Atypical Reproduction and Sexual Dimorphism of the Tropical Bonaire Island Whiptail Lizard, Cnemidophorus murinus

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III.   Characters not considered by Taylor (1968).

12. *Mesethmoid exposure.*—The mesethmoid may be covered dorsally by the frontal bones (0) or exposed between the separated frontal bones (1).

13. *Length of the premaxillary-maxillary tooth row.*—The premaxillary-maxillary tooth row may extend posteriorly to the same extent as the palatine tooth row (0); it may end 1–2 tooth positions anterior of the terminus of the palatine series (1); or it may end more than two tooth positions before the palatine series (2).

14. *Number of cusps on the premaxillary-maxillary teeth.*—These teeth may be bicuspid (0) or monocuspid (1).

15. *Number of cusps on the (pre)vomeropalatine teeth.*—These teeth may be bicuspid (0) or monocuspid (1).

16. *Choanal valves.*—The choanae may have valves near the opening into the mouth chamber (0) or not (1).

17. *Pigmentation.*—The body of adults may be nearly uniformly covered with dark pigment (0), with dark pigmentation restricted dorso-laterally (1), with a narrow dorsal band of dark pigment (2), or with no or very few melanophores resulting in a nearly uniform pinkish coloration (3).

Atypical Reproduction and Sexual Dimorphism of the Tropical Bonaire Island Whiptail Lizard, *Cnemidophorus murinus*

M. DENISE DEARING AND JOS. J. SCHALL

We investigated reproduction, sexual dimorphism in color, and sexual dimorphism in body size of *Cnemidophorus murinus*, the endemic whiptail lizard of Bonaire, Netherlands Antilles, during a year-long study and two later recapture periods. Growth rate declines as *C. murinus* increases in size. Males reach reproductive maturity at smaller snout-vent lengths (SVL) than do females (73 vs 85 mm) but continue to grow to larger final SVL (151 vs 116 mm maximum SVL). Bonaire whiptails can live at least four years. Reproduction was aseasonal; enlarged ovarian follicles and/or oviductal eggs in females and enlarged testes in males were observed in every month with no peak period of reproduction. Fat body growth, however, was strongly seasonal, and fat body mass was greatest in the months immediately after the rainy season. Amount of fat stored differed among three sites, and females stored more fat than males. Clutch size is typically one very large egg, but some females may produce two eggs. Although clutch mass/body mass ratio is typical for the genus, egg mass/body mass is greatest for any *Cnemidophorus* or *Ameiva* known and among the highest for any lizard ($x = 0.126$). Dorsal color is sexually dimorphic; females are brown, and juvenile males are also brown, changing to bright blue as they grow. However, many males never reach the brightest color morph and may retain the juvenile color form for years. Several features of the biology of *C. murinus* are unusual for the genus and for lizards in general (size at reproductive maturity, small clutch size, large relative egg mass, color variation in males).

THE natural history of some insular Caribbean species of whiptail lizards (*Cnemidophorus*: Teiidae) seems exceptional for the genus. They are herbivorous, deviating from their mainland, arthropod-eating congeners (Schall and Ressel, 1991; Dearing and Schall, 1992), and they are relatively small for herbivorous lizards (Pough, 1973). Insular populations are extremely dense compared to mainland whiptail populations, and biomass estimates are among the highest for any lizard (Schall, 1974; Bennett and Gorman, 1979). Their reproductive biology also appears peculiar: they produce typically only one exceptionally large egg per clutch (Schall, 1983; J. Wright, pers. comm.). Adult males are polymorphic in color, some displaying extravagant bright colors, but others retain juvenile colors (Schall, 1986).

We present here a study on the biology of one of these unusual species, the Bonaire island whiptail lizard, *Cnemidophorus murinus*, a species that occurs only on the Caribbean islands of Bonaire and Curaçao (Wright, 1993). Our data include body size at maturity, growth of marked animals over a four-year period, clutch size, egg size, fat storage over a year's time, testis size over the year, sexual dimorphism in color pattern, and changes in color of individuals over

time. Our goal was to determine how this species differs from congeners and lizards in general and to suggest possible explanations for these differences.

METHODS

The study was conducted on Bonaire, Netherlands Antilles. The island is tropical; mean daily temperature varied little over the year (x = 27.4 C, SD = 0.5; Netherlands Antilles Weather Service data). Rainfall, however, is strongly seasonal and highly variable among years (Fig. 1). The dry season when less than 4 cm of rain falls each month extends from Feb. to Aug. Three sites were chosen that differed in substrate and plant species composition: Karpata, Playa Frans, and Onima. Preferred foods for the lizards were most abundant at Karpata and least abundant at Onima. For a detailed description of the sites, see Dearing and Schall (1992). Except for the analysis of fat stored, data were combined for the three sites. This decision was based on a lack of three-way interaction for each sex between sites, two-month collecting intervals, and variable under study (log-linear analyses, $P > 0.05$).

Cnemidophorus murinus were shot with a .22 cal. airgun. Thirty specimens, 10 from each site, were collected every 10 days from late Aug. 1986 to mid-Aug. 1987. Permission to collect was granted by the appropriate governmental authorities. A sample of all morphological types of *C. murinus* was obtained by collecting animals without preference to size, color, or sex. Recorded were sex, snout-to-vent length to nearest mm (SVL), body mass to nearest 0.1 g, mass of both testes and inguinal fat body mass to nearest 0.001 g, dorsal color pattern, egg number and mass to nearest 0.1 g, and number and diameter of yellow, enlarged (containing yolk and >3 mm diameter) ovarian follicles.

Dorsal color in these animals is dimorphic; females are brown, but males vary from brown to bright blue. We, therefore, classified males into three dorsal color classes: (1) all brown = overall brown body, either with or without tan stripes, with greenish blue on the dorsal area of the feet; (2) blue spots = mostly brown but with pronounced blue spots on the sides; (3) all blue = overall blue dorsal color with greatest intensity on head, neck, and tail and blue spots on the sides.

Females were classified as reproductive adults if they had enlarged (>3 mm) yolking follicles in the ovaries (visible as yellow spheres) or oviductal eggs. Females were then considered adults
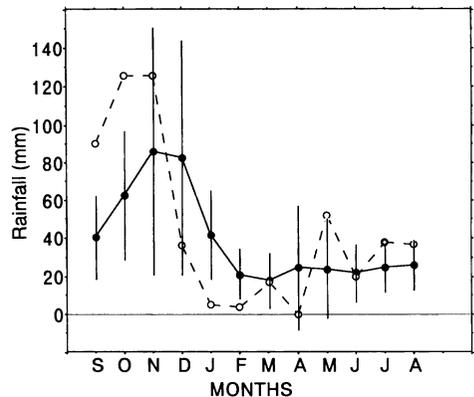

Fig. 1. Seasonal rainfall on the island of Bonaire, Netherlands Antilles. Closed circles are 20-year means with vertical lines representing one SD. Open circles represent rainfall during the study period.

if they were as large or larger (based on SVL) than the smallest reproductive female. Male lizards were considered reproductive if their testis mass was greater than 0.04 g. This cut-off point was based on Schrank and Ballinger (1973) who demonstrated that *C. gularis* with testes smaller than 0.04 g did not produce sperm. Relative clutch mass (RCM) was calculated as mass of a fully developed clutch (shelled eggs)/total mass of a female with her clutch. Relative egg mass was calculated as RCM/clutch size.

At Onima, lizards also were captured alive in wire traps, then sexed, SVL measured, color noted on males, and uniquely marked by clipping one toe per foot. Recaptures were made during the year-long study, then during three additional periods: three months later, one year later, and in Jan. 1991 (3–4.3 years after animals were marked). Sex of animals marked and released was determined by presence of postanal spurs (enlarged pointed scales) in males. This trait was 100% reliable when compared with sex determined by dissection of over 1000 animals.

RESULTS

Body size and growth rate.—Males appear to reach reproductive maturity at a smaller body size than do females but continue to grow to a larger final SVL (maximum SVL for males was 151 mm and for females 116 mm). Reproductive animals appeared in our sample in substantial numbers at 80 mm SVL for males and 85 mm for females, and the smallest reproductive male was 73 mm compared to 85 mm for the smallest reproductive female. No collected female was >116 mm SVL, and only 21% were >100 mm. In contrast,
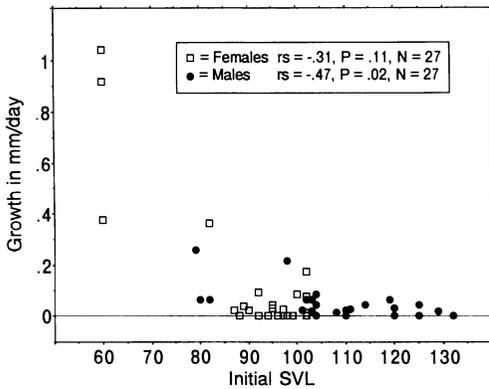
Fig. 2. Growth rate of *Cnemidophorus murinus* at the Onima site compared with initial snout-vent length (SVL). Figure demonstrates growth rate declines as the lizards grow.

approximately 25% of the sample of males had a SVL>120 mm. Mean wet body mass of males was 1.5 times greater than for females (x = 33.5 g, SD = 17.3 vs x = 22.5 g, SD = 5.4; Wilcoxon Rank Test, $P < 0.05$), and males were significantly longer than females as well (x = 106.8 mm, SD = 17.6 vs x = 97.6 mm, SD = 6.7; Wilcoxon Rank Test, $P < 0.05$; n = 587 males, 513 females). Thus, many adult males were 3.5 times the mass of reproductive females, a substantial dimorphism in body size. Over half the reproductive males were larger than the largest reproductive female in our sample.

Figure 2 presents data on growth rates for Onima lizards recaptured 28–277 days (x = 129.9; SD = 75.5) after initial measuring (data on recaptures >277 days after marking were not included because growth rates averaged over long periods would be uniformly low). Growth rate in *C. murinus* declines as the animals grow. Females appeared to cease substantial growth at about 105 mm SVL, whereas males continued to grow typically to at least 125 mm SVL. We recaptured and identified 11 animals that had been marked at the Onima site 3–4.3 yr earlier. Four females initially were 95–99 mm SVL when marked and grew to 101–109 mm. Seven males were initially 85–115 mm SVL and grew to 133– 145 mm. This confirmed that most females ceased growth at about 105 mm SVL, but males grew to a much larger size.

Juveniles (smaller than minimum reproductive size) were uncommon in the populations studied. Only 16.3% of collected lizards (n = 180/1101) were juveniles. During the entire study, we saw very few hatchlings. The smallest lizard collected was 42 mm SVL.

Clutch size, egg size, and relative clutch mass.— Only 12 (3%) of 402 adult females collected during the entire year carried oviductal eggs. Of these, 10 carried a single egg. For one female with two eggs, a single egg was in the oviduct, and another was free in the body cavity. This egg was black and appeared to be disintegrating. The other female with two shelled eggs in her oviducts had the smallest eggs we recorded (1.85 and 2.19 g). Yolking follicles were found in 105 other adult females; most had only a single enlarged follicle (81% = 1 follicle enlarged, 19% = 2 enlarged follicles). The largest yolked follicles we observed were 15–16 mm in diameter, most likely near the size when they are ovulated. Such large follicles occurred only as singletons; that is, when two enlarged follicles were seen, both were small or one was much larger than the other (examples: 14 and 5 mm, 13 and 4 mm). Therefore, the typical clutch size for this species is one egg. Mean egg mass was 2.37 g (SD = 0.21 g, n = 13). Relative clutch mass and relative egg mass (same in a species with a single egg in the clutch) was 0.126 (SD = 0.033).

Annual cycle.—The proportion of adult males and females that were reproductive varied over months but with no synchronization between the sexes (Spearman correlation, $P > 0.05$). Also, the proportion of males and females reproductive was not related to rainfall (Spearman correlations for rainfall during same time period and for rainfall in previous two-month period, $P > 0.05$). There was no significant difference in follicle size of reproductive females (n = 105) among months (Kruskal-Wallis tests, $P > 0.05$). The 12 females with shelled eggs were collected in Jan., Feb., March, June, Sept., and Dec. Females with yolked follicles near ovulation size ($\geq$10 mm diameter, n = 32) were found in every month except March. No clear peaks or trends occur for a month-by-month analysis (Fig. 3). A wet season vs dry season comparison reveals no significant difference in number of females with eggs or large yolked follicles: 9.1% vs 11.7%, G-test, $P > 0.05$. We conclude that female reproduction of *C. murinus* is not seasonal.

Testis mass did not vary seasonally (Kruskal-Wallis test for testis size by month, n = 190, $P > 0.05$). The distribution of testis mass among adult males was bimodal with modes at 0–0.04 g (67% of sample) and 0.09–0.12 g (15% of sample), supporting our use of a cut-off point of 0.04 g to distinguish reproductive activity by males, and also suggesting testis mass increases abruptly as lizards reach reproductive condition.
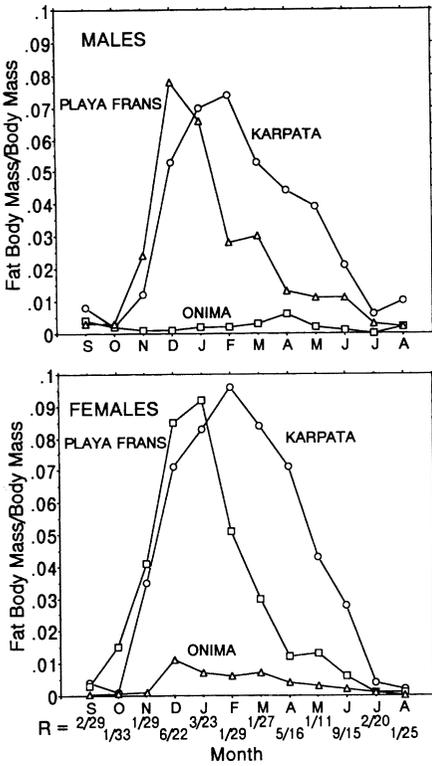
Fig. 3. Relative fat body mass stored by Bonaire whiptail lizards over time at three study sites. Points show the means. Data for males on upper graph, for females below. Numbers below axis on graph for females' data ("R") are number of females with shelled eggs and/or yolked follicles ≥ 10 mm in diameter out of sample of reproductively mature females at Karpata and Playa Frans (sites where amount of stored fat varied greatly with season). Total sample sizes for males and females at Karpata = 177 and 185, at Onima = 190 and 178, and at Playa Frans = 220 and 150.

TABLE 1. MEANS, STANDARD DEVIATIONS (SD), AND RANGES OF TESTIS MASS, BODY MASS, AND SVL IN mm BY COLOR CLASS FOR MALE BONAIRE WHIPTAIL LIZARDS. All three measures differ among color classes (Kruskal-Wallis tests, $P < 0.001$.) Testis mass of "0" means too small to dissect and weigh.

	Color class		
	1	2	3
Testis mass			
$\bar{x}$	0.015	0.039	0.128
SD	0.032	0.049	0.053
Range	0–0.140	0–0.270	0–0.280
n	198	175	98
Body mass			
$\bar{x}$	23.0	26.8	579
SD	13.13	16.08	14.11
Range	1.8–69.4	3.4–80.6	19.9–99.1
n	61	64	71
SVL			
$\bar{x}$	96.1	101.2	127.6
SD	18.70	19.06	9.57
Range	42–135	54–145	100–151
n	391	265	277

In contrast, inguinal fat appears to follow a strongly seasonal cycle (Fig. 3), with maximal fat stored just after the rainy season. Vitt and Breitenbach (1993) concluded that, in the seasonal tropics, the amount of stored fat and reproductive activity are correlated. Fat body mass and percent of females with oviductal eggs or yolked follicles ≥ 10 mm diameter were not correlated, nor was percent reproductive individuals in the previous month correlated with fat body mass (Spearman correlations, $P > 0.2$). Females stored proportionally more fat than did males at two of the three sites, Karpata and Onima (Wilcoxon Rank Tests, $P < 0.01$). Animals stored significantly different quantities of fat at each site. In particular, stored fat was very low throughout the year at Onima (Fig. 3; Multiple range tests, $P < 0.05$ for both sexes).

Body color.—All females were in color class 1, whereas adult males exhibited all three color classes. Color classes did not differ in relative proportions during the year (G-test for two-month periods to give usable sample sizes, $P > 0.05$). Color class 1 (all brown) were typically the smallest males (SVL and body mass) and had the smallest testes, and class 3 (all blue) were the largest and had the largest testes (Table 1). This suggests that males change from brown to brown with blue spots to all blue as they grow and reach sexually maturity. However, there also was considerable overlap in body size and testis mass among the three color classes (Table 1; Fig. 4). That is, some of the largest males with large testes retained the less extravagant color morphs (classes 1 and 2).

Color change over time was observed in the mark-recapture study. Animals recaptured from 28–269 days after marking (x = 137 days, SD = 68.3, n = 26) showed a color change in only four individuals. Those not changing color had increased SVL from 0–18 mm (x = 4.3), whereas those changing color had increased SVL from 7–43 mm (x = 16.8). All four males showing a change in color had increased the amount of blue on their dorsal surface. Those not changing color were of all three color classes (five class 1, 10 class 2, and seven class 3). Only one of six animals recaptured one year after mark-
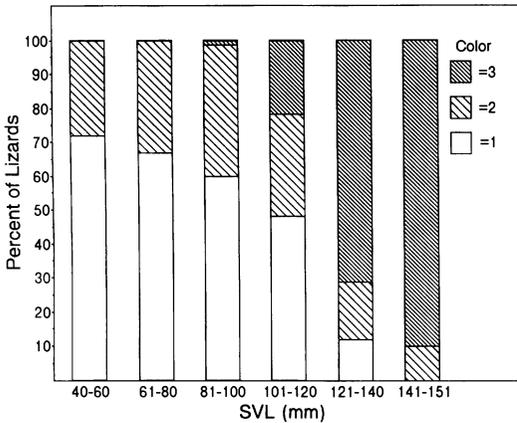
Fig. 4. Percent of male Bonaire whiptail lizards in each of three color classes: 1 = all brown, 2 = brown with blue spots, 3 = all blue. Data are for 935 lizards.
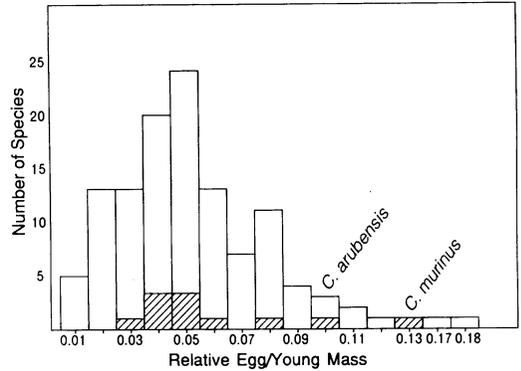

Fig. 5. Relative egg or young (for live bearers) mass for 119 species of lizards. Species of *Cnemidophorus* and *Ameiva* shown in hatching. Two species discussed in text, *C. arubensis* and *C. murinus* are indicated. Relative egg/young mass is mass of egg or young/mass of female. Data from numerous publications.

ing showed color change, also toward more blue. This animal had increased its SVL by 31 mm; the others had grown from 0–19 mm. The unchanging males were in color class 2 (two males) and 3 (three males). Five of seven males recaptured from 4–4.3 years after marking had changed color, all from class 2 to class 3. One of the unchanging males was color class 1 and the other was class 2. Again, these results suggest that some males may retain a juvenile pattern, perhaps for their entire lifetime.

DISCUSSION

Known variation in life-history traits of *Cnemidophorus*, both within and among species, is substantial. This variation has been attributed to habitat type, rainfall patterns, temperate vs tropical environments, body size, and parthenogenetic vs bisexual reproductive mode (review in Vitt and Breitenbach, 1993). Some features of the reproduction and sexual dimorphism of the Bonaire whiptail described here are typical for the genus, but others are highly unusual, both when compared with other whiptail species and for lizards in general.

Cnemidophorus murinus is similar to other tropical whiptail species in showing maximal fat deposition during or just after the rainy season (Leon and Cova, 1973; Vitt, 1983). Unlike temperate lizards or some tropical species, the *C. murinus* does not appear to recycle surplus fat into additional reproduction; there was no peak in reproduction following storage of maximal fat in Jan.–Feb. Fat body size varied among sites. At Karpata, where fat stored was the greatest, the most common food in the diet (small berries with high sugar content) was always available in

large quantities (Dearing and Schall, 1992). At Onima, with the lowest amount of fat stored, the diversity of potential food types was low, and a significant part of the diet consisted of plant types that contained substantial quantities of potential toxic secondary compounds. Estimated maximal energy content per gram of food consumed was low at Onima (2.15 kJ/g wet mass) compared to Karpata (3.77 kJ) and Playa Frans (5.03 kJ) (Dearing and Schall, 1992).

Vitt and Breitenbach (1993) note that tropical whiptail lizards (both *Cnemidophorus* and *Ameiva*) typically are reproductive year-round but have at least one peak reproductive period. *Cnemidophorus murinus*, in contrast, appears to be uniformly reproductively active, but reproductive output is low. Clutch size in *Cnemidophorus* typically increases as animals grow, and larger species tend to have larger clutches (Schall, 1978, 1981; Vitt, 1983). Vitt and Breitenbach (1993) summarize all available data on clutch size in *Cnemidophorus*; for a species of the *C. murinus*'s size, mean clutch size should be about four, with a range from 3–6. *Cnemidophorus murinus*, however, typically produces only one egg, and not more than two eggs, per clutch, similar only to *C. arubensis* of Aruba island in the Netherlands Antilles (Schall, 1983) and possibly other insular Caribbean species (J. Wright, pers. comm.). The production of a single egg is an oddity, not only when compared with other *Cnemidophorus* species but also for all lizard species in which clutch size varies among females (Pianka, 1986; Vitt, 1986).

Clutch mass/body mass for *C. murinus* is the middle of the range for the genus (Vitt and

Breitenbach, 1993), but egg size (egg mass/body mass) is very large in *C. murinus* (Fig. 5). *Cnemidophorus murinus* produces the largest egg of any species of *Cnemidophorus* or the closely related genus *Ameiva*. *Cnemidophorus arubensis*, the other *Cnemidophorus* with clutch size of one, also produces very large eggs. Only two species of lizards have been reported with larger relative egg or young size, *Typhlosaurus gariepensis*, a skink, and *Oedura tryoni*, a gecko.

Egg size in *C. murinus* may affect growth patterns. In other *Cnemidophorus*, body size at maturity is similar for males and females (Anderson and Vitt, 1990; Vitt and Breitenbach, 1993; JJS, unpubl. data), but *C. murinus* females grow to a larger size before reaching reproductive maturity than do males. There may be a minimum size necessary before a female could produce and lay such large eggs. Once female Bonaire whiptails begin to produce eggs, they may have little surplus resources to continue much growth, resulting in their remaining much smaller than most males. That is, for a female *C. murinus* to produce more than one egg per clutch, she would have to delay reproduction for an even greater period of time, perhaps increasing her chances of never reproducing.

High expenditure of resources on individual offspring is characteristic of species in highly competitive environments (Pianka, 1986). However, we doubt that intraspecific competition for food is important in this species. *Cnemidophorus murinus* is a selective feeder, but foods were abundant (Dearing and Schall, 1992). The energy challenge for this species is not a result of competition but of the limited amount of energy (and perhaps other resources, such as nitrogen and calcium) that can be extracted from plant material. Bennett and Gorman (1976) estimated a minimum energy requirement (excluding growth and reproduction) for *C. murinus* of 4.47 kJ/day per individual. Energy in the mean mass of food found in stomachs at the three sites was 2.09 kJ at Karpata, 2.42 kJ at Playa Frans, and 2.15 kJ at Onima (Dearing and Schall, 1992). Even if lizards typically took twice the amount of food per day that we found in the average stomach, they would still have little or no energy left for reproduction. Nitrogen, another nutrient critical for production of eggs, also is low in the diet of *C. murinus*, ranging from 0.0023–0.0064 g/g of food. [Values for nitrogen given in Table 6 of Dearing and Schall (1992) have the decimal point misplaced by two orders of magnitude.] Under such conditions we expect a very low reproductive output.

The large egg must produce an offspring of larger relative size than almost any other lizard species. Such large hatchlings may be necessary for two reasons. First, smaller animals may not be able to harvest the fruits, seeds, and leaves that are the common foods of the species, including juveniles. Second, smaller hatchlings may be susceptible to predation by adult Bonaire whiptails. We occasionally found small lizards, including juvenile *C. murinus*, in the stomachs of *C. murinus*. Any hatchling would be recruited to a very dense population of potential predators (i.e., adult lizards).

The nature of variation in body color in male Bonaire whiptails is perplexing. Extravagant sexually dimorphic traits in animals are always associated with greatest reproductive activity (Willson, 1990). However, some male Bonaire whiptails appear to remain dull in color throughout their lifetime and could be mistaken for very large females. No such femalelike color pattern in adult males has been seen before in *Cnemidophorus* except perhaps in *C. arubensis* of nearby Aruba island (Schall, 1986). Male-male competition for mates should be intense for the Bonaire whiptail lizard because females may not be receptive for mating very often (low reproductive rate). The extreme sexual dimorphism in body size in *C. murinus* also suggests strong male-male competition in these lizards (Vitt, 1983; Anderson and Vitt, 1990). We speculate that males retaining a color pattern closer to the female appearance might avoid aggressive interactions with other males and act as satellites, waiting for the opportunity to court and mate with unguarded females (Willson, 1990). The pattern of sexually dimorphic color seen in *C. murinus* challenges sexual selection theory and deserves further study.

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