collect all lizards of 45 mm SVL or larger found inside the boundaries of marked plots. In 2008 only, adults found up to 20 m outside of marked plots were also captured but were excluded from analyses unless observed at least once within the plot boundaries. Lizards were marked as described above and released at their site of capture, usually within 72 h.
**Home Range Estimates**

In 2005, 2006 and 2008, home range was estimated for all adults found on study plots. Starting from a randomly determined corner, an observer would walk through the plot searching for marked animals. Location of lizards was recorded by estimating position within an 11 x 11 grid marked out in 5 m increments. Data were then transcribed into the computer program Tracker (v. 1.1: Camponotus AB). This required measuring the distance of each plotted point within its respective 5-m² square on a field data sheet to each of two corners of the same square using dial calipers, then multiplying by a conversion factor for entry into a format suitable for Tracker. Modern DNA-based techniques have been used successfully to estimate reproductive success in lizards (e.g., Abell 1997, Zamudio and Sinervo 2000, Haenel et al. 2003b, Olsson et al. 2009). I used a common alternative index of male fitness in territorial lizards by estimating the extent of male-female home range overlap. A male observed to overlap with a particular female is assumed to be more likely to sire her offspring than a male that has not been observed to overlap with the same female. Studies that have incorporated both approaches have generally found good correspondence in estimates of male paternity from field observations and those verified using DNA analysis (Abell 1997, Haenel et al. 2003a, b).

**Focal Observations**

In 2005 and 2006, home range estimates were supplemented by detailed observations of male and female social behavior. Following the discovery of a marked lizard (a ‘sighting’), a single observer conducted a focal observation of each lizard for 20 min. Observers scored focal lizards for major behavior patterns (see below) and noted any
unusual activity. For all years, plots were visited up to twice daily for up to 4 h during each of two sampling periods, morning-midday (approx. 1000 - 1400 h) and afternoon-early evening (1430 - 1830 h). During a focal observation, lizard position was recorded twice, once at the start of a single sampling period and again at the end (Stone and Baird 2002). In 2008, only lizard position was recorded during observations, and so only a single position was plotted per sighting. Inclement weather (rain, fog) is common at all times of the day in the summer and fall at La Manzana, seemingly imposing a severe constraint on territorial and mating activity in this species (B. Stephenson, pers. obs.). However, weather can change quickly in the area, and so observations were often conducted during otherwise poor conditions in the event that weather improved suddenly. Many animals were located in crevices during searches, and observations of animals in crevices confirmed that little overt activity took place during these times. Thus, estimates of display rate were derived only from those observations where lizards appeared outside their refuge at least once during the 20 min focal period. However, sightings of lizards in crevices were retained for the home range analyses as lizards were commonly found to have moved to adjacent boulders between sightings.

**Displays**

Within each focal observation, I recorded the number of various social displays performed by the focal lizard. Displays performed by adjacent but non-focal lizards were not scored. Spiny lizards are characterized by the expression of stereotyped displays, and most major behavior patterns were recognizable from existing descriptions in the literature (e.g., Carpenter 1978). Although elements of displays (especially head
movements) vary across species, I found that the definitions of Ruby (1976) for *S. jarrovii* were appropriate, with slight modifications. *Headbobs* are rapid vertical movements of the head (but see below), often performed while walking. *Pushups* are vertical elevations of the anterior half of the body, usually (but not always) due to the extension of the forearms in the vertical plane. These are slower, more exaggerated displays than headbobs, and cannot be performed while walking. *Shudderbobs* are very rapid headbobs, defined as three or more up-and-down movements within 1 s. *Fullshows* are lateral compressions accompanied by a vertical extension of the throat. These expose the abdominal patches as well as the colorful throat fan. Other displays were seen in very low frequency and not entered in analysis.

Finally, it should be noted that the definition for Headbob in this study is not identical to that described for the population of *S. minor* in Escalerillas (Chapter 5). Males at both La Manzana and Escalerillas express rapid up-and-down movements of the head (headbobs) typically followed by a pause of 0.5 s or more. A single continuous movement of the head usually involves either one or two up-and-down movements. During research described in the present chapter, each of these separate (i.e., one or two) movements was scored as a separate headbob. However, later examination of video of displaying males at both sites indicated that the combination of continuous movements was a better descriptor of an individual headbob behavior pattern, and is probably closer to the definition of this behavior described by Ruby (1976) for *S. jarrovii*. Although my definitions of ‘Headbob’ are not identical for research described in Chapters 4 and 5, the same criteria were used to score the behavior pattern ‘Headbob’ for all males throughout each study. Thus, comparisons among males within each study should still be
meaningful. To eliminate confusion, it is recommended that the definition for ‘Headbob’ described in Chapter 5 be used for future studies of this display behavior in *S. minor*, unless population-specific differences suggest otherwise.

**Morph Assignment**

Assignment to male morph was conducted as described in Chapter 3. For males measured for spectral reflectance, cluster analysis was used to determine morph (blue, yellow, or red). For the subset of individuals collected when a spectrometer was unavailable, photographs were visually inspected and compared to those of males of known reflectance to assign color.

**Statistics**

Unless noted, most analyses were restricted to the months of September and October, a period coinciding with the onset and peak of the breeding season in other populations of this species (Ramírez-Bautista et al. 2008). I used nonparametric Mann-Whitney *U* tests and Kruskal-Wallis *H* tests to compare differences between sexes and male morphs. I also used ANOVA and ANCOVA to examine interactive effects between multiple factors on dependent variables. For all tests, the threshold to reject the null hypothesis was $\alpha = 0.05$ two-tailed, with Bonferroni correction for multiple tests (Rice 1989). Means are reported $\pm$ SE.
III. Results

A. Demographics

Males and Females

The number of adult males seen in each of the three main study plots (Plots A, B and C) during September and October was not significantly different (Kruskal-Wallis $H = 5.0$, $P = 0.08$). The number of females also did not differ across study plots (Kruskal-Wallis $H = 0.6$, $P = 0.73$). Thus, the number of males and females per plot during this period was stable across years (males: $\bar{X} = 4.2 \pm 0.4$ males/plot; females: $\bar{X} = 4.8 \pm 0.4$ females/plot). A full-factorial two-way ANOVA of mean lizard density with Sex and Year as factors was nonsignificant ($F_{5,12} = 1.5$, $P = 0.25$), indicating the absence of a year effect on the number of lizards per plot. There was no difference between the sexes in the absolute number of lizards found during September and October in 2005 (Mann-Whitney $U = 3.5$, $P = 0.66$), 2006 (Mann-Whitney $U = 7.5$, $P = 0.18$) or 2008 (Mann-Whitney $U = 7$, $P = 0.27$), or across all years combined (Mann-Whitney $U = 49$, $P = 0.45$; Fig. 4.1).

Male Morphs

Male morphs were not represented equally on study plots (Fig. 4.2). Yellow males were more common than blue or red males during September and October (B: $0.9 \pm 0.3$ males/plot; Y: $2.7 \pm 0.3$ males/plot; R: $0.6 \pm 0.2$ males/plot; Fig. 4.2A). A full-factorial two-way ANOVA of Morph and Year was significant ($F_{8,18} = 4.3$, $P = 0.005$); there was a significant main effect of Morph ($P = 0.002$) but not Year ($P = 0.19$) or the interaction
term (Morph x Year: \(P = 0.75\)). A reduced model without the interaction term did not change the outcome \((F_{8,18} = 8.8, P < 0.001; \text{Morph: } P < 0.001; \text{Year: } P = 0.16)\).

B. Morph Persistence/Survival

*Males and Females*

Interannual persistence was examined for males and females observed within each calendar year. A total of 42 adult males and 47 adult females were caught and released at least once from 2005-7. In 2005, 8/22 males (36.3\%) and 9/21 females (42.9\%) were found again in 2006. Of lizards marked in 2006, only 6/21 males (28.6\%) and 5/25 females (20.0\%) were seen in 2007. In 2007, 6/13 males (46.1\%) and 3/11 females (27.2\%) were found in 2008. Thus, most adults do not persist on plots for more than a year. Only 2/22 (9.1\%) adult males and 1/21 (4.8\%) adult females marked in 2005 were found again each year from 2006-2008. No lizard was seen two calendar years after release after not being seen the first year following release, indicating that adults rarely (if ever) moved off study plots only to return more than a few months later. There was no significant difference in interannual persistence between males and females captured in any single calendar year (2005: Mann-Whitney \(U = 239, P = 0.82\); 2006: Mann-Whitney \(U = 235.5, P = 0.42\); 2008: Mann-Whitney \(U = 58 P = 0.35\); Fig. 4.3) or across all years combined (Mann-Whitney \(U = 930.5, P = 0.72\)).
Male Morphs

No difference was found among morphs in interannual persistence among males captured in 2005 (Kruskal-Wallis $H = 2.0, P = 0.36$; Fig. 4.4A) or 2007 (Kruskal-Wallis $H = 0.1, P = 0.94$; Fig. 4.4C). Among males captured in 2006—including surviving males from 2005—there was a difference (Kruskal-Wallis $H = 8.3, P = 0.016$; Fig. 4.4B); blue males had higher interannual persistence from that year forward than yellow males (Mann-Whitney $U = 55, P = 0.005$) but not red males (Mann-Whitney $U = 12, P = 0.16$). Red males did not differ in persistence from yellow males (Mann-Whitney $U = 24, P = 0.29$). Males did differ in persistence across all years (Kruskal-Wallis $H = 6.2, P = 0.044$). Specifically, yellow males tended to exhibit lower persistence than other males, though no difference attained statistical significance following Bonferroni correction (B > Y: Mann-Whitney $U = 135.5, P = 0.024$; R > Y: Mann-Whitney $U = 142, P = 0.08$). Blue and red males did not differ (Mann-Whitney $U = 34.5, P = 0.42$).

C. Home Range

As a minimum of three observations is necessary to establish a home range, lizards sighted only once or twice were necessarily excluded from home range analyses. Estimates of home range area are expected to increase with the number of sightings per animal (Rose 1982, Stone and Baird 2002); thus, to increase the number of sightings I performed most home range analyses for a given year with all observations. However, I also tested for differences in home range size using the subset of observations available from September and October for comparison.
Males and Females

Males had larger home ranges than females (2005: Mann-Whitney $U = 107, P = 0.09$; 2006: Mann-Whitney $U = 67, P = 0.008$; 2008: Mann-Whitney $U = 22, P = 0.020$; Fig. 4.5A, Table 4.3). However, the number of sightings per lizard varied substantially within and among years (Table 4.3) and was usually related to home range area, for both males (2005: $r^2 = 0.19, P = 0.055$; 2006: $r^2 = 0.49, P = 0.002$; 2008: $r^2 = 0.73, P = 0.006$), and females (2005: $r^2 = 0.02, P = 0.63$; 2006: $r^2 = 0.50, P = 0.001$; 2008: $r^2 = 0.29, P = 0.047$). Thus, I used ANCOVA to control for the effect of the number of sightings on estimated home range in males and females in 2005, 2006 and 2008. There was a marginally nonsignificant difference in home range size between sexes in 2005 (overall model: $F_{3,32} = 3.9, P = 0.017$; sex: $P = 0.059$; sightings: $P = 0.12$; sex x sightings: $P = 0.23$; reduced model: $F_{2,33} = 5.1, P = 0.001$; sex: $P = 0.074$; sightings: $P = 0.030$), but there was a significant difference in 2006 (overall model: $F_{3,30} = 14.5, P < 0.001$; sex: $P = 0.036$; sightings: $P = 0.005$; sex x sightings: $P = 0.34$; reduced model: $F_{2,31} = 21.4, P < 0.001$; sex: $P = 0.050$; sightings: $P < 0.001$), and 2008 (overall model: $F_{3,18} = 28.7, P < 0.001$; sex: $P < 0.001$; sightings: $P < 0.001$; sex x sightings: $P = 0.002$). There was no significant effect of body size on male or female home range across all three years (Males: 2005: $r^2 = 0.00, P = 0.94$; 2006: $r^2 = 0.00, P = 0.86$; 2008: $r^2 = 0.00, P = 0.73$; Females: 2005: $r^2 = 0.01, P = 0.71$; 2006: $r^2 = 0.10, P = 0.22$; 2008: $r^2 = 0.01, P = 0.77$). I also tested whether home range size during September and October differed; although fewer subjects were available for analysis (Table 4.3), there was a significant difference in home range size between males and females for all three years (Mann-Whitney $U =$...
Male home range size did not predict overlap by rivals. No significant correlation between home range area and the number of rival males found in a male’s home range was seen in 2005 ($r^2 = 0.17, P = 0.071$), 2006 ($r^2 = 0.08, P = 0.27$), or 2008 ($r^2 = 0.00, P = 0.92$). Male home range size did predict female overlap in some years, however. A significant positive relationship between a male’s home range and the number of females observed within it was found in 2006 ($r^2 = 0.45, P = 0.003$), but not in 2005 ($r^2 = 0.09, P = 0.20$). No significant difference was found in 2008 ($r^2 = 0.36, P = 0.11$); however, sample size for this year was small ($N = 8$). Thus, I ran an additional analysis including males from the two additional plots constructed in 2008 (Plots D and E), and a significant positive relationship was found ($r^2 = 0.38, P = 0.011$). Addition of these extra males to the data set did not change the interpretation from the analysis of male intruders in 2008 ($r^2 = 0.01, P = 0.92$).

**Male Morphs**

Home range data were available for only two red males in 2006, and for only one blue male and one red male in 2008. I therefore excluded 2008 data from statistical analyses, and only compared blue and yellow males in 2006. Blue, yellow and red morphs did not differ in home range size in 2005 (Kruskal-Wallis $H = 1.5, P = 0.47$; Table 4.4, Fig. 4.6A), and there was no difference between blue and yellow males in 2006 (Mann-Whitney $U = 35.5, P = 0.08$; Table 4.4, Fig. 4.6A). Therefore, I also used ANCOVA to test for differences in home range area with the number of sightings as a covariate.
However, controlling for the number of sightings did not change the outcome. There was no significant overall effect for 2005 (overall model: $F_{5,14} = 1.3$, $P = 0.30$; reduced model: $F_{3,16} = 1.6$, $P = 0.22$). In 2006, there was a significant overall effect ($F_{3,11} = 5.6$, $P = 0.014$). However, this was evidently a function of the number of sightings ($P = 0.02$), as there was no significant main effect of color ($P = 0.19$) or the interaction term (Morph x Sightings: $P = 0.30$). A reduced model without the interaction term confirmed this interpretation (Overall model: $F_{2,12} = 7.6$, $P = 0.007$; Morph: $P = 0.42$; Sightings: $P = 0.02$). I also tested whether home range size in September and October differed between morphs. There were no significant differences in home range size between morphs across years during this period (2005: Kruskal-Wallis $H = 0.2$, $P = 0.90$; 2006: Mann-Whitney $U = 12$, $P = 0.62$; Fig. 4.6B) though sample sizes were low (Table 4.6).

D. Display Behavior

Males and Females

Males tended to be seen more frequently outside of their refuges than females during September and October of 2005 (Mann-Whitney $U = 82.5$, $P = 0.031$) and 2006 (Mann-Whitney $U = 34$, $P = 0.049$; Table 4.5), however neither difference was significant following Bonferroni correction. As expected, males exhibited higher rates of most displays than females in both 2005 (Headbobs: Mann-Whitney $U = 42$, $P < 0.001$; Pushups: Mann-Whitney $U = 31.5$, $P < 0.001$; Shudderbobs: Mann-Whitney $U = 64$, $P < 0.001$; Full Shows: Mann-Whitney $U = 136$, $P = 0.35$; Table 4.5) and 2006 (Headbobs: Mann-Whitney $U = 5$, $P < 0.001$; Pushups: Mann-Whitney $U = 13$, $P = 0.001$;
Shudderbobs: Mann-Whitney $U = 30, P = 0.008$; Full Shows: Mann-Whitney $U = 50, P = 0.11$; Table 4.5).

**Male Morphs**

Because only one red male was encountered during September-October of 2006 it was excluded from analysis. Blue, yellow and red morphs did not differ in the number of sightings during September and October of 2005 (Kruskal-Wallis $H = 2.3, P = 0.32$). Blue and yellow morphs did not differ in the number of sightings during the same period in 2006 (Mann-Whitney $U = 25, P = 0.12$). There was no significant difference in rates of displays among all three morphs in 2005 (Headbobs: Kruskal-Wallis $H = 1.3, P = 0.51$; Pushups: Kruskal-Wallis $H = 1.1, P = 0.57$; Shudderbobs: Kruskal-Wallis $H = 1.9, P = 0.38$; Full Shows: Kruskal-Wallis $H = 0.8, P = 0.67$; Fig. 4.7, Table 4.6) or between blue and yellow morphs in 2006 (Headbobs: Mann-Whitney $U = 28, P = 0.041$; Pushups: Mann-Whitney $U = 25, P = 0.13$; Shudderbobs: Mann-Whitney $U = 20, P = 0.47$; Full Shows: Mann-Whitney $U = 21, P = 0.26$; Table 4.6). Although a trend towards a difference in rate of Headbobs was found between blue and yellow males in 2006, this difference was not significant following Bonferroni correction.

**IV. Discussion**

Alternative reproductive tactics confer fitness on individuals of one sex by exploiting vulnerabilities in mate acquisition and defense created by the expression of other mating tactics in other individuals of the same sex (e.g., Shuster and Wade 2003). Morphs arise
by disruptive selection of multiple correlated traits (Sinervo and Svensson 2002) and are commonly revealed by observations of discontinuities in the expression of behavioral, morphological, and physiological traits. Males of the saxicolous lizard *Sceloporus minor* occur in one of three discrete color morphs: blue, yellow, and red. Yellow males are morphologically and physiologically distinct from blue and red males in several ways (Chapter 3). Yellow males are smaller, and express proportionately smaller heads in relation to their body size. They also differ in performance: yellow males have greater stamina than blue and red males (Chapter 3). Thus, it is conceivable that males of this species express ARTs. I tested whether male morphs of *S. minor* differed in aspects of territorial behavior in the field. Territoriality is relevant to testing hypotheses about the relationship of color morphs to ARTs, because female and resource defense polygyny increases variance in male mating success, which in turn favors the evolution of ARTs (Shuster and Wade 2003). I also measured aspects of female space usage and social displays for comparison, since ARTs in some other lizards (Sinervo and Lively 1996, Whiting et al. 2009) have been characterized as female mimicry. Thus, if any male morph of *S. minor* exhibits a tactic that might be considered to be (at last partly) female mimicry, I would expect these males to exhibit behavioral patterns that more closely resemble those seen in females than other morphs.

A. Demographics

The absolute number of males and females did not differ across plots, either within or between years (Fig. 4.1A). Visual inspection of Fig. 4.1B indicates that females may have increased in representation relative to males during this period. Interannual variation in
sex ratio has been observed in another close relative (*S. jarrovii*: Ruby 1976). Morphs of *S. minor* differed in their representation among males. Yellow males were more common on each plot than other morphs during September and October (Fig 4.2) and appeared to increase in representation relative to other males between 2005 and 2008.

B. Persistence

Persistence is the tendency of subjects to remain in defined areas, and reflects both migration and survivorship. The disappearance of adult lizards on plots is probably closely linked to mortality (e.g., Sinervo et al. 2000a), especially as adult lizards tend to disperse relatively shorter distances than juveniles (Calsbeek 2009). In this study mortality contributed to estimates of persistence, as predation on marked subjects was observed on multiple occasions (B. Stephenson, pers. obs.). Nevertheless, differences in persistence may also reflect differential migration as well as detectability, and disentangling the relative contribution of these factors to persistence is not possible in my data set.

Males and females did not differ in persistence across years (Fig. 4.3). However, male morphs did significantly differ in persistence; yellow males remained on plots for fewer calendar years than blue or red males (Fig. 4.4). This overall difference is primarily attributable to a strong difference in persistence between blue and yellow morphs in 2006. In that year, 4/5 blue males were seen again at least one year later, whereas only 1/13 yellow males was seen again at least one year later.
C. Home Range

A territory is a defended space (Ruby 1976), whereas a home range is all the area that an animal uses as part of its daily activities (e.g., Jones and Droge 1980). The home range may not be the same as the territory, to the extent that males may actively defend only a subset of total visited space. At least some adult males of *S. minor* at La Manzana appear to be territorial, in part because males were occasionally seen engaging in fights with neighboring males (B. Stephenson, pers. obs.). Nevertheless, home range provides a measure of the extent to which adults move through the environment.

Males had larger home ranges than females during the months of September-October only, and across all months combined (Fig. 4.5). Analyses of the combined data sets showed that the males had larger home ranges even controlling for significant differences in the number of sightings; specifically, males were more commonly encountered than females. This is probably at least partly a function of the greater conspicuousness of males compared to females as perceived by human observers, but there may also be behavioral differences. For example, females generally appeared to move into refuges more quickly than males upon approach by observers (B. Stephenson, pers. obs.).

Larger adult males did not have larger home ranges than smaller adult males, a surprising finding in light of the significant positive relationship between male home range size and the number of females overlapped observed in 2006 and 2008. A correlation between male home range size and the number of overlapping females has been shown to strongly predict male fitness by DNA fingerprinting in other species of *Sceloporus* (e.g., Abell 1999, Haenel et al. 2003a, b). There were no differences among
male morphs in home range size (Fig. 4.6), or the extent of male and female overlap (Table 4.4).

D. Display Behavior

Males exhibited higher rates of all measured displays than females during focal observations, consistent with many other field studies of lizards (e.g., Ruby 1976, Martins 1993). In males, headbobs and pushups were performed most frequently, followed by shudderbobs and fullshows (Fig. 4.7). However, females were never observed to perform fullshows or shudderbobs during focal observations. This is in contrast to the work of Ruby (1977) with *S. jarrovii*, who found that females frequently performed each of these displays in response to the approach of adults of either sex. There were no differences among male morphs in rates of any display (Table 4.6).

Do males of *S. minor* exhibit alternative reproductive tactics?

In *S. minor*, males occur in one of three discrete color morphs: blue, yellow and red. Prior research showed that males differ in morphometric and performance traits, consistent with expectations for alternative reproductive tactics in other lizards. If males of *S. minor* exhibit alternative reproductive tactics, I predicted that morphs would differ in home range size, access to females, or overlap with males. Contrary to predictions, I found no difference among male morphs of *S. minor* in any of these three key variables, although sample sizes within years were small.
Morphs of *S. minor* also did not differ in rates of several common display behaviors, indicating that all morphs were capable of producing the stereotypical displays characteristic of the genus associated with territory advertisement and defense, as well as courtship. Whether morphs are equally likely to use these displays in specific social contexts is unknown, however. One approach for investigating this question is to simulate territorial intrusions by use of tethered introductions of different morphs. Such experiments can reveal differences in resident male aggressive behavior that may be hard to detect with exclusively observational data, such as those presented in this study.

Although I found no differences among morphs in home range size, overlap with male and females, or display rates, morphs differed in other attributes that plausibly could be linked to ARTs. For one, morphs were not represented equally on plots; yellow males represented between 56% and 81% of all males across all years studied. The fact that morphs are not represented at equal frequency does not by itself indicate ARTs, but is not inconsistent with this hypothesis. More notable is the finding that yellow males had lower interannual persistence than other males. If survival contributes substantially to my estimates of persistence, then yellow males probably have higher annual mortality than other morphs. If so, then the observation that yellow males are maintained at high frequency despite higher mortality is intriguing. Presumably, high mortality of yellow morphs among younger adult age classes would have to be offset by high reproductive success, since lifetime reproductive success in these males would be concentrated in a single breeding season. Further research coupling experiments on male social behavior with DNA paternity analyses would be illuminating with respect to the question of ARTs in *S. minor*. 
Figure 4.1 Representation of males and females in three main study plots during September-October of 2005, 2006 and 2008. M = Males, F = Females. A: Mean number of males and females per plot. B: Mean proportion (%) of males and females per plot.
Figure 4.2 Representation of male morphs in three main study plots during September-October of 2005, 2006 and 2008. B = Blue, Y = Yellow, R = Red. A: Mean number of male morphs per plot. B: Mean proportion (%) of morphs per plot.
Figure 4.5 Home range of males and females in three main study plots in 2005, 2006 and 2008. M = Males, F = Females. A: All months. B: September and October only.
Figure 4.6 Home range of three male morphs in three main study plots in 2005, 2006 and 2008. B = Blue, Y = Yellow, R = Red. A: All months. B: September and October only.
**Figure 4.7** Mean rate of displays during focal observations of adult *S. minor* at La Manzana during September-October 2005. A: Display rates for all males and females. M = Males, F = Females. B: Display rates for male morphs only. B = Blue, Y = Yellow, R = Red.
Table 4.1 Number of males and females observed in the three main study plots between 2005 and 2008 at La Manzana.

| Month | Males | | | | | | Males | | | | | |
|-------|-------|---|---|---|---|---|---|---|---|---|---|
| May   |       |      |      |      | 13    | 13    |      |      |      |      |
| June  |       |      |      |      | 18    | 21    |      |      |      |      |
| July  | 21    | 14   |      |      | 20    | 14    |      |      |      |      |
| August| 20    | 13   | 10   |      | 17    | 14    | 12   |      |      |      |
| October| 13   | 11   | 9    |      | 14    | 16    | 14   |      |      |      |
| November|     |      |      | 8    | 14    |      |      |      |      |


<table>
<thead>
<tr>
<th></th>
<th>Blue</th>
<th></th>
<th>Yellow</th>
<th></th>
<th>Red</th>
<th></th>
</tr>
</thead>
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<td>June</td>
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</tr>
<tr>
<td>July</td>
<td>4</td>
<td>4</td>
<td>11</td>
<td>11</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>August</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>12</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>September</td>
<td>3</td>
<td>4</td>
<td>1</td>
<td>8</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>October</td>
<td>1</td>
<td>6</td>
<td>0</td>
<td>0</td>
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</tr>
</tbody>
</table>

Table 4.2 Number of male morphs observed in the three main study plots between 2005 and 2008 at La Manzana.
Table 4.3 Descriptive statistics for home range and territory overlap in *S. minor* in 2005 (August-October), 2006 (July-October) and 2008 (September-November).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Males (N = 20)</th>
<th>Females (N = 16)</th>
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<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
<td>SE</td>
</tr>
<tr>
<td>Sightings</td>
<td>14.7</td>
<td>2.0</td>
</tr>
<tr>
<td>Home Range (m$^2$)</td>
<td>78.4</td>
<td>18.8</td>
</tr>
<tr>
<td>Male Overlap (%)</td>
<td>22.7</td>
<td>7.2</td>
</tr>
<tr>
<td>Total Females</td>
<td>1.6</td>
<td>0.2</td>
</tr>
<tr>
<td>Total Males</td>
<td>1.5</td>
<td>0.2</td>
</tr>
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<table>
<thead>
<tr>
<th>Trait</th>
<th>Males (N = 17)</th>
<th>Females (N = 17)</th>
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<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
<td>SE</td>
</tr>
<tr>
<td>Sightings</td>
<td>23.5</td>
<td>4.4</td>
</tr>
<tr>
<td>Home Range (m$^2$)</td>
<td>119.0</td>
<td>31.1</td>
</tr>
<tr>
<td>Male Overlap (%)</td>
<td>35.0</td>
<td>7.5</td>
</tr>
<tr>
<td>Total Females</td>
<td>2.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Total Males</td>
<td>1.6</td>
<td>0.3</td>
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<table>
<thead>
<tr>
<th>Trait</th>
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<th>Females (N = 14)</th>
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<td></td>
<td>$\bar{X}$</td>
<td>SE</td>
</tr>
<tr>
<td>Sightings</td>
<td>11.6</td>
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</tr>
<tr>
<td>Home Range (m$^2$)</td>
<td>125.9</td>
<td>37.8</td>
</tr>
<tr>
<td>Male Overlap (%)</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Total Females</td>
<td>2.1</td>
<td>0.7</td>
</tr>
<tr>
<td>Total Males</td>
<td>0.5</td>
<td>0.2</td>
</tr>
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</table>
Table 4.4 Descriptive statistics for home range and territory overlap in *S. minor* in 2005 (August-October) and 2006 (July-October).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Blue ($N = 4$)</th>
<th>Yellow ($N = 12$)</th>
<th>Red ($N = 4$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
<td>SE</td>
<td>range</td>
</tr>
<tr>
<td>Sightings</td>
<td>20.5</td>
<td>6.2</td>
<td>7 – 37</td>
</tr>
<tr>
<td>Home Range (m$^2$)</td>
<td>75.9</td>
<td>21.7</td>
<td>22.9 – 128.7</td>
</tr>
<tr>
<td>Male Overlap (%)</td>
<td>20.6</td>
<td>17.3</td>
<td>0 – 72.3</td>
</tr>
<tr>
<td>Total Females</td>
<td>2.2</td>
<td>0.6</td>
<td>1 – 4</td>
</tr>
<tr>
<td>Total Males</td>
<td>1.5</td>
<td>0.6</td>
<td>0 – 3</td>
</tr>
</tbody>
</table>

Table 4.4 Descriptive statistics for home range and territory overlap in *S. minor* in 2005 (August-October) and 2006 (July-October).
Table 4.5 Descriptive statistics for common behavior patterns observed in males and females during observational studies during September and October in 2005 and 2006.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Males (N = 18)</th>
<th>Females (N = 16)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \bar{x} )</td>
<td>SE</td>
</tr>
<tr>
<td>Sightingss</td>
<td>4.6 0.7</td>
<td>1 – 11</td>
</tr>
<tr>
<td>Home Range†</td>
<td>59.1 12.3</td>
<td>0.6 – 159.4</td>
</tr>
<tr>
<td>Headbobs/min</td>
<td>0.9 0.2</td>
<td>0 – 2.5</td>
</tr>
<tr>
<td>Pushups/min</td>
<td>0.6 0.1</td>
<td>0 – 1.4</td>
</tr>
<tr>
<td>Shudderbobs/min</td>
<td>0.0 0.2</td>
<td>0 – 0.2</td>
</tr>
<tr>
<td>Fullshows/min</td>
<td>0.1 0.1</td>
<td>0 – 1</td>
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<table>
<thead>
<tr>
<th>Trait</th>
<th>Males (N = 13)</th>
<th>Females (N = 10)</th>
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<tbody>
<tr>
<td></td>
<td>( \bar{x} )</td>
<td>SE</td>
</tr>
<tr>
<td>Sightings</td>
<td>3.9 0.7</td>
<td>1 – 8</td>
</tr>
<tr>
<td>Home Range††</td>
<td>94.5 25.8</td>
<td>14 – 285</td>
</tr>
<tr>
<td>Headbobs/min</td>
<td>1.3 0.3</td>
<td>0.2 – 3.6</td>
</tr>
<tr>
<td>Pushups/min</td>
<td>0.6 0.1</td>
<td>0.1 – 1.2</td>
</tr>
<tr>
<td>Shudderbobs/min</td>
<td>0.1 0.0</td>
<td>0 – 0.4</td>
</tr>
<tr>
<td>Fullshows/min</td>
<td>0.1 0.0</td>
<td>0 – 0.5</td>
</tr>
</tbody>
</table>

† (M = 17, F = 14)  †† (M = 10, F = 10)
Table 4.6 Descriptive statistics for common behavior patterns observed in among male color morphs during observational studies during September and October in 2005 and 2006.

<table>
<thead>
<tr>
<th>Trait</th>
<th>2005</th>
<th>2006</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Blue ($N = 4$)</td>
<td>Yellow ($N = 10$)</td>
</tr>
<tr>
<td></td>
<td>$\bar{x}$ SE range</td>
<td>$\bar{x}$ SE range</td>
</tr>
<tr>
<td>Sightings</td>
<td>6.0 1.8 1 – 10</td>
<td>3.9 0.9 1 – 11</td>
</tr>
<tr>
<td>Home Range†</td>
<td>62.6 32.2 21.0 – 126.0</td>
<td>59.7 16.6 0.6 – 159.4</td>
</tr>
<tr>
<td>Headbobs/min</td>
<td>1.0 0.5 0.1 – 2.3</td>
<td>0.7 2.2 0 – 2.2</td>
</tr>
<tr>
<td>Pushups/min</td>
<td>0.6 0.2 0 – 1.0</td>
<td>0.6 0.3 0 – 0.9</td>
</tr>
<tr>
<td>Shudderbobs/min</td>
<td>0.1 0.0 0 – 0.2</td>
<td>0.0 0.0 0 – 0.1</td>
</tr>
<tr>
<td>Fullshows/min</td>
<td>0.0 0.0 --</td>
<td>0.1 0.1 0 – 1</td>
</tr>
</tbody>
</table>

2006

<table>
<thead>
<tr>
<th>Trait</th>
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<th>2006</th>
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<tbody>
<tr>
<td></td>
<td>Blue ($N = 4$)</td>
<td>Yellow ($N = 8$)</td>
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<tr>
<td></td>
<td>$\bar{x}$ SE range</td>
<td>$\bar{x}$ SE range</td>
</tr>
<tr>
<td>Sightings</td>
<td>5.2 1.2 2 – 8</td>
<td>2.9 0.7 1 – 7</td>
</tr>
<tr>
<td>Home Range††</td>
<td>89.4 26.0 14 – 132.7</td>
<td>60.5 22.2 18.8 – 134.9</td>
</tr>
<tr>
<td>Headbobs/min</td>
<td>2.3 0.6 0.9 – 3.6</td>
<td>0.9 0.3 0.2 – 2.3</td>
</tr>
<tr>
<td>Pushups/min</td>
<td>0.8 0.2 0.4 – 1.2</td>
<td>0.5 0.1 0.1 – 0.9</td>
</tr>
<tr>
<td>Shudderbobs/min</td>
<td>0.2 0.1 0 – 0.4</td>
<td>0.0 0.0 0 – 0.1</td>
</tr>
<tr>
<td>Fullshows/min</td>
<td>0.1 0.0 0 – 0.2</td>
<td>0.1 0.1 0 – 0.5</td>
</tr>
</tbody>
</table>

† (B = 3, Y = 10, R = 4)  †† (B = 4, Y = 5, R = 1)
A Test of the Sensory Exploitation Hypothesis in the Lizard *Sceloporus minor*

I. Background

In many species, males are larger and more colorful than females, and exhibit complex behavioral displays that females do not express. These traits can be costly to produce and maintain; nevertheless, theory and empirical evidence show that these traits can confer high reproductive success in males. Such traits evolve by two major mechanisms, female mate choice and male contest competition (Andersson 1994). In female choice, females exhibit a preference for certain males as a function of variation in male traits; males with more elaborate traits are preferred as mates. In male contest competition, males engage in contests for access to a limited resource (e.g., food or mates) and assess the quality of opponents by evaluating traits that predict opponent resource holding potential (RHP), or fighting ability (Andersson 1994). Typically, males with more elaborate traits defeat their less showy rivals, even in the absence of direct physical contact (Andersson 1994). Since it was first proposed by Darwin (1871) the notion of female choice has been controversial. As a consequence, female choice has received extensive theoretical attention with researchers seeking to explain how such traits can arise and be maintained (e.g., Fisher 1930, Zahavi 1975, Grafen 1990, Iwasa and Pomiankowski 1999, Johnstone et al. 2009).

A pre-existing sensory bias is a bias in the sensory system that generates a preference for certain stimuli over others (Endler and Basolo 1998). The evolution of
male secondary sex traits in response to female sensory biases is termed sensory exploitation (Kirkpatrick and Ryan 1991). Sensory exploitation is distinct from other major classes of models for female choice in that female preferences evolve prior to the evolution of preferred male traits (Ryan and Rand 1993). Crucially, this hypothesis can only be tested within the context of a phylogeny (Endler and Basolo 1998). As originally formulated, support for sensory exploitation requires several conditions to be met (Basolo 1995). First, within a clade of closely related taxa, males of a derived species or population should express a secondary sex trait that females use in mate choice. Second, males in a closely related ancestral taxon should lack this trait entirely, or exhibit only a reduced form. Third, females of the ancestral populations should mate preferentially with males with the derived trait (or a synthetic analog) rather than with males that lack this trait. More recent models predict that female preferences may be only weakly expressed in derived taxa (e.g., Holland and Rice 1998). Nevertheless, the sensory exploitation hypothesis has received some empirical support, and has been invoked to explain the evolution of male traits in a wide range of taxa (water mites: Proctor 1991, 1992; damselflies: Córdoba-Aguilar 2002; crickets: Sakaluk 2000, Sakaluk et al. 2006; spiders: Stålhandske 2002, Cross et al. 2009, Herberstein et al. 2009; swordtails: Basolo 1990; guppies: Rodd et al. 2002; splitfins: Macias Garcia and Ramirez 2005; cichlids: Tobler 2006; salamanders: Karuzas et al. 2004; túngara frogs: Ryan et al. 1990, but see Ron 2008; bowerbirds: Madden and Tanner 2003, but see Borgia and Keagy 2006; cotton-top tamarins: Miller et al. 2004).

A relatively unexplored question is whether signals that are important in male-male contests could also arise via sensory exploitation. Endler (1992) noted that there is
no obvious restriction to this possibility, since the traits used in signals to rivals should be subject to the same design constraints as those used in mate attraction. Nevertheless, surprisingly few studies have directly addressed this issue (e.g., Quinn and Hews 2000). Interestingly, multiple predictions might be consistent with this hypothesis. For example, cheaters might win contests with males of high fighting ability by producing a signal that induces reduced aggression in opponents. Trait reliability could be established if a correlation between RHP and signal quality evolved rapidly (Maynard Smith and Harper 2003); such a mechanism may partly explain the evolution of the descended larynx in male red deer (Reby and McComb 2003). Alternatively, males that produce the signal might generate increased aggression from rivals. If only males with high RHP produce the signal, and these males win contests against aggressive but poor-quality fighters, then the signal could be maintained as a reliable indicator of male quality. Thus, multiple outcomes could be consistent with male-biased sensory exploitation; however, the key prediction is that opponents with the derived form of the trait would elicit different levels of aggression relative to controls.

Since many male traits can serve to both attract females and deter rivals, evidence of sensory exploitation of male traits may be more readily detected in taxa where male contest competition is especially intense and where female choice of traits is relatively weak. Members of the spiny lizards, *Sceloporus* (Squamata: Phrynosomatidae) would seem to fit these criteria. *Sceloporus* is a diverse assemblage of diurnal New World lizards (Wiens and Reeder 1997) characterized by the use of bright blue color patches in stereotyped social displays (Carpenter 1978). Adult males defend territories that typically contain multiple females (Abell 1999, Haenel et al. 2003a) and attempt to exclude rivals...
from access to females (Ruby 1978). In most species only males possess abdominal and
throat color patches (Wiens 1999), features revealed to conspecifics during courtship and
aggressive interactions (Cooper and Burns 1987). There is relatively little evidence of
overt female mate choice in spiny lizards (Quinn 2001) but good evidence that the
outcome of male-male competition predicts mating success (e.g., Haenel et al. 2003b).

Given that the color blue appears to be of importance in *Sceloporus* social
displays (e.g., Cooper and Burns 1987, Quinn and Hews 2000) and was probably present
in the common ancestor of the genus (Wiens 1999), blue may be of fundamental
importance in the evolution of sexual signaling in *Sceloporus*. In this context, a study by
Quinn and Hews (2000) on the role of blue abdominal color in social signaling in *S.
virgatus* is intriguing. In *S. virgatus*, males lack blue abdominal patches that were present
in a recent common ancestor (Wiens 1999). Males paired with opponents whose ventral
patches were painted blue (but not other color combinations) were significantly more
likely to retreat following presentation of these patches by an opponent (Quinn and Hews
2000). The response by males of *S. virgatus* to males with the replaced blue signal may
be analogous to the ‘residual preference’ pre-existing bias model (Basolo 1995). In this
model, trait and preference co-occur at some point in time, but the trait is subsequently
lost (e.g., offsetting costs of increased predation). Females retain the preference for the
lost trait, and this bias is available for males to co-opt in the future (Basolo 1995). In *S.
virgatus*, males may have retained a response to blue as an aggressive signal, following a
secondary loss of the signal. Although the results of Quinn and Hews (2000) do not
demonstrate sensory exploitation, they do suggest that males exhibit a sensory bias that
could be exploited by males in the future.
Study Species

The minor lizard *Sceloporus minor* is a common and conspicuous inhabitant of boulders and rock outcroppings throughout the southern Chihuahuan Desert of central México (Chrapliwy 1964). Like most congeners, adult males exhibit bright blue ventral and throat coloration (Smith 1936). However, a phylogenetic analysis of this species revealed unusual patterns of dorsal color expression across populations (Wiens et al. 1999). Derived populations in the states of Tamaulipas and Hidalgo exhibit strongly sexually dimorphic dorsal color (See Chapter 1: Fig. 1.1). All males in these populations exhibit a bright blue head, legs and tail, and some males express a uniform blue dorsum, whereas other males express orange or yellow shoulder patches (Chrapliwy 1964; see Chapter 1). Alternatively, males from ancestral populations in the state of San Luis Potosí express brown or orange dorsal color, and more closely resemble females in this regard than do males from Tamaulipas or Hidalgo (Chapter 1: Fig. 1.1). Crucially, bright blue dorsal color appears to be absent in the common ancestor of *S. minor* (Wiens et al. 1999).

I tested whether adult males from a population (Escalerillas, San Luis Potosí: 22° 5' N, 101° 4' W; Fig. 5.1) that express the hypothesized ancestral condition of dorsal color (brown/orange: *sensu* Wiens et al. 1999) respond differently to males painted to mimic the dark blue phenotype characteristic of derived populations (e.g., La Manzana, Hidalgo: Fig. 5.1) relative to control groups. I predicted that if sensory exploitation explains the existence of blue color in derived populations, blue males would receive either increased or decreased aggression relative to orange males (to mimic the putative ancestral phenotype) and green males (a novel stimulus control).
II. Materials and Methods

Research was conducted near the community of Escalerillas, San Luis Potosí, Mexico, between 11 October and 23 November 2007, a period coinciding with the expected peak of male breeding behavior in this population (Ramírez-Bautista et al. 2008). Resident males (N=27) and intruder males (N=29) were collected at separate sites (Fig. 5.1) since previous interactions between lizards may predict the outcome of future contests (Forster et al. 2005). In all cases, resident and intruder pairs were found at locations separated by at least 500 m, a dispersal distance almost twice as great as that observed for any individual in another population of *S. minor* (B. Stephenson, unpubl data).

Lizards were captured by noose on their territories, and brought to a nearby field house within a few hours. Both resident and intruder males were measured for color using a portable spectrometer and light source. In addition, several common morphometric measurements were collected for each male, including mass, snout-vent length (SVL), intact and total tail length, jaw length, head width and head depth. Details on protocols for spectrometric and morphological measurements are described elsewhere (Chapters 1-2). Each resident male was marked by applying a unique sequence of colored beads to the base of the tail, then released back onto its territory within 24 h of capture. Intruder males were not marked with beads, but instead were assigned to one of three paint treatment groups (Fig. 5.2). Orange intruders were painted orange on the dorsum to mimic the most common phenotype found in males at Escalerillas (see Chapters 1-2). Blue intruder males were painted blue to resemble the derived phenotype present in some males from La Manzana. A third class of intruder was painted green, a phenotype that does not occur in *S. minor* (Wiens et al. 1999), its sister taxon *S. serrifer* (Martínez-
Méndez and Méndez-de la Cruz 2007) or in other squamate reptiles found at the study site (Grant and Smith 1959; B. Stephenson, unpubl. data). Color change following drying of paint was confirmed by spectroradiometry (Fig. 5.3). All paints used were of a brand certified non-toxic to humans (Chromacryl: Stuart-Fox and Johnston 2005).

Trials were conducted 1-3 days following capture of intruders. Intruder males were introduced onto the territory of residents by fishing pole and tether (e.g., Cooper and Burns 1987), with approximately 1 m of line to allow intruders to move freely. The fishing pole attained a length of approximately 5m when fully extended, and so the minimum distance by researchers to each resident male at the start of each trial was 3-5 m. A trial started when an intruder was placed on a resident male’s boulder and judged to be clearly within the line of sight of the resident. If the resident was determined to have not seen the intruder after 20 min, the trial was postponed for 24 h or canceled entirely. Most resident males retreated to crevice refuges following initial approach by researchers, but usually reappeared where initially seen within 10 min. Due to time constraints, marked males were rejected for use as residents if they failed to re-emerge from crevices within the line of sight of observers within approximately one hour on at least two separate occasions. Trials lasted up to 20 min, but were preemptively stopped if sustained physical contact was maintained for more than 60 s, or if the risk of injury to either lizard was considered excessive (i.e., sustained biting; retreating to a boulder crevice with tether, etc.). Experiments were recorded using a Panasonic PV-GS300 video camera positioned 3-5 m from the resident male at the start of the trial. Each resident male and intruder male was used in only one trial. The responses of residents to intruders were scored from viewing videotapes of each trial. At the conclusion of each trial
intruders were cleaned of stimulus paint, marked with a small white paint dot at the base of the tail to indicate previous use, and released at their site of capture.

If sensory exploitation explains the initial evolution of blue coloration, I predicted that residents should exhibit either reduced or increased aggression to blue-painted intruder males relative to orange- and green-painted intruders. However, if there is no difference in aggressive behavior (either reduced or increased) towards blue males as opposed to green males, this would suggest that any observed difference between blue and orange males is most likely due to resident males responding to an unfamiliar stimulus.

Statistics

Rates of all display variables were adjusted in proportion to the length of the trial and the proportion of time the resident was visible to the camera during the trial. I used non-parametric tests to test for differences among residents in responses to different intruder treatment groups. Principal components analysis was used to transform 16 behavioral variables (Table 5.1) to a smaller subset of orthogonal variables. I used the broken-stick criterion advocated by Jackson (1993) to determine the number of PCs to retain for analysis. Because data failed to meet conditions for parametric tests, I used non-parametric tests for all comparisons. For all tests, alpha was set to 0.05 with Bonferroni adjustment for multiple tests (Rice 1989).
III. Results

Following release, 26/27 marked resident males (96%) were resighted, and all exhibited behavior consistent with normal territorial activity. Of those located, most (23/26) were found at or near their capture site within 72 h of release. Two of the remaining three males were subsequently located but failed to meet behavioral criteria necessary to carry out a trial (i.e., failing to reappear within 1 h of researcher approach on two separate occasions). Thus, these males were not used in the experiment. Overall, 24 successful trials were performed representing eight trials per treatment group.

Resident males and intruder males did not differ in body size (SVL: Mann-Whitney $U = 340$, $P = 0.28$) or condition (Mann-Whitney $U = 348$, $P = 0.22$). No difference was found between the three resident male groups in body size (Kruskal-Wallis $H = 5.07$, $P = 0.08$) or condition (Kruskal-Wallis $H = 2.13$, $P = 0.34$). Similarly, intruder males did not differ in body size (Kruskal-Wallis $H = 2.31$, $P = 0.31$) or condition (Kruskal-Wallis $H = 0.45$, $P = 0.80$) as a function of paint treatment. The first principal component (PC1) of the behavioral response scores was found to explain 37.8% of the variation among behavioral variables, and was positively correlated with all display variables except Escapes, Latency to approach, Latency to first display, and Latency to first fullshow, indicating that PC1 was correlated with aggressive behavior. Only PC1 was retained for analysis, since PC2 explained less variation (14.2%) than that required (14.8%) under the broken-stick model (Shaw 2003). A Kruskal-Wallis test of PC1 by intruder color was non-significant (Kruskal-Wallis $H = 1.11$, $P = 0.57$; Fig. 5.4). Thus, resident males did not differ in the intensity of aggressive behavior directed
towards intruder males of any color type. Removal of a single extreme outlier from analyses did not change the outcome ($\text{Kruskal-Wallis } H = 1.79, P = 0.41$).

### IV. Discussion

Endler (1992) proposed that animal signals evolve in predictable directions due to biophysical constraints on signal design, changes in the physical features of the environment, or the sensory properties of receivers, a phenomenon he termed sensory drive. An extension of sensory drive is sensory exploitation (Endler and Basolo 1998), which posits that secondary sex traits can evolve solely in response to preceding changes in the sensory properties of receivers, rather than via any intrinsic correlation between the expressed trait and receiver benefits (Ryan and Rand 1993). This idea was developed partly to account for the observation that females can exhibit preferences for traits that do not occur within their population or species (Burley and Symanski 1998) but which appear in derived taxa (Basolo 1995). Similar models (e.g., sensory traps: Christy 1995) have been applied to other signaling contexts including aposematism (Smith 1977), predator/prey strategies (Fleishman 1992, Nelson et al. 2010), and floral pollination syndromes (Schaefer and Ruxton 2009). Collectively these studies suggest that much of signal diversity may be explained by receiver biases and sensory exploitation.

An intriguing question is whether traits important in male contest competition could evolve the same way. Males of many lizards make use of conspicuous visual traits in social interactions, and variation in these display traits has been shown to predict contest outcome (Olsson 1994, Stapley and Whiting 2006) and reproductive success (Anderholm et al. 2003). I tested the hypothesis of male-biased sensory exploitation in
the lizard *Sceloporus minor*. Males in at least two populations have independently evolved bright blue dorsal color, whereas ancestral populations express a yellow, orange or red color and blue color is rare or absent (Wiens et al. 1999; see Chapters 1-2). Blue color is relevant to the sexual signaling of other species of *Sceloporus* (Cooper and Burns 1987, Quinn and Hews 2000) and its expression on the abdomen and throats of males probably represents the ancestral character state for the genus (Wiens 1999). Thus, males that express bright blue color on the dorsum might exploit a pre-existing sensory bias in males. Nevertheless, I found no effect of intruder color on aggressive behavior of males in a population with the ancestral phenotype (Table 5.2, Figure 5.4). As sample size was small ($N = 8$ for all treatments), I also tested the response of resident males to only blue and orange males. However, there was no significant difference in aggressive behavior directed towards males of these two groups alone (data not shown).

If male-biased sensory exploitation cannot explain the evolution of blue color in *S. minor*, what other factors might be responsible? One alternative hypothesis is that blue dorsal color evolved by sensory exploitation of females. Until recently, demonstrations of female mate choice were rare in lizards (Tokarz 1995) and when detected, preferences were generally found to be correlated with male body size and condition (e.g., Cooper and Vitt 1993, Censky 1997) rather than color (e.g., Olsson 2001, Quinn 2001). However, several recent studies suggest that females may indeed exhibit preferences for color traits. For example, Hamilton and Sullivan (2005) tested whether several morphological and behavioral traits in males predicted female choice in the tree lizard *Urosaurus ornatus*. They found that no single trait predicted choice in univariate analyses, but that abdominal patch size and tail color contributed to female choice in a multivariate analysis; males
with larger blue abdominal patches and bluer tails tended to be preferred. In the side-blotched lizard *Uta stansburiana*, females exhibited positive mating assortment on the basis of male throat color prior to their first clutch. Orange females then switched preferences to yellow males prior to the second clutch whereas yellow females did not (Bleay and Sinervo 2007). Another unusual pattern was seen in the painted dragon *Ctenophorus pictus* (Healey et al. 2008). Females of this species exhibited no preference for orange and yellow males in choice trials, but did prefer to associate with mixed-morph pairs as opposed to single-morph pairs, indicating that male color may influence mating decisions. Finally, a study by Kwiatkowski and Sullivan (2002) on sexual selection in chuckwallas (*Sauromalus ater*) found that females from a population that lacked males with bright orange tails tended to prefer males with this phenotype over males with yellow-white tails, the phenotype naturally occurring in that population. This suggests that some populations of female chuckwallas may exhibit a pre-existing bias for orange-colored males.

Another possibility is that any responses by conspecifics to male dorsal color in *S. minor* did not evolve prior to the evolution of blue dorsal color, but instead evolved simultaneously with it or subsequent to it. These predictions would conform to expectations for several models of female choice. In Fisher’s (1930) runaway process, females evolve a preference for male traits, such that males with more elaborate traits are preferred as mates. The genes for preference and trait become linked, and female preferences will drive male traits to extremes until balanced by offsetting costs for trait expression in males (Ryan and Rand 1993). Thus, male traits and female preferences evolve in synchrony. Similar scenarios are postulated for good genes models; preference
and trait should evolve together, with the strength of the female preference increasing with increasing correlation of the preferred male trait and signaler quality. Alternatively, the male trait could precede the preference (Ryan and Rand 1993). Such a scenario would be expected under direct benefits models for female choice; males evolve traits that advertise their ability to provide resources to females, and females subsequently evolve preferences for these traits (Ryan and Rand 1993). However, this latter scenario is unlikely to explain the evolution of blue dorsal color in *S. minor* as males probably do not provide resources to females.

**Blue males at Escalerillas**

In this study, I asked whether males from a population that exhibits the ancestral phenotype for *S. minor* (orange-brown) modified their aggressive responses to blue males but not to green and orange controls. While dark blue males that resemble those from La Manzana are clearly absent from Escalerillas, blue phenotypes per se may not be. At least one uniform pale blue male was seen during this study (Chapter 1: Fig. 1.2A); this individual exhibited spectral attributes that resembled those of dark blue males from La Manzana. In addition, males with a light blue phenotype were reported from a nearby locality by Grant and Smith (1959), indicating that this color pattern may be more common than previously suspected. One implication is that males from Escalerillas may have had encounters with blue males previously, in opposition to a key assumption of this experiment. One possibility is that blue males are normally present at very low frequencies in the population. Alternatively, the frequency of blue males may change across years. Such an outcome would be consistent with the expression of alternative
reproductive tactics maintained by frequency dependent selection, with morph frequencies oscillating over time. One interpretation of these observations is that the population at Escalerillas may not be as suitable for testing the sensory exploitation hypothesis as originally thought.

Nevertheless, other lines of evidence indicate male-biased sensory exploitation may help explain the evolution of male sexually dimorphic traits. Corl et al. (2010) studied the evolutionary relationships of the side-blotched lizard (U. stansburiana) across much of its range in the United States and Mexico. Male throat trimorphism was recovered as the ancestral character state for this species, but multiple losses of yellow and blue morphs were observed in derived populations. Although the authors did not find evidence for the reappearance of a morph subsequent to its loss, further sampling of populations in Mexico might be informative in this regard. In addition, unpublished research on the evolutionary history of Sceloporus indicates that multiple morphs (blue, yellow, and orange/red) have evolved repeatedly within the genus (Sinervo et al. unpubl.). One possible explanation (among others) to explain the rapid evolution of similar color phenotypes in distant relatives is that males with novel phenotypes exploit pre-existing sensory biases in males or females. Further experimental approaches should be revealing in this regard.
**Figure 5.1** Aerial view of study site near Escalerillas, San Luis Potosí. Capture localities of males indicated by colored circles. Red = Resident, Blue = Intruder.
Figure 5.2 Examples of each of three male treatments used in staged intrusions. A = Blue, B = Green, C = Orange.
Figure 5.3 Mean reflectance spectrum for each of three paints (blue, green and orange) following application to dorsum of males used in intruder experiments ($N=9$ males/paint). Spectra plotted as average of medians of 10 nm bins; standard error bars plotted at 20 nm increments for clarity. Mean spectrum for blue males from La Manzana and red males from Escalerillas provided for comparison.
Figure 5.4 The effect of male intruder color on resident aggression in male *S. minor* at Escalerillas.

Kruskal-Wallis $H = 1.11$, $P = 0.57$
Table 5.1 Ethogram of behavior patterns scored from videotaped trials of *Sceloporus minor* at Escalerillas.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Headbob</td>
<td>One or two rapid and continuous up-and-down vertical movements of the head followed by pause of 0.5 s or more. May be performed while walking or standing still. A headbob sequence is a continuous series of headbobs with a pause of &lt; 3 s between consecutive headbobs.</td>
</tr>
<tr>
<td>Pushup</td>
<td>Slow, exaggerated vertical movement of the head, usually accompanied by an extension of the forelimbs that results in an elevation of the anterior half of the torso. Cannot be performed while walking. A pushup sequence is a continuous series of pushups with a pause of &lt; 3 s between consecutive pushups.</td>
</tr>
<tr>
<td>Throat Fan</td>
<td>Extension of the throat in the vertical plane exposing the blue throat fan (dewlap).</td>
</tr>
<tr>
<td>Fullshow</td>
<td>Lateral compression that exposes the blue abdominal patches accompanied by an extension of the throat fan.</td>
</tr>
<tr>
<td>Hop</td>
<td>Short hop, often in a lateral direction, that results in at least two but usually all four limbs lifted into air.</td>
</tr>
<tr>
<td>Chase</td>
<td>A. Sprinting towards an opponent that results in displacement of the opponent, or B. Sprinting towards opponent &lt; 2 s after opponent runs in opposite direction.</td>
</tr>
<tr>
<td>Escape</td>
<td>Sprinting away from opponent.</td>
</tr>
<tr>
<td>Straddle</td>
<td>Placement of body across midsection of opponent, typically in a longitudinal orientation.</td>
</tr>
<tr>
<td>Head Butt</td>
<td>Push of opponent lizard with head (often around midsection) without biting.</td>
</tr>
<tr>
<td>Bite</td>
<td>Opponent lizard is seized with jaws.</td>
</tr>
</tbody>
</table>
Table 5.2 Descriptive statistics for individual response variables of resident males to intruders in staged introduction trials. Means reported ± SE. \( N = 8 \) for each treatment.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Male Category</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Blue</td>
</tr>
<tr>
<td>Headbobs/min</td>
<td>2.3 ± 0.6</td>
</tr>
<tr>
<td>Headbob sequences/min</td>
<td>0.7 ± 0.1</td>
</tr>
<tr>
<td>Headbobs/sequence</td>
<td>2.8 ± 0.5</td>
</tr>
<tr>
<td>Pushups/min</td>
<td>1.5 ± 0.3</td>
</tr>
<tr>
<td>Pushup sequences/min</td>
<td>0.6 ± 0.1</td>
</tr>
<tr>
<td>Pushups/sequence</td>
<td>2.0 ± 0.5</td>
</tr>
<tr>
<td>Throat fans/min</td>
<td>0.1 ± 0.0</td>
</tr>
<tr>
<td>Fullshows/min</td>
<td>0.4 ± 0.1</td>
</tr>
<tr>
<td>Chases/min</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td>Bites + Headbutts/min</td>
<td>0.5 ± 0.3</td>
</tr>
<tr>
<td>Straddles/min</td>
<td>0.1 ± 0.0</td>
</tr>
<tr>
<td>Hops/min</td>
<td>0.7 ± 0.4</td>
</tr>
<tr>
<td>Escapes/min</td>
<td>0.1 ± 0.0</td>
</tr>
<tr>
<td>Latency to first approach</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>Latency to first display</td>
<td>0.4 ± 0.2</td>
</tr>
<tr>
<td>Latency to first fullshow</td>
<td>2.8 ± 2.5</td>
</tr>
</tbody>
</table>


Olsson, M., Healey, M., and Astheimer, L. 2007a. Afternoon T: Testosterone level is higher in red than yellow male polychromatic lizards. *Physiology and Behavior* 91:531-534.


