

## Original Article

Male aggression varies with throat color in 2  
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We describe discrete variation in throat color, an important sexual signal, in males of 2 populations of the mesquite lizard (*Sceloporus grammicus*). At one locality, males exhibit orange, yellow, and blue morphs; whereas at the other, males exhibit orange, yellow, and white morphs. We performed dyadic agonistic behavior trials in both populations and found that variation in throat color is associated with variation in aggression level. However, the association between color and behavior is not the same between these 2 populations. The association between color and behavior in the mesquite lizard is also not consistent with some of the associations documented in closely related species with variable throat color. Our findings suggest that although the tendency for discrete color variation to signal alternative reproductive tactics is phylogenetically widespread, both the color signals and the behaviors associated with them may change rapidly over evolutionary time.

**Key words:** agonistic behavior, color morphs, interpopulation variation. [*Behav Ecol*]

## INTRODUCTION

Numerous animals exhibit color morphs, or discrete variation in coloration, and this variation is known to be at least partially genetically based (i.e., to be a true polymorphism) in a growing number of species (Gray and McKinnon 2007; Hugall and Stuart-Fox 2012). In many cases, color morphs represent variation in secondary sexual coloration, often in species experiencing strong sexual selection (Sinervo and Calsbeek 2006; Gray and McKinnon 2007; Forsman et al. 2008). This phenomenon occurs most frequently in males (Thompson et al. 1993; Sinervo and Lively 1996; Knapp et al. 2003; Pryke and Griffith 2006; Huyghe et al. 2007; Korzan and Fernald 2007; Olsson et al. 2007; Dijkstra, Hemelrijk, et al. 2009), although several cases also occur in females (Forsman and Shine 1995; Sinervo et al. 2000; Sinervo 2001; Svensson et al. 2005; Vercken et al. 2006; Calisi et al. 2008; Dijkstra, Van Dijk, et al. 2009; Vercken et al. 2010; Pellitteri Rosa 2012). In keeping with their links to sexual selection and sexual signals, intrapopulation color morphs have been associated with variation in alternative reproductive tactics and/or strategies (sensu Gross 1996) in one or both sexes in a range of taxa, including lizards, birds, fish, and insects (Thompson et al. 1993; Sinervo and Lively 1996; Sinervo et al. 2000; Sinervo 2001; Pryke and Griffith 2006; Healey et al.

2007; Huyghe et al. 2007; Korzan and Fernald 2007; Olsson et al. 2007; Vercken and Clobert 2008a; Dijkstra, Van Dijk, et al. 2009). These alternatives often encompass variation in aggression levels (Rand 1988; Sinervo and Lively 1996; Pryke and Griffith 2006; Healey et al. 2007; Korzan and Fernald 2007; Vercken and Clobert 2008a, 2008b; Dijkstra, Van Dijk, et al. 2009; Dijkstra, Hemelrijk, et al. 2009). However, they may also involve other aspects of reproduction and reproductive behavior, such as reproductive investment (Forsman and Shine 1995; Zamudio and Sinervo 2000; Sinervo 2001; Svensson et al. 2005; Sinervo et al. 2006; Vercken et al. 2006; Lancaster et al. 2008; Pellitteri Rosa 2012), maternal effects (Lancaster et al. 2007; Lancaster et al. 2010), or mate choice (Bleay and Sinervo 2007; Lancaster et al. 2009).

Theoretical expectations (West-Eberhard 1983; West-Eberhard 1986; Ritchie 2007; Forsman et al. 2008) and empirical observations (Gray and McKinnon 2007; Corl, Davis, Kuchta, and Sinervo 2010; Hugall and Stuart-Fox 2012) have linked both color polymorphisms and alternative reproductive strategies to rapid interpopulation divergence and increased rates of speciation. Selection, perhaps due to divergent sensory drive, may cause different morphs to be favored in neighboring populations (Seehausen and Schluter 2004; Dijkstra et al. 2005). When combined with divergence in mating preference, interpopulation differences in sexual signal polymorphisms or reproductive behavior may accelerate the evolution of reproductive isolation (Coyne and Orr 2004; Maan and Seehausen 2011).

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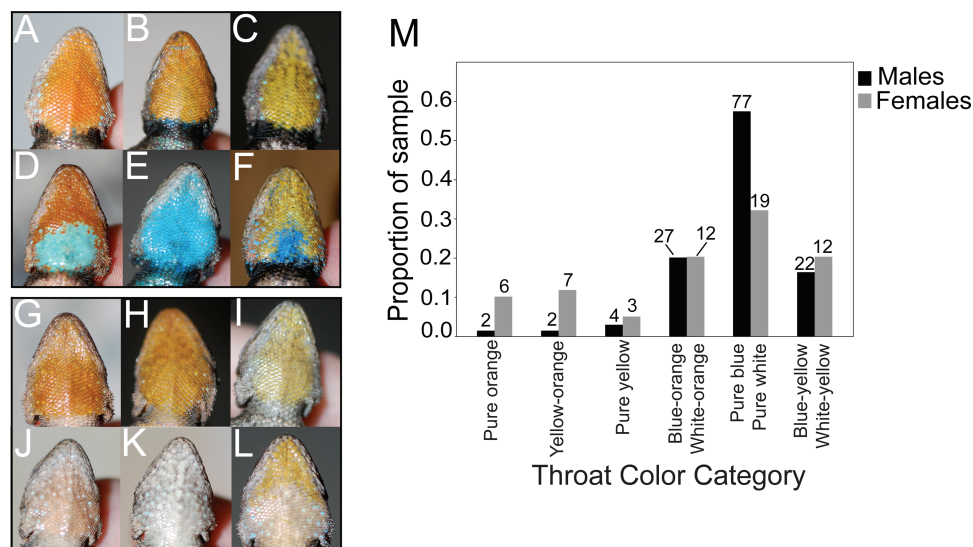
Stochastic processes such as genetic drift or founder effects can also cause neighboring populations to differ in the presence or frequency of morphs, which may contribute to reproductive isolation between them (Gray and McKinnon 2007; Forsman et al. 2008; Alonzo and Calsbeek 2010; Corl, Davis, Kuchta, and Sinervo 2010). Species with alternative strategies (reproductive or otherwise) may also be less vulnerable to extinction and better able to adapt to new environments than monomorphic species. This reduced extinction vulnerability and increased adaptive potential may occur because the presence of multiple behavioral morphs allows these species to occupy more than 1 ecological niche and because the evolutionary forces maintaining the polymorphism may also maintain high levels of standing genetic variation (West-Eberhard 1986; Forsman et al. 2008; Hugall and Stuart-Fox 2012; Pizzatto and Dubey 2012).

We investigated the association between throat color morphs and variation in male agonistic behavior in 2 populations of the mesquite lizard (*Sceloporus grammicus*) species complex, which is a taxon of small, phrynosomatid lizards that inhabit most desert and montane regions of México (Hall 1973; Marshall et al. 2006). Previous research found these lizards to be highly karyotypically variable, with diploid numbers ranging from 32 to 46 (Hall 1973; Sites 1983; Sites et al. 1995; Marshall et al. 2006). Populations of the *S. grammicus* complex also inhabit a wide variety of habitats, between which there may occur differences in life history and reproductive characteristics (Ramírez-Bautista et al. 2004; Hernández-Salinas et al. 2010). These characteristics have caused several authors to suggest that the *S. grammicus* complex represents a case of incipient speciation (Lara-Gongora 1983; Sites 1983; Porter and Sites 1986; Sites and Davis 1989; Reed et al. 1995a; Marshall et al. 2006; Hall 2009).

Here, we show that 2 closely related populations of the *S. grammicus* species complex have also diverged both in the associations between color and male agonistic behavior and in which male throat color morphs are present in the populations. One of our study populations exhibits orange, yellow, and blue throat color morphs in males (Figure 1A–F). This discrete color variation is similar in appearance to a well-studied, heritable polymorphism

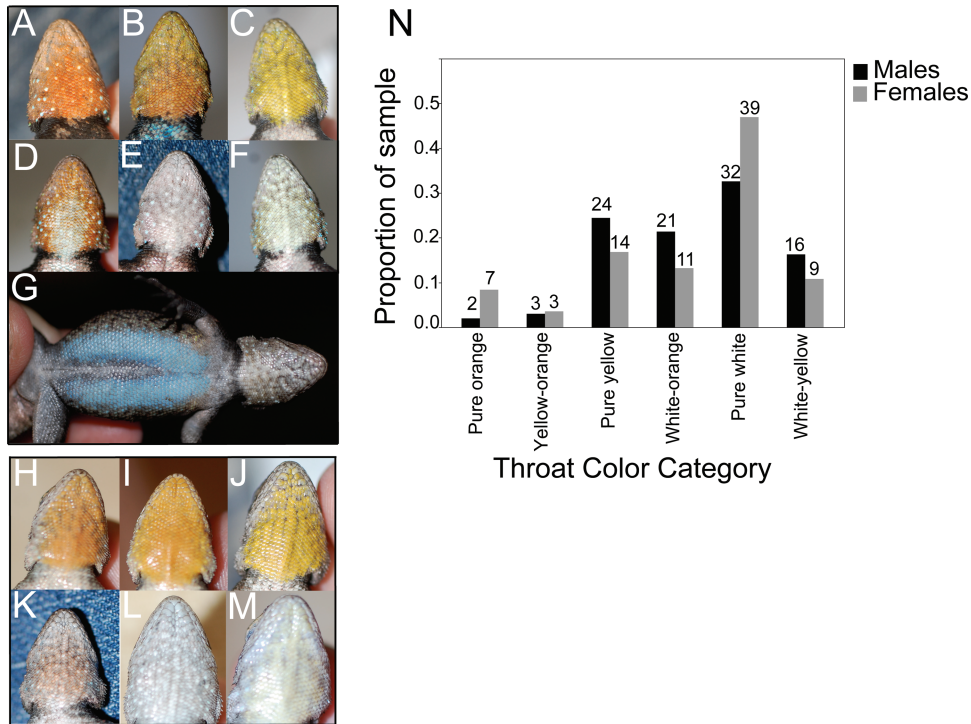
present in another phrynosomatid species, *Uta stansburiana* (Sinervo and Lively 1996; Sinervo 2001). The other population we studied exhibits orange, yellow, and white color morphs in males (Figure 2A–G). This variation appears somewhat more similar to discrete color variation observed in some populations of another sceloporine, *Sceloporus consobrinus* (formerly *Sceloporus undulatus erythrocheilus*; Rand 1990; Rand 1992; Leaché and Reeder 2002; Jones and Lovich 2009). However, whereas white-throated male *S. consobrinus* appear to be rare mutants with melanized ventral and dorsal coloration (Rand 1990, 1992), the white male morph in *S. grammicus* exhibited similar belly (Figure 2G) and dorsal (Bastiaans E, unpublished data) coloration to the orange and the yellow morphs and was the most common morph in the population we studied (Figure 2N). White, orange, and yellow color morphs are also associated with variation in reproductive behavior in the European common lizard, *Zootoca vivipara* (Sinervo et al. 2007; Vercken and Clobert 2008a).

Other populations of the *S. grammicus* species complex also exhibit these 2 categories of color variation (orange/yellow/blue and orange/yellow/white); however, blue and white male morphs never co-occur within the same population (Bastiaans E, unpublished data). Regardless of whether males exhibit orange/yellow/blue or orange/yellow/white color morphs, females of the *S. grammicus* species complex exhibit orange/yellow/white throat color morphs (Figure 1G–L, Figure 2H–M). In a different population, we found that individual coloration is stable from one reproductive season to the next and that maternal and offspring throat colors are correlated, based on a study in which lizards born in the laboratory were recaptured at reproductive maturity (Bastiaans E, in preparation). This correlation suggests that variable throat color in *S. grammicus* may have a heritable component, as it does in *U. stansburiana*, where gene mapping studies indicate that the expression of a similar throat color polymorphism is largely controlled by a single locus (Sinervo et al. 2006). Thus, the *S. grammicus* complex appears likely to represent another example of a lizard with discrete color morphs, similar to the morphs observed



**Figure 1**

Representative examples of male and female throat color morphs present in *S. grammicus* from Cerro Peña Nevada, Nuevo León, México. (A–F) Male morphs. (A) Pure orange. (B) Yellow-orange. (C) Pure yellow. (D) Blue-orange. (E) Pure blue. (F) Blue-yellow. (G–L) Female morphs. (G) Pure orange. (H) Yellow-orange. (I) Pure yellow. (J) White-orange. (K) Pure white. (L) White-yellow. (M) Proportions of each male and female throat color morphs in our sample. Sample sizes appear above bars.



**Figure 2**

Representative examples of male and female throat color morphs present in *S. grammicus* from San Antonio de las Alazanas, Coahuila, México. (A–G) Male morphs. (A) Pure orange. (B) Yellow-orange. (C) Pure yellow. (D) White-orange. (E) Pure white. (F) White-yellow. (G) Pure white male showing blue belly patches. (H–M) Female morphs. (H) Pure orange. (I) Yellow-orange. (J) Pure yellow. (K) White-orange. (L) Pure white. (M) White-yellow. (N) Proportions of each male and female throat color morphs in our sample. Sample sizes appear above bars.

in *S. consobrinus*, *Urosaurus ornatus*, *U. stansburiana*, *Zootoca vivipara*, and *Podarcis melisellensis* (Rand 1988; Rand 1990; Thompson et al. 1993; Sinervo and Lively 1996; Sinervo et al. 2006; Vercken et al. 2006; Huyghe et al. 2007).

In this study, we assess behavioral variation among lizards of different color morphs within 2 different populations. In these 2 populations, we test whether orange/yellow/blue throat color variation and orange/yellow/white throat color variation are associated with variation in male agonistic behavior. We also compare the behavior of corresponding male morphs in different populations to one another (i.e., orange to orange, yellow to yellow, and blue to white). We find that male throat colors can be consistently assigned to discrete categories and that throat color variation is associated with variation in aggression level during male agonistic interactions in both populations. Specifically, orange coloration is associated with decreased aggression in the population where blue-throated males occur, whereas white coloration is associated with decreased aggression in the population where white-throated males occur. A combined analysis of the 2 populations reveals that the blue and white male morphs differ in their agonistic behavior. This research thus expands the list of species in which discrete color morphs are associated with behavioral variation while shedding new light on how color signals and the behaviors associated with them may change over evolutionary time.

## MATERIALS AND METHODS

This project was conducted in accordance with guidelines from the Chancellor's Animal Research Committee at the University of California, Santa Cruz (permit Sineb0902) and under collection

permits issued by the Secretaría del Medio Ambiente y Recursos Naturales of México (folio FAUT007).

## Field sites

We studied lizards from 2 locations: San Antonio de las Alazanas, Coahuila, México (25.22193°N, 100.39331°W; 2800 m above sea level) and Cerro Peña Nevada, Nuevo León, México (23.83154°N, 99.89381°W; 2800 m above sea level). Henceforth, we will refer to these 2 sites as SAA and CPN, respectively. We chose these sites during summer 2010, when we first observed abundant populations of *S. grammicus* at each location and discovered the different throat color morphs occurring at each of them (Figures 1 and 2). Both localities are coniferous forests dominated by *Pinus*, *Abies*, and *Pseudotsuga* spp. (Villanueva-Díaz et al. 2007; Encina-Domínguez et al. 2008), although numerous *Agave* spp. were also present at CPN (Bastiaans E, personal observation). Lizards at SAA were primarily observed and captured from the walls of vacant or abandoned houses, whereas those at CPN primarily inhabited fallen pine logs and dead agaves. Previous research using allozyme electrophoresis indicated that these populations are closely related within the *S. grammicus* complex (Sites and Greenbaum 1983), and preliminary mitochondrial DNA sequence data support this conclusion (Bastiaans E, unpublished data). Thus, differences in coloration and behavior between lizards from SAA and CPN are likely to have evolved recently.

## Lizard capture and husbandry

From late June to early September 2011, we captured 98 adult male *S. grammicus* from SAA and 134 adult male *S. grammicus* from

CPN. Males were considered adult if they had a snout-vent length (SVL) greater than 40 mm and secondary sexual characteristics such as blue belly patches and colored throat patches (Lemos-Espinal et al. 1998; Zúñiga-Vega et al. 2008). We captured all lizards either by noose or by hand and gave them unique toe clips for individual identification. To prevent interactions among males during transport, we placed each lizard into an individual cloth bag. During fieldwork, captured lizards were kept in hard-sided coolers and cool environments to minimize their stress levels and metabolic rates. On capture, we measured each lizard's SVL to the nearest 0.5 mm using a clear ruler and mass to the nearest 0.05 g using a Pesola © spring scale.

Within 1 week of capture, we transported lizards to the Universidad Juárez del Estado de Durango (UJED), Gómez Palacio, Durango, México. We maintained lizards in individual plastic terraria (22.5 × 14.6 × 13.5 cm), covered with opaque paper to prevent visual interactions among males prior to behavioral trials. Each terrarium contained peat moss as a substrate and a folded piece of cardboard as a refuge for the lizard. We provided lizards with water daily by misting terrarium walls and fed them 4–5 crickets (*Acheta domestica*) every other day. Heat was provided by Flexwatt © heating tape placed under the terraria, with a ZooMed © thermostat set to 32°C and a timer that limited the provision of heat to daylight hours (7 AM–8 PM). However, given the high summer temperatures in Gómez Palacio, the ambient temperature was generally high enough for the lizards to be active, and the thermostat almost never activated the heat tape (Bastiaans E and Morinaga G, personal observation). The animal room had large windows open to the ambient air, so the lizards were exposed to the natural photoperiod and UV light. Before performing behavior trials, we gave lizards at least 5 days to acclimate to the laboratory environment and recover from the stress of transport (Denardo and Licht 1993). At the conclusion of our experiment, we released all males at their original capture sites.

### Throat color scores

We scored each individual's throat color on capture, using methods developed for *U. stansburiana*, a lizard from the same family as *S. grammicus* with a discrete color polymorphism that is phenotypically similar to the color variation we documented at CPN (Sinervo and Lively 1996; Sinervo et al. 2001; Lancaster et al. 2007; Lancaster et al. 2009; Lancaster et al. 2010). Although we have not assessed the genetic basis of the color variation we observed at CPN or SAA specifically, previous work on color morphs in closely related species (Rand 1992; Thompson et al. 1993; Sinervo 2001; Sinervo et al. 2001; Sinervo et al. 2006) supports the idea that this variation is at least partly genetically based. Also, maternal and offspring throat colorations were found to be correlated in a different population, when lizards born in the laboratory were released into the field and recaptured at sexual maturity (Bastiaans E, in preparation). Although this result is consistent with both additive genetic variation and maternal effects as bases for throat color variation, it indicates that the cause of the variation is unlikely to be purely environmental (Pemberton 2008).

We classified throat coloration by assigning scores from 0 to 2 along orange, yellow, and blue or white axes (Tables 1 and 2; Figures 1 and 2). This system was based on the scoring system previously used with *U. stansburiana* (Sinervo 2001; Sinervo et al. 2006), with white substituted for blue in the case of females at CPN (Figure 1G–L) and both sexes at SAA (Figure 2). Although we scored female throat color at both sites and calculated the

**Table 1**  
**Throat color scoring system used at CPN**

Throat color score	Orange axis	Yellow axis	Blue axis	Corresponding photo
Pure orange	2	0	0	Figure 1A
Yellow-orange	1	1	0	Figure 1B
Pure yellow	0	2	0	Figure 1C
Blue-orange	1	0	1	Figure 1D
Pure blue	0	0	2	Figure 1E
Blue-yellow	0	1	1	Figure 1F

**Table 2**  
**Throat color scoring system used at SAA**

Throat color score	Orange axis	Yellow axis	White axis	Corresponding photo
Pure orange	2	0	0	Figure 2A
Yellow-orange	1	1	0	Figure 2B
Pure yellow	0	2	0	Figure 2C
White-orange	1	0	1	Figure 2D
Pure white	0	0	2	Figure 2E
White-yellow	0	1	1	Figure 2F

frequencies of each female color morph in our sample (Figure 1M; Figure 2N), we did not use females in the experiment whose results we report here. We assigned a score of 2 on a given axis when a color was very intense and not mixed with any other color (Figure 1A,C,E,G,I,K; Figure 2A,C,E,G,H,J,L). If a lizard's throat color appeared intermediate between 2 other colors (Figure 1B,H,J; Figure 2F,I,K,M) or 2 patches of different colors were present on different parts of the throat (Figure 1D,E,L; Figure 2B,D), we assigned a score of 1 on each of those 2 color axes. If a color was absent from a lizard's throat, we assigned a score of 0 on that axis. No lizards displayed more than 2 colors on their throats, so this scoring system resulted in 6 possible scores for each sex at each site (Figures 1 and 2). Occasionally, a few isolated individual blue or white scales were present near a lizard's jawline (Figure 1A,C,D,F–H,J–L; Figure 2A–G,K–L). The presence of these colored scales appeared to be unrelated to background coloration because isolated blue scales were sometimes present near the jawlines of females from both sites and males from SAA (Figure 1G–H,J–L; Figure 2A–G,K,L). This occurred even though neither males from SAA nor females from either site ever exhibited blue background coloration on the throat or large patches of blue scales. We thus did not consider these isolated colored scales to represent color patches and did not use them in assigning throat color scores. In males from CPN, blue patches were clearly distinguishable from these isolated blue scales because the patches were located in the middle of the throat and consisted of many contiguous blue scales (Figure 1D,F).

We also documented each lizard's throat color soon after capture using digital photography. To ensure relatively consistent lighting in all images, photographs were taken in shaded, indoor environments, using the flash of a Nikon D40 camera with a macro lens attachment (Langkilde and Boronow 2010). Although UV reflectance is present in color patches used for intraspecific communication in some lizards, (Fleishman et al. 1993; Stoehr and McGraw 2001), previous research on sceloporines (Stoehr and McGraw 2001; Langkilde and Boronow 2010), as well as our own spectrophotometric measurements of throat color in several

other populations in the *S. grammicus* species complex (Bastiaans E, unpublished data), indicate that the contribution of UV reflectance to coloration in the lizards used in this study is likely to be low. Thus, human vision and digital photography should capture the essential elements of the lizards' throat colors (Healey et al. 2007; Langkilde and Boronow 2010).

### Selection of dyads for agonistic behavior trials

We assigned lizards from the same population to dyads randomly, with the constraints that the 2 males in a dyad could not differ by more than 2 mm in SVL and had been captured at least 40 m apart. The distance cutoff was intended to avoid "dear enemy" effects, in which males from neighboring territories exhibit fewer agonistic interactions than males from nonadjacent territories (Whiting 1999; López and Martín 2002; Husak 2004). We selected the distance cutoff by uploading the coordinates of all male capture locations to ArcGIS 10.0 (Environmental Systems Research Institute, 2011), calculating the average nearest neighbor distance for each population (the mean distance between a focal capture point and the nearest other capture point; approximately 20 m at both sites) and doubling that distance. We considered this to represent a conservative cutoff because despite intensive sampling effort, it is unlikely we captured every male present at either of our field sites. The average nearest neighbor distance calculated from our data is thus probably an overestimate and doubling it should minimize the likelihood that males paired for agonistic behavior trials had extensive previous interactions. Each individual male was used in only 1 trial (Carpenter 1995a). This experimental design resulted in unequal distributions of trials across throat color scores (Table 3), but given the rarity of certain color classes at both sites (Figures 1 and 2), a more balanced design would have required us to either use individual males in multiple trials or perform a very small number of total trials. Both these alternatives would have resulted in low statistical power. We, therefore, sacrificed a balanced experimental design in favor of maximizing the number of trials we could perform while using each individual male only once. The rarity of certain homozygous classes has been observed in a species in which similar polymorphisms are controlled by a single locus with 3 alleles (Sinervo et al. 2001, 2007), so the rarity of "pure" color classes relative to "mixed" color classes (Figures 1 and 2) may provide further support for the hypothesis that there is a genetic basis for throat color in *S. grammicus*.

### Agonistic behavior trials

We conducted behavior trials in a chamber measuring 70 cm wide × 46 cm long × 46 cm tall, with a plywood floor and Plexiglas ©

walls covered in opaque paper. The floor of the chamber was covered in sand procured from the UJED campus, and this sand was changed after every trial to prevent scent cues from influencing future trials (Duvall 1979; López and Martín 2002). We placed a rock in the center of the trial chamber to provide a substrate for male displays. After each trial, we scrubbed the rock with water to remove scent cues. Heat was provided by a 40-W incandescent light bulb in a lamp clamped to 1 wall of the chamber and angled to shine directly on the rock. Temperature measurements indicated that this raised the temperature of the rock to 30–35 °C, the approximate preferred body temperature of *S. grammicus* (Andrews et al. 1997), thus providing an incentive for the lizards to approach the rock and engage in agonistic interactions (Garland et al. 1990).

We performed trials from late July to late September 2011, a period which corresponds to the reproductive season for *S. grammicus* in northern México (Guillette and Casas-Andreu 1980, 1981). Trials were performed between 10 AM and 4 PM, which represent the approximate time during which males were observed to be active at our 2 field sites (Bastiaans E and Morinaga G, personal observation). Before each trial, 2 cardboard barriers were used to divide the chamber into 3 sections. We placed lizards in the 2 outer sections for at least a 5-min acclimation period prior to each trial (Sheldahl and Martins 2000). Lizards were randomly assigned to either the left or the right side of the trial chamber via coin toss. Trials commenced when both cardboard dividers were simultaneously lifted, and each trial lasted 20 min. We selected this trial duration based on pilot trials conducted in summer 2010, when we observed that this period of time was usually sufficient for agonistic interactions to cease or reach equilibrium (Bastiaans E, unpublished data). No lizards were injured during the pilot experiment we conducted, so we did not consider it necessary to observe trials in order to stop them as soon as 1 male achieved dominance. We thus eliminated the influence of human observers on the lizards' behavior by videotaping trials using a Flip Video digital camera (Cisco Systems) mounted on a tripod above the trial chamber.

### Behavior scoring

We defined the behaviors to be scored based on literature descriptions of male agonistic behavior in lizards of the genus *Sceloporus* and closely related taxa such as *Uta* and *Urosaurus* (Table 4). We also used our pilot experiment to determine which of these previously documented display behaviors *S. grammicus* males would exhibit under our experimental conditions (Bastiaans E, unpublished data). All trials were scored by 1 observer (E.B.), without knowledge of the color morphs of the lizards involved (Garland et al. 1990). Because

**Table 3**  
Distribution of trials between focal and opponent male throat color scores

Population		Throat color score								
		Orange			Yellow			Blue		
CPN	Male status	0	1	2	0	1	2	0	1	2
	Focal	38	10	0	41	7	0	2	15	33
	Opponent	36	12	0	39	9	0	0	21	27
SAA		Orange			Yellow			White		
	Male status	0	1	2	0	1	2	0	1	2
	Focal	19	8	0	16	5	6	6	13	8
	Opponent	21	6	0	12	9	6	6	15	6

**Table 4**  
**Definitions and sources of behaviors scored during agonistic behavior trials.**

Behavior name	Behavior description	Sources
Push-up	Entire body moves up and down vertically due to bending and straightening of front legs (occasionally with some involvement of hind legs)	Purdue and Carpenter (1972), Carpenter (1978), Cooper and Burns (1987), Martins (1993), Smith and John-Alder (1999)
Lateral compression	Lizard compresses sides and gular region laterally, displaying belly patches and throat; may be performed alone or in combination with push-ups but was scored separately	Purdue and Carpenter (1972), Carpenter (1978); Cooper and Burns (1987), Martins (1993), Smith and John-Alder (1999), Sheldahl and Martins (2000)
Substrate taste	Lizard touches snout to sand	Bleay and Sinervo (2007)
Lick	Lizard touches opponent with snout	Bastiaans E, personal observation
Approach	Lizard moves toward opponent while looking at opponent	Cooper and Burns (1987)
Retreat	Lizard moves away from opponent, soon after some interaction between them	Garland et al. (1990)
Bite	Lizard grasps opponent's body with its teeth	Cooper and Burns (1987), Garland et al. (1990)
Lunge	Lizard vigorously hurls entire body against opponent but does not bite	Bastiaans E, personal observation
Tail wave	Tail is raised and waved vigorously back and forth	Carpenter (1978), Sheldahl and Martins (2000)
Tail vibration	Tail tip vibrates; tail is not raised	Carpenter (1978)
Touch	Lizard comes into physical contact with opponent other than licking, lunging, or biting	Bastiaans E, personal observation

the video camera was mounted above the trial chamber, the lizards' throat colors were not visible to the observer scoring the videos. Each video was viewed twice, with the observer focusing first on 1 male and then on the other. To avoid any possible influence of artificial markings on male behavior or opponent response, we did not mark the males used in behavior trials. During trial scoring, individual males were identified as "left male" or "right male," based on the acclimation chamber to which they had been assigned before the trial. The observer identified individual males during the trials based on slight variations in dorsal pattern and used the frame-by-frame function of the video viewer (QuickTime Player) to ensure that the correct male was followed after physical contact between the 2 males. We recorded the time that elapsed before each lizard's first behavior and tallied the numbers of each behavior (Table 4) performed by each lizard over the course of each 20-min trial. We tallied bouts of push-ups, tail waves, and tail vibrations rather than individual movements for 2 reasons. First, these movements are extremely rapid, making counts of individual motions logistically challenging. Second, all bouts observed consisted of multiple push-ups, tail waves, or tail vibrations; these behaviors were never observed singly. Although most behaviors were clearly discrete, the boundaries between 2 incidences of the behaviors "approach" or "retreat" and between bouts of push-ups, tail waves, and tail vibrations were sometimes less clear. We tallied these behaviors twice only if there was an obvious pause (indicated by the lizard relaxing its body posture) between the 2 incidences of the behavior.

### Data analysis

To assess the consistency of our throat color scoring method, the same individual who made the initial field scores (E.B.) used digital photographs to rescore all males in spring 2012, approximately 1 year after the lizards were captured. Rescoring was performed without reference to our original field notes. We used Cohen's Kappa coefficient (Cohen 1960) to measure the repeatability of throat scores within individual lizards, when scored in the field versus based on digital photographs.

The unit of replication for our experiment was the trial, but each trial included 2 males. To avoid pseudoreplication, we defined 1 male from each trial as the focal individual and the other male as the opponent. We chose the males initially assigned to the left side of the trial chamber as focal individuals at SAA and the males

initially assigned to the right side of the trial chamber as focal individuals at CPN. We based this assignment on which male's aggression scores (see below) showed the most nearly equal variances across throat color scores of particular interest in each population (orange at CPN, white at SAA) and thus best satisfied the assumptions of regression analyses testing for effects of these throat color scores on aggression. Because our initial assignment of males to the left and right sides of the chamber was random, the choice of a focal male should not introduce bias into our analyses. We characterized the behaviors of focal males from each population using principal components analysis (PCA) on a correlation matrix containing the number of incidences of each behavior or bout (Table 4) during a trial and the latency to (i.e., time elapsed before) each lizard's first behavior or bout (Nishikawa 1985; Carpenter 1995a; Smith and John-Alder 1999; López et al. 2005). In all cases, principal component 1 (PC1) showed positive, significant loadings (Table 5) from behaviors such as lateral compression, push-ups, lunging, and tail waving, which are associated with male aggression in closely related taxa (Garland et al. 1990; Smith and John-Alder 1999). We thus considered PC1 to be a proxy for male aggression. At both CPN and SAA, PC1 was positively correlated with male SVL (CPN:  $r^2 = 0.29$ ,  $F_{1,47} = 31.6$ ,  $P < 0.0001$ ; SAA:  $r^2 = 0.21$ ,  $F_{1,25} = 6.5$ ,  $P = 0.018$ ). This result further supports our choice of PC1 as an index of male aggression, as larger male lizards are usually more aggressive (Tokarz 1985; Carpenter 1995a). Before performing further analyses, we removed the effect of male body size on PC1 by performing linear regression of PC1 on male SVL and saving the residuals (Tsuji et al. 1989; Schulte-Hostedde et al. 2005). These residuals were our indices of male aggression for all subsequent analyses.

To assess the reliability of our behavior scoring, the same individual who originally scored the behavior trials (E.B.) rescored a randomly selected sample of 10 trials (5 from CPN and 5 from SAA). PC1 scores were calculated from these rescored trials using the loadings resulting from the analysis described above (Table 5), and we used a paired Wilcoxon signed-rank test to determine whether focal males' PC1 scores differed between the first and the second scorings of each trial.

To assess whether male throat color affected agonistic behavior, we used multiple regression to analyze the effect of a focal male's

Table 5

**Loading scores, eigenvalues, and percent variation explained by principal component 1 for behaviors exhibited during agonistic behavior trials by focal male lizards from CPN and SAA**

Behavior	PC1 loading (CPN)	PC1 loading (SAA)	PC1 loading (combined)
Time to first behavior	-0.103	-0.204	-0.275
Push-up	<b>0.786</b>	<b>0.718</b>	<b>0.724</b>
Lateral Compression	<b>0.905</b>	<b>0.907</b>	<b>0.905</b>
Substrate Taste	-0.374	-0.324	-0.251
Lick	<b>0.553</b>	<b>0.789</b>	<b>0.684</b>
Approach	0.073	0.382	0.455
Retreat	0.188	0.350	0.368
Bite	0.260	0.784	0.731
Lunge	<b>0.831</b>	<b>0.815</b>	<b>0.779</b>
Tail Wave	<b>0.608</b>	<b>0.605</b>	<b>0.651</b>
Tail Vibration	0.038	0.764	0.399
Touch	<b>0.500</b>	<b>0.907</b>	<b>0.775</b>
Eigenvalue	3.54	5.43	4.62
% Variation explained	32.2%	45.2%	38.5%

Significant scores are in bold.

Columns 1 and 2 show the results of PCAs performed separately for each population, whereas column 3 shows the results of a PCA on the combined data set.

own color and the opponent's color on focal male aggression. Because knowledge of 2 of an individual's color axis scores allows the third to be determined, we never used more than 2 color axis scores per individual in any analysis (Sinervo et al. 2001; Lancaster et al. 2007; Lancaster et al. 2010). We compared all models that included no more than 2 color scores per male and report the results of the models with the lowest Akaike Information Criterion scores for small sample sizes (AICc) (Sugiura 1978). At both CPN and SAA, pure orange males (Figures 1A and 2A) were very rare (Figures 1M and 2N). Thus, only 2 agonistic behavior trials in each population included pure orange males, and there were only 2 data points per population with values of 2 on the orange color axis. Pure yellow males (Figure 1C) were very rare at CPN (Figure 1M), and only 1 pure yellow male could be matched with another male under the body size and capture location requirements of our experimental design. Thus, only 1 data point had a value of 2 on the yellow color axis at CPN. We excluded from our analyses all trials with pure orange males from both populations, and the trial with a pure yellow male from CPN, to prevent outliers from biasing our regressions.

To determine whether males with corresponding throat colors behaved differently in the 2 populations we studied, we performed analysis of covariances (Ancovas) on a combined data set, seeking to detect interaction effects of orange score by population, yellow score by population, or blue/white score by population. We also included opponents' color scores in the model to control for their effects. We considered blue and white throat colorations to represent corresponding morphs because blue and white males never co-occur in the same population within the *S. grammicus* complex, and populations with a blue male morph always include a white female morph (Bastiaans E, unpublished data). We combined data from CPN and SAA, continuing to use the same focal individuals we had used in the separate analyses and excluding trials that involved pure orange males, as well as the trial from CPN that included a pure yellow male. As before, we characterized focal male behaviors using PCA (Table 5), regressed PC1 on male SVL ( $r^2 = 0.26$ ,  $F_{1,74} = 26.4$ ,  $P < 0.0001$ ), and saved the residuals as an index of aggression. Aggression scores were not normally distributed ( $n = 75$  trials, Shapiro–Wilk test  $W = 0.913$ ,  $P < 0.0001$ ), but we found that this deviation from normality was caused by 2 trials from SAA that were

outliers due to their very high focal male aggression scores. When these 2 trials were excluded, remaining aggression scores exhibited a normal distribution ( $n = 73$  trials, Shapiro–Wilk test  $W = 0.967$ ,  $P = 0.054$ ). We performed our analysis with and without these 2 trials included and present both sets of results for comparison.

We conducted all statistical analyses using JMP 9.0 (SAS Institute, 2010) and assessed the normality of dependent variables with goodness-of-fit tests before using parametric statistics. If necessary, variables were log-transformed to achieve normality.

## RESULTS

### Throat color morphs present in each population

At both localities, we observed 6 discrete color classes in males and females, with the 3 “pure” color classes considerably less common than the 3 “mixed” color classes (Figures 1 and 2). Male *S. grammicus* from CPN displayed varying degrees of orange, yellow, or blue coloration on their throats (Figure 1A–F), whereas females in this population displayed varying degrees of orange, yellow, or white coloration (Figure 1G–L). The orange and yellow throat color morphs were also present in both sexes at SAA, but the blue male morph was absent (Figure 2). Instead, we observed white-throated males that lacked all throat color, except for a few small blue dots (Figure 2E). However, this lack of coloration was not indicative of immaturity or an inability to produce blue coloration because white-throated males possessed the blue belly patches typical of adult males in many species of *Sceloporus* (Figure 2G), as well as other secondary sexual characteristics such as enlarged femoral pores (Wiens 2000; Stebbins 2003).

According to Cohen's kappa coefficient ( $K$ ), repeatability of individual male throat color scores between initial field scores, and scores made from photographs in spring 2012 was high for both populations (SAA:  $K = 0.86$ ,  $P < 0.0001$ ; CPN:  $K = 0.89$ ,  $P < 0.0001$ ). In no case did a lizard's photograph-based score differ by more than 1 color rank from its original field score. For example, although a small number of lizards from SAA that were scored “white-yellow” (Figure 2F) in the field were scored “pure white” (Figure 2E) based on their photographs, no lizards initially scored “pure yellow” (Figure 2C) were later scored “pure white” (Figure 2E). Initial field scores were used for subsequent analyses

because they were made immediately after capture, with the animals “in hand” and thus represent a more detailed assessment of the lizards’ coloration that avoids the potential for color change or decline in captivity (Carpenter 1995b).

After rescoreing 10 randomly selected behavior trials (5 from CPN and 5 from SAA), we recalculated the value of PC1 for each focal male, using the coefficients generated from the original PCA in each population (Table 5). We used a paired Wilcoxon signed-rank test to compare the values of PC1 obtained for each focal male during his original trial and after rescoreing the trial, and we found no significant difference between the 2 scoring sessions ( $S = -10.5$ ,  $P = 0.32$ ).

**Agonistic behavior differences between color morphs**

At CPN, focal male aggression scores were normally distributed ( $n = 48$  trials, Shapiro–Wilk test  $W = 0.98$ ,  $P = 0.58$ ). The multiple regression model with the lowest AICc score (188.5) included focal male orange score, which had a significant negative effect on focal male aggression ( $F_{1,45} = 6.3$ ,  $P = 0.016$ ) and opponent orange score, which had a nonsignificant (but also negative in direction) effect on focal male aggression ( $F_{1,45} = 1.7$ ,  $P = 0.20$ ). Qualitatively, focal males with orange axis scores of 1 tended to perform fewer aggressive behaviors than males with orange axis score of 0 (Table 6).

At SAA, focal male aggression scores were normally distributed after a  $\log_{10}$  transformation ( $n = 27$  trials, Shapiro–Wilk test  $W = 0.95$ ,  $P = 0.22$ ). The multiple regression model with the lowest AICc score (11.98) revealed a significant negative effect of focal male white score on focal male aggression ( $F_{1,24} = 7.8$ ,  $P = 0.010$ ) and a nonsignificant (but negative in direction) effect of opponent yellow score on focal male aggression ( $F_{1,24} = 2.3$ ,  $P = 0.14$ ). Qualitatively, focal males with higher white axis scores tended to perform fewer aggressive behaviors than males with lower white axis scores (Table 7). An alternative regression model including focal male yellow score and opponent male yellow score was a very slightly worse fit according to the AICc (AICc = 0.33). As expected, given the complementary nature of white and yellow scores, focal male yellow score had a positive effect on aggression ( $F_{1,24} = 7.4$ ,  $P = 0.012$ ), whereas the effect of opponent yellow score was negative in direction but not significant ( $F_{1,24} = 1.9$ ,  $P = 0.18$ ).

To compare the effects of blue and white coloration on male aggression while accounting for the effects of opponent coloration,

we performed an ANCOVA on our combined data set, with focal male aggression score as dependent variable. We tested the effects of population (CPN or SAA), focal male blue/white score, opponent yellow score, opponent orange score, and the interaction focal male blue/white score by population. The analysis revealed a significant interaction effect of focal male blue/white score by population ( $F_{1,69} = 10.2$ ,  $P = 0.0019$ ; Figure 3), indicating that the effect of blue coloration on the agonistic behavior of males from CPN differed from the effect of white coloration on the behavior of males from SAA, controlling for opponents’ color scores. None of the other effects included in this model were significant (all  $P > 0.05$ ). These results were qualitatively the same if we excluded the 2 high-aggression outlier trials from SAA.

To assess whether orange and yellow males from CPN behaved differently from males of the same color morphs at SAA, we performed 2 similar ANCOVAs, testing for interaction effects of orange score by population and yellow score by population. An ANCOVA including population, focal male orange score, opponent blue/white score, opponent yellow score, and the interaction population by focal male orange score revealed a significant negative effect of focal male orange score when the 2 outlier trials we previously identified were included ( $F_{1,69} = 4.29$ ,  $P = 0.042$ ). None of the other effects in the model were significant (all  $P > 0.05$ ). When we excluded the 2 high-aggression outlier trials from SAA, however, the negative effect of focal male orange score was no longer significant ( $F_{1,67} = 2.45$ ,  $P = 0.12$ ).

An ANCOVA including population, focal male yellow score, opponent blue/white score, opponent orange score, and the interaction population by focal male yellow score revealed no significant effects (all  $P > 0.05$ ), although the positive effect of focal male yellow score was nearly significant ( $F_{1,69} = 2.95$ ,  $P = 0.090$ ), and the interaction effect of focal male yellow score by population was also nearly significant ( $F_{1,69} = 2.91$ ,  $P = 0.092$ ). However, when we excluded the 2 high-aggression outlier trials from SAA, the 2 effects that had been nearly significant were considerably less so (focal male yellow:  $F_{1,67} = 1.93$ ,  $P = 0.17$ , focal male yellow by population:  $F_{1,67} = 1.58$ ,  $P = 0.21$ ).

**DISCUSSION**

Orange throat coloration has previously been associated with variation in aggression level in 3 species of the lizard family

**Table 6**

**Mean ( $\pm$ standard error) number of aggressive behaviors performed by lizards receiving each orange color score value at CP**

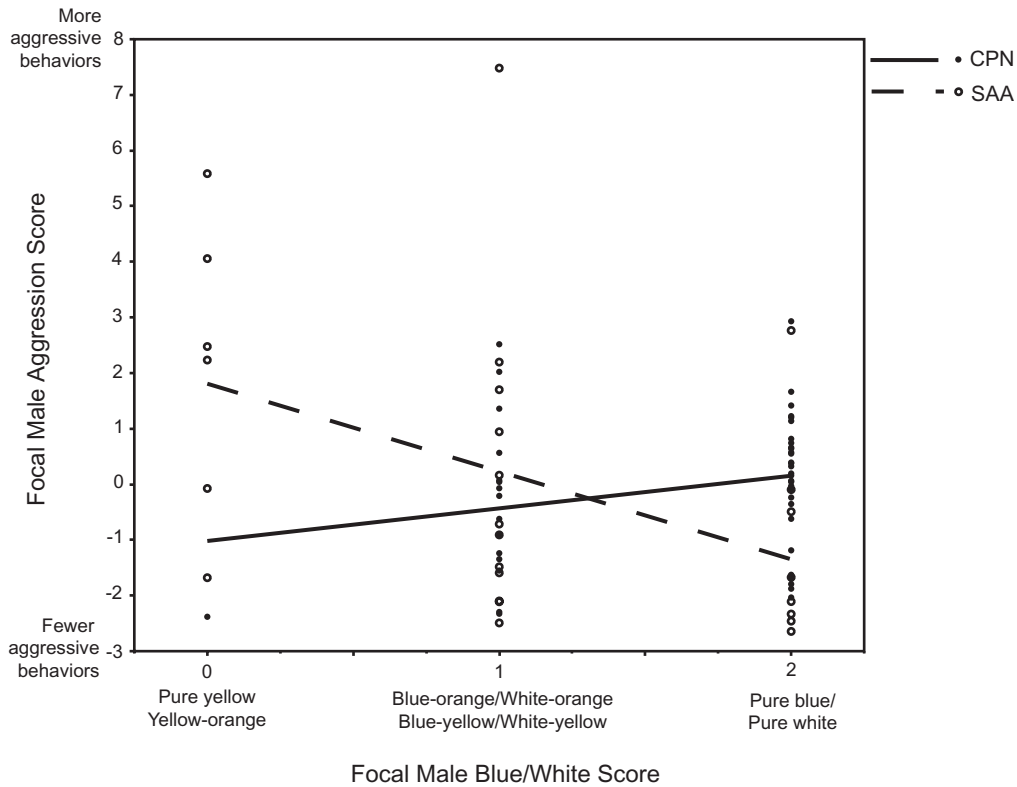
Orange color score	Push-ups	Lateral compressions	Licks	Lunges
0	5.4 $\pm$ 0.73	13.4 $\pm$ 1.4	1.5 $\pm$ 0.51	6.3 $\pm$ 1.2
1	3.2 $\pm$ 1.4	8.4 $\pm$ 2.6	0.90 $\pm$ 0.46	5.0 $\pm$ 1.7

**Table 7**

**Mean ( $\pm$ standard error) number of aggressive behaviors performed by lizards receiving each white color score value at SAA**

White color score	Push-ups	Lateral compressions	Licks	Lunges
0	9.2 $\pm$ 2.9	25.7 $\pm$ 6.1	9.2 $\pm$ 4.0	13.5 $\pm$ 3.6
1	4.7 $\pm$ 1.7	13.0 $\pm$ 3.6	6.7 $\pm$ 4.0	5.9 $\pm$ 2.7
2	5.5 $\pm$ 1.5	12.9 $\pm$ 4.5	3.4 $\pm$ 1.7	2.9 $\pm$ 2.1





**Figure 3**

Interaction plot showing the contrasting effects of blue throat color score (males from CPN, closed dots, solid line) and white throat color score (males from SAA, open dots, dashed line) on male aggression during agonistic behavior trials. Aggression scores were derived by performing a PCA on the incidences of the behaviors scored, regressing PC1 on male SVL, and saving the residuals.

Phrynosomatidae: orange males are a highly aggressive morph in *U. stansburiana* (Sinervo and Lively 1996; Sinervo et al. 2000; Sinervo 2001; Sinervo et al. 2006) and *S. consobrinus* (Rand 1988) but one of the less-aggressive morphs in populations of *U. ornatus* with multiple color morphs (Hover 1985; Thompson et al. 1993; Carpenter 1995a). At CPN, males with higher orange scores were less aggressive during agonistic encounters. Although the color variation exhibited by *S. grammicus* at CPN is phenotypically very similar to the orange/yellow/blue polymorphisms present in many populations of *U. stansburiana* (Sinervo and Lively 1996; Corl, Davis, Kuchta, and Sinervo 2010), the negative effect of orange throat score on focal male aggression at CPN suggests that the behavior of the *S. grammicus* orange morph in this population may be more similar to that of orange-throated *U. ornatus* (Hover 1985; Thompson et al. 1993; Carpenter 1995a). Of the 3 other phrynosomatid species in which similar studies have been performed, *S. grammicus* is most closely related to *S. consobrinus*, next most closely related to *U. ornatus*, and least closely related to *U. stansburiana* (Wiens et al. 2010). Surprisingly, therefore, the meaning of orange coloration appears to be most similar in pairs of species that are not sister taxa: *U. stansburiana* and *S. consobrinus*, and *U. ornatus* and *S. grammicus*. This suggests the association between color and strategy is labile over evolutionary time, even when colors themselves are conserved. However, the extremely low frequency of the pure orange phenotype (Figure 1A,M) at CPN prevented us from including these males in our analysis. Our results thus only reflect behavioral differences between yellow-orange and blue-orange males (Figure 1B,D) and other morph categories. Repeating experiments similar to those performed in this study in populations with higher frequencies of the pure orange male morph

could shed further light on the meaning of orange coloration in the *S. grammicus* complex. An additional caveat when comparing the behavior of orange-throated males of different species arises from the fact that behavioral trials were performed in the field in species where orange coloration was associated with increased aggression (Rand 1988; Sinervo and Lively 1996) but in laboratory or semi-natural enclosures in species where orange coloration was associated with decreased aggression (Hover 1985; Carpenter 1995a; this study). These methodological differences may have occurred because both *U. ornatus* and *S. grammicus* are primarily arboreal (Hall 1973; Jones and Lovich 2009), making field behavioral experiments logistically challenging. However, standardized experimental conditions would improve our ability to compare results across taxa. In general, further study of the association between agonistic behavior and orange coloration in other phrynosomatid species where similar color morphs occur would help to place the variation we have observed into a clearer phylogenetic context.

At SAA, males with more yellow throat color were more aggressive. This association of yellow coloration with increased aggression contrasts with the behavior of the phenotypically similar yellow morph in *U. stansburiana*, where yellow males are female mimics who exhibit a sneaker strategy and low aggression levels (Sinervo and Lively 1996; Zamudio and Sinervo 2000). However, yellow ventral coloration is associated with increased aggression in females of the distantly related European common lizard, *Zootoca vivipara* (Vercken and Clobert 2008a). Further investigation of the behavior of yellow-throated males in other species of the genus *Sceloporus* could help shed light on how the meaning of this signal has changed over evolutionary time.

Although similar phenotypes to the white male morph we observed at SAA (Figure 2E,G) have been reported from other sceloporines (Rand 1990; Wiens and Reeder 1997), our observations appear to represent the first time both blue and white throat color morphs have been observed within the same species. The fact that these 2 morphs do not co-occur within the same population (Bastiaans E, unpublished data) suggests that they may have replaced one another during the diversification of the *S. grammicus* complex. The observation that populations in the *S. grammicus* species complex with orange/yellow/blue variation in males (Figure 1A–F) always display orange/yellow/white variation in females (Figure 1G–L; E. Bastiaans, unpublished data) further supports the hypothesis that blue and white coloration may result from a single allele that produces different phenotypes in males and females. If throat color in the *S. grammicus* complex has a similar genetic basis to throat color in *U. stansburiana* (i.e., 1 locus with 3 alleles; Sinervo et al. 2001), it is also possible that the blue and white male morphs are produced by homologous alleles. However, further investigation of the genetic basis of throat color in populations displaying both orange/yellow/blue and orange/yellow/white male color morphs will be required to elucidate the relationship between the blue male morph and the white female morph, as well as the relationship between the blue and white male morphs.

We sought to determine whether blue-throated males from CPN and white-throated males from SAA were behaviorally similar. We found a significant statistical interaction between population and blue/white score, which confirmed that the effect of increased blue throat coloration was significantly different from the effect of increased white coloration (Figure 3). When we analyzed populations separately, males with higher white scores exhibited decreased aggression at SAA. At CPN, males with more orange coloration were less aggressive, which indicates that blue males (with their low orange scores) tended to be more aggressive. In *S. consobrinus*, both orange and yellow morphs (in both sexes) develop bright coloration in response to testosterone treatment, but the rare white male morph fails to do so (Rand 1992). This may suggest that white coloration is associated with decreased responsiveness to testosterone in *S. grammicus*, which could help explain the white male morph's decreased aggressiveness relative to the blue male morph. In addition, *Sceloporus virgatus*, a species in which males do not exhibit blue belly patches, exhibits decreased plasma testosterone levels and reduced sexual dimorphism in brain regions that respond to testosterone compared with *Sceloporus undulatus*, a species in which males do exhibit blue belly patches (Hews et al. 2012).

However, there are important differences between the white color morph in *S. grammicus* and “white” males in *S. consobrinus* or *S. virgatus*. Unlike white-throated male *S. consobrinus*, white-throated male *S. grammicus* are not rare relative to the other color morphs and do not exhibit increased melanization (Figure 2G,N; Rand 1992; Bastiaans E, unpublished data). Unlike male *S. virgatus*, white-throated male *S. grammicus* retain blue belly patches (Figure 2G). Further experimentation will, therefore, be required to understand the proximate basis of white throat coloration and the behavior of white-throated males in the *S. grammicus* species complex.

Tests for interaction effects of population by yellow score and population by orange score did not reveal significant interactions, indicating that these color morphs were similar in their behavior across the 2 populations we studied. However, combining the data sets from SAA and CPN reduced or eliminated the significant effects of yellow coloration (at SAA) and orange coloration (at CPN)

we had found when we analyzed the populations separately, even though the combined analyses had larger sample sizes. This may indicate that the colors most important in signaling male aggression level differ between the 2 populations, with yellow coloration more important at SAA and orange coloration more important at CPN.

The use of orange (or reddish), blue, and/or yellow color patches as signals during aggression or courtship is widespread among lizards. It is particularly striking that similar colors are observed across a wide range of taxa, including phrynosomatids (Cooper and Crews 1987; Rand 1990; Thompson and Moore 1991; Lemos-Espinal et al. 1996; Sinervo and Lively 1996; Wiens 2000; Weiss 2006; Martínez-Méndez et al. 2012), lacertids (Vercken et al. 2006; Huyghe et al. 2007; Sinervo et al. 2007; Pellitteri Rosa 2012), anoles (although these lizards display additional colors besides orange, blue, or yellow; Nicholson et al. 2007), agamids (Gibbons and Lillywhite 1981; Healey et al. 2007; Olsson et al. 2007; Stuart-Fox et al. 2007), tropidurids (Pinto et al. 2005), and liolaemids (Verrastro et al. 2003; Verrastro 2004; Salica and Halloy 2009). The most recent common ancestor of all these taxa likely lived at least 175 million years ago (Hedges and Vidal 2009), indicating that the use of these colors as signals either is an ancient characteristic of squamates or has arisen multiple times during their evolution (Sinervo et al. 2007). This widespread apparent convergence may suggest a physiological constraint on the colors lizards are most easily able to produce (Morrison et al. 1995; Steffen and McGraw 2009), selection imposed by similar environments on what colors are most effective for communication (Nicholson, Harmon, and Losos 2007; Feldman, et al. 2011), or a combination of these factors.

In several other taxa, males of some species display blue color patches, whereas males of closely related species exhibit white or colorless patches on the same part of the body (Rand 1990; Morrison et al. 1995; Wiens and Reeder 1997; Quinn and Hews 2000; Vercken et al. 2006; Huyghe et al. 2007; Sacchi et al. 2007). To our knowledge, however, this is the first time blue and white color patches have been reported from different populations within the same species. *S. grammicus* populations from CPN and SAA appear to be very closely related within the *S. grammicus* species complex, based on karyotype and allozyme data (Sites 1983; Sites and Greenbaum 1983). Preliminary genetic results (Bastiaans E, unpublished data) appear to confirm the close relationship between the 2 populations we studied, which suggests that changes between the 2 types of color variation (orange/yellow/blue and orange/yellow/white) can occur rapidly. In future, phylogenies of taxa exhibiting color morphs that include multiple populations of each species, in combination with data on coloration from each population, would help ascertain whether this lability of coloration is a common phenomenon and if so, under what conditions changes from 1 type of color variation to another occur.

Variation among populations in morph presence or frequency has been observed in several species of lizards known to exhibit throat color morphs. In *U. stansburiana*, the loss of 1 or more morphs is associated with rapid evolutionary changes in body size and sexual dimorphism (Corl, Davis, Kuchta, and Sinervo 2010). Variation among populations or closely related species in morph presence and/or frequency has also been observed in the phrynosomatid genus *Urosaurus* (Hews et al. 1997; Feldman et al. 2011) and several populations of *S. consobrinus* (Rand 1992). Similar variation has been recorded in the more distantly related lacertid genus *Podarcis* (Sacchi et al. 2007) and the reproductively bimodal species *Z. vivipara*, where a switch from male-limited to

female-limited polymorphism appears to be associated with a switch from oviparity to viviparity (Sinervo B, in preparation). Interpopulation variation in polymorphic state has also been observed in other color-polymorphic taxa, including several in which color morphs are associated with alternative reproductive tactics (Gray and McKinnon 2007). Most previous research into the alternative reproductive tactics associated with color morphs, however, has focused on single populations (Sinervo and Lively 1996; Vercken et al. 2006; Huyghe et al. 2007; Dijkstra, Van Dijk, et al. 2009), and studies that find variation in morph presence or frequency among populations often do not test whether the relationship between color and strategy is the same in all of them. However, 1 previous study of *U. ornatus* found that orange males were less aggressive than other morphs from the same population when blue, blue-green, green, orange-green, and orange morphs were present, but more aggressive than other morphs from the same population when only orange or orange-green morphs were present (Carpenter 1995a). These findings from *U. ornatus*, in addition to the results we report here, indicate that the behaviors associated with a particular color may vary even among populations of the same species, even though the general tendency for color variation to signal alternative reproductive tactics is taxonomically widespread (Rand 1988; Sinervo and Lively 1996; Sinervo 2001; Svensson et al. 2005; Pryke and Griffith 2006; Vercken et al. 2006; Huyghe et al. 2007; Korzan and Fernald 2007; Sinervo et al. 2007; Vercken and Clobert 2008a; Dijkstra, Van Dijk, et al. 2009; Dijkstra, Hemelrijk, et al. 2009). Variation among populations in the meaning of color signals is consistent with previous empirical and theoretical works, suggesting that behavioral traits are more evolutionarily labile than morphological traits such as coloration (Wiens 2000; Blomberg et al. 2003; Martins et al. 2004, but see de Queiroz and Wimberger 1993). When alternative reproductive tactics are found in 1 population with discretely varying sexual signals, it may, therefore, be valuable to repeat those studies in other populations of the same species, particularly those with different morphs or different numbers of morphs. Further documentation of these patterns across a greater range of species may allow us to develop hypotheses regarding the phylogenetic, environmental, and/or physiological factors that influence the association between signals and behavioral tactics.

Previous work on the *S. grammicus* species complex has focused on its karyotypic variability and the possibility that the chromosome races of which the species complex is comprised represent an example of speciation in progress (Hall 1973; Hall and Selander 1973; Sites 1983; Sites and Davis 1989; Arévalo et al. 1994; Marshall et al. 2006). Our findings may further support this possibility because both color polymorphism and alternative behavioral tactics within populations are expected to increase rates of divergence among populations (West-Eberhard 1983; West-Eberhard 1986; Corl, Davis, Kuchta, and Sinervo 2010; Corl, Davis, Kuchta, Comendant, et al. 2010; Hugall and Stuart-Fox 2012). Numerous hybrid zones are known to occur among populations of the *S. grammicus* complex (Arévalo et al. 1993; Reed et al. 1995a; Reed and Sites 1995; Sites et al. 1995; Reed et al. 1995b; Marshall and Sites 2001), and the presence of potential pre-mating isolating factors (i.e., different sexual signals) and known postzygotic isolating factors (i.e., chromosomal differences; Reed and Sites 1995) may make this taxon an excellent system for the study of how the presence of isolating factors at each of these stages influence the dynamics of gene flow among diverging populations.

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