

Social behavior and sexual dimorphism in the Bonaire whiptail, *Cnemidophorus murinus* (Squamata: Teiidae): the role of sexual selection

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Abstract: We measured body dimensions and coloration and quantified the behavior of females and males of two color phases in the Bonaire whiptail, *Cnemidophorus murinus*, to begin addressing the ultimate causation for sexual dimorphism in this species. Examination of size-adjusted body dimensions revealed that males have wider, longer, and deeper heads as well as somewhat longer forelegs and hind legs. Males were characterized by two distinct coloration patterns. Blue males displayed purple–blue dewlaps, blue–gray background coloration on the head and anterior torso, numerous light blue spots on the flanks, brown–orange coloration on the posterior torso, and a turquoise section on the proximal portion of the tail. By contrast, brown males were uniform olive–green to yellow–brown, with the exception of light blue spots on the lateral torso. Females were colored like brown males but lacked the blue spots. Testis length scaled with body size. Testes of only 26% of brown males were active, whereas all blue males had active testes. Blue males initiated aggressive encounters involving chases and displays directed toward other males much more frequently than females were aggressive with conspecifics or with either type of male. Brown males were not observed to initiate aggression. Most blue male aggression was directed toward other blue males (70.6% of encounters), whereas 29.4% of encounters were with brown males. Blue males initiated 85.7% of the courtship encounters observed compared with only 7.1% initiated by brown males and 7.2% by females. Male-biased dimorphism in head and leg dimensions as well as coloration, together with higher rates of intrasexual aggression and courtship activity by blue males, are consistent with the hypothesis that sexual selection explains the evolution of sexual dimorphism in *C. murinus*.

Résumé : Dans le cadre d'une exploration préliminaire des causes ultimes du dimorphisme sexuel chez le lézard arc-en-ciel de Bonaire, *Cnemidophorus murinus*, nous avons mesuré les dimensions du corps, déterminé les colorations et quantifié les comportements chez les femelles et les mâles des deux phases de couleur. L'analyse des dimensions corporelles corrigées d'après la taille montre que les mâles possèdent une tête plus large, plus longue et plus haute, ainsi que des pattes antérieures et postérieures un peu plus allongées. Les mâles possèdent deux types distincts de coloration. Les mâles bleus ont des fanons bleu violacé, une coloration de base gris bleu sur la tête et le tronc antérieur, de nombreux points bleu pâle sur les flancs, une coloration brun orangé sur le tronc postérieur et une bande turquoise dans la région proximale de la queue. En revanche, les mâles bruns ont une coloration uniforme brun olive à brun jaunâtre, à l'exception des points bleu pâle sur les côtés du tronc. Les femelles ont une coloration semblable à celle des mâles bruns, mais sans les points bleus. La longueur des testicules est en proportion de la taille du corps. Tous les mâles bleus, mais seulement 26 % des mâles bruns, ont des testicules actifs. Les mâles bleus provoquent des rencontres agressives comprenant des poursuites et des parades avec les autres mâles beaucoup plus fréquemment que ne le font les femelles entre elles ou avec l'un ou l'autre type de mâles. Les mâles bruns ne semblent pas provoquer d'agression. La plupart des agressions (70,6 % des rencontres) des mâles bleus sont dirigées contre d'autres mâles bleus, alors que les mâles bruns sont visés dans 29,4 % des agressions. Les mâles bleus provoquent 85,7 % des rencontres de cour; les mâles bruns sont responsables de seulement 7,1 % et les femelles de 7,2 % de ces rencontres. Le dimorphisme dans les dimensions de la tête et des pattes et dans la coloration qui favorise les mâles, ainsi que les taux plus élevés d'agression intrasexuelle et d'activité chez les mâles bleus, sont compatibles avec l'hypothèse qui veut que la sélection sexuelle explique l'évolution du dimorphisme sexuel chez *C. murinus*.

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Introduction

Intraspecific differences between the sexes in total body size, the size of particular body dimensions, and (or) coloration have captivated the interest of both theoretical and empirical evolutionary biologists for well over a century (Darwin 1871; Fisher 1930; Andersson 1994). Numerous hypotheses have been proposed to explain the evolution of sexual size dimorphism in particular (Hedrick and Temeles 1989). Dimorphism in size and color may be a product of contests between same-sex individuals, mate choice, or both. Large size or bright coloration may confer advantages to males in contests with consensual competitors over mates (e.g., Rowland 1982; Clutton-Brock et al. 1988; Howard 1988; Hews 1990), or females may show mating preferences for males with exaggerated traits (e.g., Basolo 1990; Warner and Schultz 1992; Johnson et al. 1993). Dimorphic structures associated with prey capture and feeding (e.g., jaw and head size) may also evolve owing to sexual differences in use of food resources (Selander 1966; Schoener 1967; Fitch 1982; Shine 1989; Perry 1996). In other cases, even though large size may be selected in both sexes, males may grow larger because young females allocate more of their available energy to egg production (Hedrick and Temeles 1989; Sandell 1989; Anderson and Vitt 1990). If males actively search for females to maximize reproductive success, then large male size may be selected because it reduces vulnerability to predators when searching for mates (Anderson and Vitt 1990). Apparent sexual dimorphism may also result from differences in mortality that produce disparate size-age distributions of the sexes (Dunham 1981; Anderson and Vitt 1990). Lastly, large size may be advantageous for males in some cases if it promotes the ability of males to forcibly inseminate females (Berry and Shine 1980; McKinney et al. 1983; O'Neill and Evans 1983; Birkhead et al. 1985).

Lizards have proven well suited for examining the numerous evolutionary mechanisms leading to sexual dimorphism (Stamps 1983, 1993; Anderson and Vitt 1990). Studies on lizards have provided evidence that sexual dimorphism may result from differences in food resource partitioning (Rand 1967; Roughgarden 1974; Simon and Middendorf 1976; Shoener 1977; Powell and Russell 1985) and sexual differences in energy allocation to growth (Cooper and Vitt 1989; Mouton and Van Wyk 1993; Cordes et al. 1995; Watkins 1996; Mouton et al. 1999). Both intrasexual competition and mate choice have resulted in dimorphism in size and coloration in sit-and-wait foraging lizards (Stamps 1983; Iguania; Baird et al. 1997; McCoy et al. 2003), as well as in those that use wide-foraging tactics (e.g., Scincidae, Teiidae; Vitt and Cooper 1985; Cooper and Vitt 1987, 1993; Censky 1995, 1997). The possibility that sexual dimorphism may be a consequence of sexual selection can often be evaluated in lizards by studying social behavior patterns in the field (Fox et al. 2003).

Previous studies have shown that males of the Bonaire whiptail, *Cnemidophorus murinus*, are larger than females in snout-vent length (SVL), but unlike males in many size-dimorphic lizards, males of this species mature at a smaller size but then continue to grow to a larger maximum size (Dearing and Schall 1994). Different maturation schedules and maximum size make it plausible that the sexes differ in

allocation of energy to reproduction and growth, with females being more energetically stressed perhaps owing to the high cost of egg production (Trivers 1972). However, some male *C. murinus* also show striking color differences from females, whereas the coloration of other males is only subtly different from that of females (Dearing and Schall 1994). Sexual differences in coloration are generally a consequence of sexual selection in other lizards (McCoy et al. 1997; Whiting et al. 2003; Zamudio and Sinervo 2003). Because no quantitative data have been collected on either social behavior or body dimensions other than SVL in this species, the extent to which sexual selection may be operating in *C. murinus* is unknown.

We recorded data on the sex, body dimensions, coloration, and social behavior of the endemic Bonaire whiptail as a first step toward evaluating the ultimate causation of sexual dimorphism. If sexual dimorphism is a consequence of differential food resource use and female *C. murinus* are more stressed energetically, we expected female-biased dimorphism in one or more dimensions of the head because large heads may favor acquisition of larger food items (Carothers 1984). If, on the other hand, male dimorphism in size and color is driven by sexual selection, we expected male-biased dimorphism in head and possibly other body dimensions because larger size (and disproportionately larger structures) may promote success in contests with other males (Vitt and Cooper 1985). Under the sexual selection hypothesis, we also expected that intrasexual aggression would be initiated more frequently by large, brightly colored males, these aggressive acts should be directed towards consensual competitors, and the large, brightly colored males should engage in courtship interactions more frequently than drably colored males.

Methods and materials

Morphology

To examine dimorphism in body dimensions, we collected lizards ($n = 65$ males and 35 females) at Boca Kokolishi and near Buena Vista, Bonaire, from 2 to 10 March 2001. Some lizards were collected by shooting with a pneumatic rifle (Anonymous 1987). Other specimens were trapped using sections of plastic pipe (10 cm diameter \times 60 cm long) closed at one end using duct tape, baited with cut pears, and propped up against rocks at an angle (45°–75°). All live-collected specimens were killed with Nembutal and measured immediately prior to preservation. One of us (L.J.V.) recorded the following measurements using dial calipers accurate to the nearest 0.01 mm: SVL, head length from the anterior edge of the external ear to the tip of the snout (mouth closed); head width at its widest point; head depth from the gular area (hyoid relaxed) to the top of the head on the midline; body width and body depth; at their greatest dimensions, length of the right foreleg and hind leg from the limb's insertion to the end of the longest toe; width of the base of the tail at its widest point; and length of the tail. We measured total body mass to the nearest gram using a spring scale (Pesola). Sex was determined by the presence (males) and absence (females) of spurs on the postanal scales (Dearing and Schall 1994). After measurements, we necropsied specimens to confirm sex and reproductive matu-

rity by inspection of the gonads, and we categorized the color of males (blue or brown) (*sensu* Dearing and Schall 1994). We measured the length of the left testis in males and classified them as sexually active when the testes contained enlarged convoluted epididymides and sexually inactive when the epididymides were nonconvoluted. Sacrificed specimens were later preserved and deposited in the Sam Noble Oklahoma Museum of Natural History, Norman, Okla.

Prior to analyzing morphometric data, we adjusted for variation in body size by regressing each log-transformed body dimension against log-transformed SVL and calculated residuals (Miles 1994). We then used principal component analysis (PCA) on residuals to characterize patterns of variation in size-adjusted measurements. Because we could not obtain measurements for all body dimensions on 12 lizards collected by air rifle, these individuals were eliminated from the PCA, reducing our sample size ($n = 88$). We tested for sexual dimorphism using ANOVA to compare the PCA factor scores for males and females.

On 13–14 March 2000 and 8 March 2001, we captured lizards by hand ($n = 22$ blue males, 100–130 mm SVL; $n = 6$ brown males, 95–105 mm SVL; $n = 16$ females, 79–126 mm SVL) at Boka Kokolishi and Boka Onima to describe coloration of males and females using Munsell Color Charts for Plant Tissues. Color estimates were made on living lizards in full sun when the air temperature ranged from 32 to 36 °C.

Behavior

To compare the behavior of blue and brown males and females, two of us (T.A.B. and T.D.B.) conducted focal animal studies (*sensu* Altmann 1974) between 4 and 10 March from 0900 to 1400 when substrate temperatures ranged from 30 to 38 °C, the range over which this species is emergent and active (L.J. Vitt, unpublished data). On 4 March, we recorded focal observations at Boka Kokolishi. Most of the focal observations (5–10 March) were recorded 9.4 km from Boka Onima within 1 km north and south of Shaw Wash and within 100 m of the ocean shoreline. *Cnemidophorus murinus* occurred in large numbers throughout these habitats. Walking two visual transects (350 m \times 10 m) indicated that the density of *C. murinus* ranged from 0.14 to 0.66 lizards/10 m² at Boka Onima. At both sites, we observed lizards occupying fossil coral “rocks” (0.25–5 m in diameter) and sand substrata with little vegetation (Cooper et al. 2003), allowing continuous viewing of focal subjects. Because female and male *C. murinus* become reproductively mature at 85 and 80 mm SVL, respectively (Dearing and Schall 1994), we opportunistically chose subjects that we estimated to be at least 90 mm SVL for observation by walking slowly through the habitat searching with binoculars for perched lizards. When we sighted a subject, we positioned ourselves at a good vantage point (10–30 m away) and began recording behavior patterns by speaking into a tape recorder while viewing the lizard through binoculars. We attempted to observe focal lizards for 5 min, but some sessions were shortened when subjects retreated beneath vegetation where we could no longer observe their behavior. We restricted quantitative analysis of behavioral frequencies to focal observations that were at least 1 min long. The durations of focals on blue males (4.5 ± 0.15 min (mean \pm

1.0 SE)), brown males (4.4 ± 0.33 min), and females (4.0 ± 0.17 min) were not different (one-way AVOVA, $F_{[2,167]} = 2.30$, $P = 0.104$). Altogether, we recorded 334 min of focal observations on blue males, 98 min on brown males, and 262 min on females. We took three precautions to minimize the possibility of recording repeated observations on the same subjects. After each focal observation, we located a subject on a different perch, the two observers worked in different parts of the study area, and on each day, we moved to a different portion of the study site.

The sex of focal subjects was determined based on observation through binoculars of color patterns. Blue males are distinct because they have conspicuous blue coloration on the head, dorsal body, and tail (Dearing and Schall 1994; this study). Brown males appeared similar to females, but lizards of the size that we chose for focal observations (≥ 90 mm) could be distinguished by the presence of light blue spots on the sides of the torso, neck, and anterior surface of the hind legs (Dearing and Schall 1994). Some brown males also had slight blue coloration on the top of the head, but they lacked the fully developed body and tail coloration of blue males. Brown lizards that lacked the light blue spots of brown males were classified as females. We recorded focal observations on 77 blue males, 23 brown males, and 69 females. During focal observations, we recorded when lizards were traveling or stationary for at least 1 s to determine percent time moving and the number of starts as general indices of activity. We recorded bouts of feeding (biting on vegetation or strikes on insects). We also recorded the frequency with which lizards circumducted their forelegs (*sensu* Carpenter and Ferguson 1977). Circumduction involved lifting either forelimb (one at a time) and flexing the distal forelimb downward in a circular motion once or several times (see below).

To quantitatively compare the behavior of the three classes of lizards, we recorded when focal individuals initiated intra- and inter-sexual encounters with conspecifics as well as the serial behavioral acts during these encounters. We recorded an aggressive intrasexual social encounter when the focal lizard initiated a directed approach to within 1 m of a conspecific (usually to within one body length) and performed multiple acts including various displays, biting, and (or) chasing (described below) the recipient lizard. Recipients responded with return displays, chases, or by fleeing. Therefore, aggressive intrasexual encounters (and similarly intersexual encounters, see Results) involved an exchange of numerous behaviors. Although we also recorded the behaviors received by focal subjects, because sexual selection theory predicts that the sexes and different classes of males should differ in the extent to which they initiate aggression, we analyzed the aggressive behavior initiated by focal subjects.

Because the duration of focal observations varied, we converted the number of encounters and individual acts within encounters to frequencies per minute by dividing the total number of behaviors by the total observation time for that individual. When variances were homogeneous, we used parametric one-way ANOVA to compare the frequencies of behavior among the two types of males and females. When variances were heterogeneous, we computed one-way Kruskal–Wallis ANOVA on ranked data. We used Tukey’s

Table 1. Factor scores from the first three principal components on log-transformed, size-adjusted morphological variables in *Cnemidophorus murinus*.

Variable	Factor I	Factor II	Factor III
Mass	<0.001	0.099	0.146
Head width	0.741	-0.021	-0.030
Head length	0.680	-0.051	0.037
Head depth	0.626	-0.144	0.007
Body width	<0.001	0.078	0.931
Body depth	-0.308	0.616	0.526
Hind-leg length	0.518	0.491	-0.283
Foreleg length	0.482	0.385	-0.055
Tail width	0.080	-0.120	-0.046
Eigenvalues	4.183	1.471	0.792
% of variation	46.5	16.3	8.8

Note: High loading variables are in boldface type.

tests to compare means. All data for these and analyses below are presented as means \pm 1.0 SE.

Results

Morphometry

SVL of all males pooled (107.6 ± 3.5 mm, range 55–147 mm) was larger ($U_{[66,34]} = 1539$, $P = 0.005$) than that of females (94.0 ± 2.56 mm, range 60–123 mm), and the SVL of blue males (130.9 ± 1.30 mm, range 120–147 mm) was larger ($U_{[33,31]} = 999.0$, $P < 0.0001$) than that of brown males (83.5 ± 3.6 mm, range 55–130 mm). Four PCA axes accounted for 78.3% of size-adjusted morphological variation in body dimensions (Table 1). The first axis (46.5%) described a gradient based on relative head width, length, and depth, and relative hind-leg and foreleg lengths (for non-size-adjusted dimensions see Table 2). The second axis (16.3%) described a gradient based primarily on relative body depth. The third axis (8.8%) described a gradient primarily in body width, whereas the fourth axis was a gradient in tail width and body mass (Table 1). Size-adjusted relative head dimensions and limb lengths (PCA factor I) were significantly different ($F_{[1,87]} = 8.806$, $P < 0.039$) between the sexes (Fig. 1). However, ANCOVA's with log SVL as the covariate and sex as the class variable revealed that all three head dimensions differed by sex ($F_{[1,87]} = 4.94$ – 5.41 , $P = 0.022$ – 0.029), whereas length of the forelegs and hind legs did not ($F_{[1,87]} = 0.674$ and 0.394 , $P = 0.414$ and 0.565). Therefore, most of the variation in the first PCA factor results from sexual differences in head size. Although considerable variation was evident in relative body depth (PCA factor II), no significant differences between the sexes were apparent ($F_{[1,87]} = 0.297$, $P = 0.5870$).

Testis length was positively correlated ($r^2 = 0.82$, $P < 0.0001$) with male SVL (Fig. 2). All blue males had mature testes with convoluted epididymides, whereas only 9 of 35 (25.7%) brown males were mature. Testes of mature blue males were not longer ($F_{[1,33]} = 0.13$, $P = 0.72$) than those of mature brown males after controlling for effects of SVL (Fig. 2).

Table 2. Mean (range) non-size-adjusted body dimensions in male and female *C. murinus*.

Body dimension (mm)	Male	Female
Head length	22.6 (12.0–29.4)	19.3 (13.4–24.6)
Head width	14.9 (8.4–22.9)	12.2 (8.2–16.8)
Head depth	12.4 (6.9–20.7)	10.3 (7.0–13.4)
Hind-leg length	75.6 (41.5–103.5)	66.4 (46.1–87.6)
Foreleg length	38.8 (11.4–54.7)	33.3 (22.0–45.8)

Coloration

All lizards regardless of gender and other coloration had bright turquoise (Munsell hues = 2.5–7.5 green, values = 5–7, chromas = 2–6) patches on the dorsal surface of each pes. Both females and brown males had a similar olive-green to brown-yellow coloration (hues = 2.5–5 yellow, 7.5 green-yellow, 7.5 yellow-red) on the dorsal surfaces of the torso, limbs, and head (values and chromas = 2–5). Although we did not make measurements, the ventral surfaces were similar hues but lighter. Brown males had spots on the sides of the torso and upper forelimbs and hind limbs that were similar in color to those of blue males (see below) but appeared less intense. Females lacked these spots. Both brown males and females lacked the blue tail coloration present in blue males (see below).

The coloration of blue males was strikingly more complex. The top of the head and the anterior one third of the torso and upper forelimbs were dark blue-gray (hue = 2.5 blue, values = 3–8, chromas = 2–6). The dewlap was dark blue-purple (hues = 2.5 blue or 5 red-purple, values = 5–7, chroma = 2). Posterior to the pectoral girdle, the blue color graded into brown-orange (hues = 2.5–5 yellow, values = 4–5, chromas = 2) covering the posterior and ventral torso, the hind legs, and the proximal tail. Several prominent light blue spots (hue = 2.5 blue, values = 7–8, chromas = 2–4) were scattered on the sides of the head, torso, and upper forelimbs and hind limbs. One to 2 cm posterior to the tail base, alternating rows of scales that ringed the tail were the same bright turquoise blue as the patches on the pes (see above). More distal on the tail, each row of scales was pigmented, resulting in a section (2–5 cm long) of the tail that was bright turquoise. Posterior to the end of the turquoise pigments, the tail was the color of the posterior torso.

General behavior

We usually sighted observation subjects while lizards were perched on elevated rocks in full sun. Whiptails were frequently observed to burrow under coral rocks, and most of the rocks at Boka Onima had one or more tunnel entrances leading beneath them. Tracks on the sand outside burrow entrances suggested that lizards moved in and out of them frequently. Lifting rocks in the morning prior to lizard emergence revealed that tunnels led into shallow (5–15 cm depth) chambers that were occupied by whiptails at night. Entrances to three burrows had dried carcasses of *C. murinus*.

Neither percent time traveling ($r^2 = 0.007$, $P = 0.286$) nor frequency of starts ($r^2 = 0.006$, $P = 0.32$) was correlated with substrate temperature over the range that we recorded behavioral data. Percent time traveling did not differ among

Fig. 1. Principal component analysis scores for factor I versus factor II in male and female *Cnemidophorus murinus*. Factor I scores for males (-0.597 ± 0.236 (mean ± 1.0 SE)) were significantly different ($F_{[1,87]} = 8.806$, $P = 0.039$) from those for females (0.234 ± 0.149).

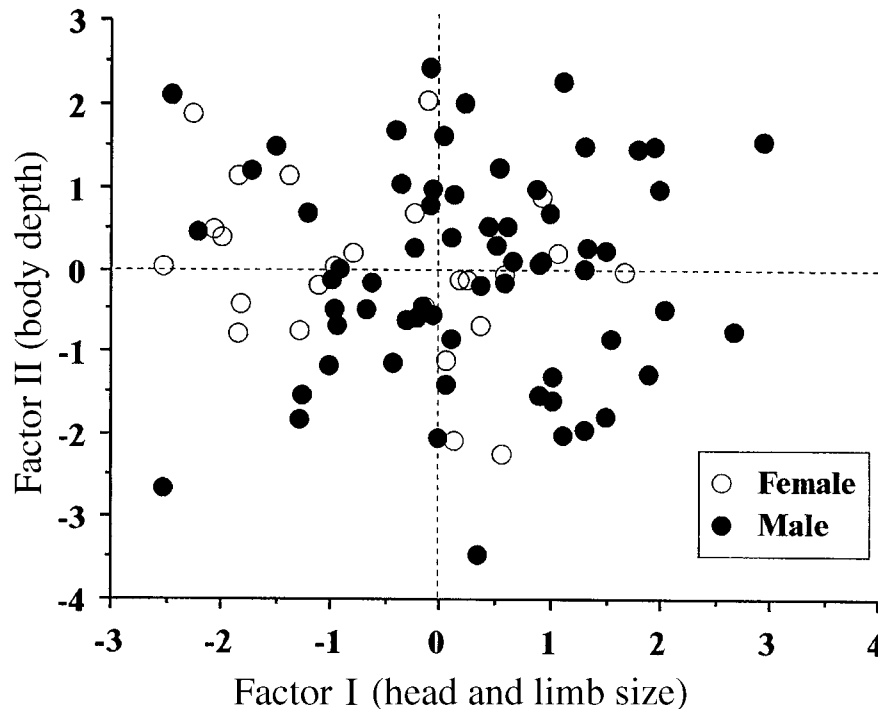
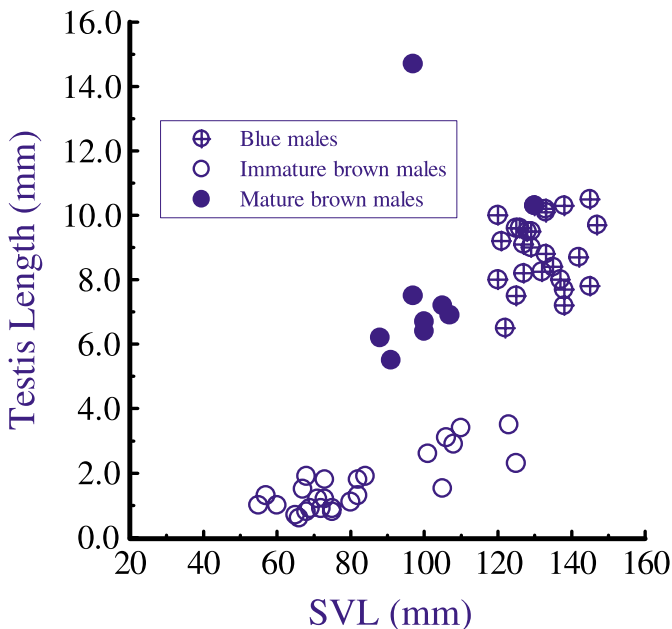


Fig. 2. Testis length versus snout–vent length (SVL) in blue and immature and mature brown male *C. murinus*.



the three classes of lizards (one-way ANOVA, $F_{[2,167]} = 0.59$, $P = 0.56$) (Table 3). The frequency of starts differed (one-way ANOVA, $F_{[2,167]} = 4.65$, $P = 0.011$) by lizard class, with the frequency being higher in females than in brown males (Tukey's test, $P < 0.05$), but was similar in the two types of males and in blue males and females (Table 3). We observed feeding only infrequently (Table 3). Although, on average, females fed more than twice as often as either blue or brown males, frequencies were not different statisti-

cally owing to high variation (one-way ANOVA on ranks, $F_{[2,167]} = 2.30$, $P = 0.10$).

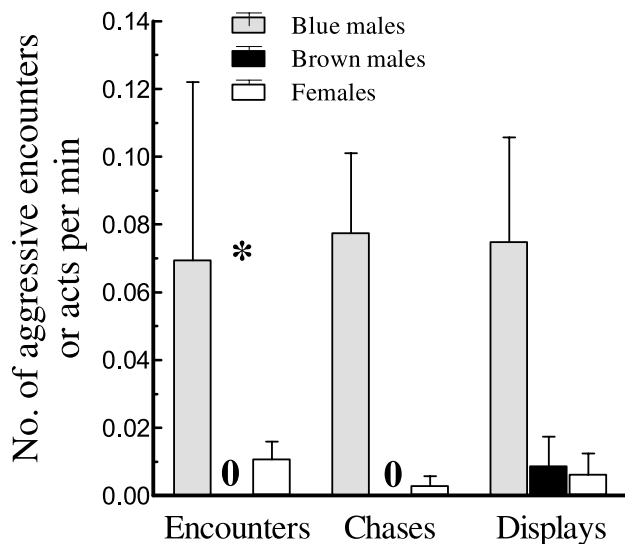
Lizards circumducted their forelimbs either when they had been stationary or during brief pauses (1–5 s) while traveling. The frequency of total (either forelimb) circumductions differed by social class (one-way ANOVA on ranks, $F_{[2,167]} = 4.48$, $P = 0.013$), with the mean frequency in females being higher (Tukey's test, $P < 0.05$) than that of blue males but similar in the two types of males and in brown males and females (Table 3).

Social behavior

The frequency with which whiptails initiated intrasexual aggressive encounters differed by sex and color class (one-way ANOVA, $F_{[2,167]} = 5.33$, $P = 0.0057$) (Fig. 3). In 262 min of total observation, we observed only three aggressive encounters between females, and it was common for two to four females to perch within one body length of one another without exhibiting aggression. By contrast, in 334 min of total observation, blue males initiated a total of 17 aggressive encounters with conspecifics, with the average frequency of aggressive encounters by blue males being 6.5 times higher (Tukey's test, $P < 0.05$) than that initiated by females. Brown males were not observed (98 min of observation) to initiate aggressive encounters with either blue or brown conspecifics. Frequencies of chases and displays (described below) also differed by social class (one-way ANOVA on ranks; chases, $F_{[2,167]} = 7.48$, $P = 0.0008$; displays, $F_{[2,167]} = 3.56$, $P = 0.037$) with patterns similar to that of encounters (Fig. 3). Mean frequencies of displays and chases in the three lizard classes did not differ statistically owing to large variances. However, on average, blue males performed displays 8.6 and 12.0 times more frequently than did brown males and females, respectively, and blue males

Table 3. Mean (± 1.0 SE) measures of activity and foraging in three classes of *C. murinus*.

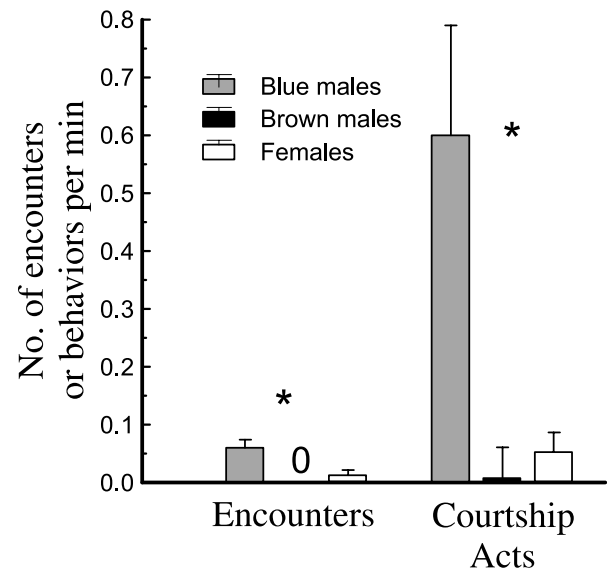
Lizard class	% time traveling	Starts/min	Feeding bouts/min	Circumductions/min
Blue male ($n = 77$)	15.66 (1.97)	1.19 (0.13)	0.05 (0.03)	0.43 (0.11)
Brown male ($n = 23$)	14.57 (3.68)	0.79 (0.21)*	0.04 (0.04)	0.90 (0.49)
Female ($n = 69$)	18.40 (2.31)	1.59 (0.19)	0.12 (0.05)	1.75 (0.43) [†]

*Significant differences ($P < 0.05$) between adjacent classes.[†]Significant differences ($P < 0.05$) between females and blue males.**Fig. 3.** Mean (± 1.0 SE) frequencies of intrasexual aggressive encounters and the chases and displays within these encounters initiated by blue and brown male and female *C. murinus*. The asterisk indicates pairwise statistical differences ($P < 0.05$) in aggressive encounter frequencies between blue males and both brown males and females.

chased conspecifics more than 26 times more frequently than did females. Brown males did not chase conspecifics (Fig. 3).

Of the intrasexual encounters initiated by blue males, 70.6% (12 of 17) were with other blue males, whereas 29.4% (5 of 17) were with brown males. In six encounters with other blue males, the recipient quickly moved away or fled, causing the aggressor to chase him usually for 2–15 m. In one exceptional chase, a blue male sprinted 30 m toward an opponent, running the first 10 m bipedally. In the other six encounters, when blue males neared their opponents, the aggressor lowered his snout while arching (dorsally) his neck and pectoral girdle, compressing his torso laterally for 5–15 s while holding his tail on the ground. Aggressor males and opponents also displayed by extending their dewlaps one or more times while they were near (within 1 m) one another, bobbing their heads and pectoral girdles in a dorsoventrally oriented S-shaped undulating motion while moving slowly forward. In two such encounters, the aggressor male bit its opponent. During two other intrasexual encounters, aggressor males flattened their bodies to the substratum and turned in a circle that was approximately one body length in diameter. These males turned four to six times, first in one direction and then in the opposite direction.

Intersexual encounters usually involved males approaching females to within one body length and making physical

Fig. 4. Mean (± 1.0 SE) frequencies of intersexual encounters and courtship acts within these encounters initiated by blue or brown male and by female *C. murinus*. The asterisks indicate pairwise statistical differences ($P < 0.05$) in the frequency of intersexual encounters initiated by blue and both brown males and females.

contact while performing displays (see below). Of the 28 intersexual encounters observed, 24 (85.7%) were initiated by blue males. Two encounters were initiated by females (one each with a blue and a brown male), and brown males initiated two encounters with females. The frequency of intersexual encounters initiated varied statistically by sex and color class ($F_{2,167} = 5.87$, $P = 0.003$), with blue males initiating encounters over four times more frequently (Tukey's test, $P < 0.05$) than either females or brown males (Fig. 4). We did not observe any encounters initiated by blue or brown males that appeared to involve copulation.

Similar to intrasexual encounters, blue males approached females while lowering the snout, arching the back and pectoral girdle while laterally compressing the torso, and holding the tail on the ground. While holding this posture as they moved toward the female, blue males displayed by bobbing the head and shoulders in a dorsoventral undulating pattern and by holding their dewlaps stiffly in an extended position. Encounters between blue males and females often involved the two lizards sitting facing the same direction with heads and (or) bodies touching. In other cases, the two perched with the limbs, tail, or torso of either lizard superimposed over the partner or the lizards sitting motionless facing one another with only the tips of the snouts touching. The frequency with which these courtship acts were initiated varied

by sex and color class (Kruskal–Wallis ANOVA, $F_{[2,167]} = 7.49$, $P = 0.0008$), with blue males initiating more courtship acts (Tukey's test, $P < 0.05$) than brown males and females (Fig. 4).

Discussion

Our data show that not only are *C. murinus* males dimorphic in coloration (similarly see Dearing and Schall 1994) but that males have relatively larger heads than females. Blue males had larger SVL than brown males, and all blue males were reproductively active compared with about 26% of brown males. All three classes of lizards spent similar amounts of time traveling, and the number of starts was similar in blue and brown males. Blue males were far more aggressive toward conspecifics than either brown males or females, and blue males exhibited much higher rates of courtship than did brown males.

We saw no indication that circumduction of forelimbs had a social function in *C. murinus*, even though this behavior is reportedly used during aggressive contests in some lizards (Carpenter et al. 1970; Brattstrom 1971; Carpenter and Ferguson 1977). Females circumducted their forelimbs more frequently than either type of male, yet females had the lowest rates of aggression, and there was no obvious relationship between circumduction and either the proximity or the activity of conspecifics.

Although we did not quantify the diets of male and female *C. murinus*, it seems unlikely that feeding niche separation explains the evolution of dimorphism in head dimensions because this species is a generalist herbivore (Cooper et al. 2002), taking small (<1 cm) flowers, leaves, and berries from a wide variety of plants (Dearing and Schall 1992, 1994). Size is probably not a significant factor limiting which foods can be eaten by males and females because all three of the mean head dimensions of males and females were larger than the food items found in the stomachs of *C. murinus*, and lizards favored tender leaves and flowers, both of which could probably be torn and eaten by animals with smaller heads (Dearing and Schall 1992). The herbivorous diet of *C. murinus*, however, may limit its reproduction, particularly at the Boka Onima site where Dearing and Schall (1992, 1994) found that the energy content of foods was low. Male *C. murinus* mature at a smaller size than do females, but female growth slows when they begin producing eggs (Dearing and Schall 1994). The higher energetic cost of egg production, therefore, may curtail growth in female SVL, head, and limb size, especially if food is scarce, whereas males may be able to continue growing at higher rates following maturity. Such an explanation alone, however, does not account for our finding of size-adjusted sexual differences in head and limb dimensions among smaller males and females.

Taken together, our observations are most consistent with the hypothesis that sexual dimorphism in *C. murinus* is under sexual selection. Because other teiids, including two congeners (*Cnemidophorus ocellifer* and *Cnemidophorus lemniscatus*), also show male dimorphism in SVL, head size, and leg length (L.J. Vitt, unpublished data), similar dimorphism in *C. murinus* may be pleisiomorphic. On the other

hand, dimorphism in these characters may also be maintained by current selection because large total size, larger heads, and long limbs appear to promote success in intrasexual contests over mates in this family (Anderson and Vitt 1990; Vitt et al. 1993; Censky 1995) as well as in other lizards (Vitt and Cooper 1985; Hews 1990; McCoy et al. 1994; Hasegawa 2003). The degree of male sexual dimorphism among related species is expected to be directly related to the intensity of intrasexual male competition (Alexander et al. 1979), and the potential for polygyny should be higher in larger species (Reiss 1989). Among teiids (22 *Cnemidophorus* spp. and 5 *Ameiva* spp.), the degree of sexual dimorphism shows a strong positive correlation with body size (Fig. 4 in Anderson and Vitt 1990). *Cnemidophorus murinus* falls above this regression line (within the upper 95% confidence interval), with the mean size of Bonaire whiptails being larger than that of all but two species of *Cnemidophorus* and *Ameiva ameiva* (Anderson and Vitt 1990), suggesting that male–male competition may be relatively intense in this species.

Few data are available on rates of aggression in other teiids with which to compare those on *C. murinus*. In *Ameiva plei*, males are aggressive when guarding mates (Censky 1995), but we saw no indication of mate guarding in *C. murinus*. In *Cnemidophorus deppi*, only 3% of lizards on transects were involved in social interactions (Vitt et al. 1993), and *Ameiva exul* displaced conspecifics less than once per hour (Lewis and Saliva 1987). Extrapolation from data on *Cnemidophorus sexlineatus* observed in enclosures suggests rates of social encounters that varied from 0.05 to 1.23/h (Carpenter 1960), but since the gender of individuals was not known in this study, aggressive encounters could have been initiated by either males or females. By comparison, on average, blue male *C. murinus* initiated aggression with other males approximately four times per hour. These data are consistent with the hypothesis that intrasexual male aggression is relatively frequent in *C. murinus*, although many other factors such as variation in the timing of observations and population densities across studies on these different teiids make this interpretation tentative.

Because Bonaire whiptails occur at extremely high densities, frequent aggression by blue males may simply be a consequence of increased contact with conspecifics. Female *C. murinus* reproduce all year, but low-energy intake limits reproductive rate such that relatively few females are receptive at any particular time (Dearing and Schall 1994). Another possibility, therefore, is that frequent aggression and size attributes that promote success in contests may be favored if these increase male access to females that are receptive. Owing to the high lizard densities and open habitats on Bonaire (Cooper et al. 2002, 2003), *C. murinus* females should have ample opportunity to assess multiple potential male mates, and females prefer to consort with large males in some teiids (Censky 1997) and other lizards (Vitt and Cooper 1985). Although bright coloration sometimes promotes success in male–male contests (Baird et al. 1997), brightness is most usually associated with female preferences for mates (Andersson 1994), including some lizards (Baird et al. 1997). Therefore, both increased success in contests over mates by large-headed brightly colored males and

female preference for such males remain viable hypotheses to explain the evolution of sexual dimorphism in *C. murinus*.

The pattern of reproductive maturity in relation to SVL and coloration suggests that male reproductive tactics may change ontogenetically. Nine of 33 brown males (88–130 mm SVL) had mature testes. Testes of eight mature brown males fell into a relatively narrow size range (5.5–7.5 mm), but two had testes that were among the largest that we measured. By contrast, two brown males were immature, even though they were as large as blue males (Fig. 2). Long-term recapture of marked males revealed that brown males sometimes transform into blue males (Dearing and Schall 1994), prompting these authors to suggest that males in the two color morphs use alternative mating tactics. Because some brown males are mature, one possibility is that retention of female-like coloration promotes avoidance of aggression from blue males and allows brown males to sneak mating opportunities (Dearing and Schall 1994). We observed brown males to initiate only two intersexual encounters, however, even though they were near numerous females during focal observations. These observations may suggest that males postpone reproductive effort and development of blue coloration until they enter a social setting in which they are large enough and (or) there are enough mature females that they can compete effectively for matings (Zamudio and Sinervo 2003). Under this hypothesis, brown males with mature testes might be in the process of gonadal maturation prior to color change. Testis and body sizes in most brown males smaller than those of blue males are consistent with this hypothesis, but not exclusively so. The presence of two immature brown males larger than 120 mm SVL and the presence of two other brown males with relatively large testes suggest a third possible reproductive pattern. If food availability on Bonaire is limited, as suggested by Dearing and Schall (1992, 1994), energy intake may be insufficient to sustain the high rate of social activity characteristic of blue males. Under this hypothesis, as an energy-saving strategy, mature males may cycle between the blue and brown morphs with a correlated enlargement and recrudescence of their testes. Although our observations strongly suggest that sexual selection plays an important role in the behavior and morphology of *C. murinus*, the reproductive life history of this species clearly merits further study to examine these and other hypotheses.

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