Copeia, 2003(4), pp. 858–864

Positive Relationship between Abdominal Coloration and Dermal Melanin Density in Phrynosomatid Lizards

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Phrynosomatid lizards show considerable variation among species in the occurrence of a secondary sexual trait, blue abdominal coloration. The production of blue skin may be controlled by at least two cellular components, melanin in melanophores, and guanine in iridophores. To examine the hypothesis that a mechanism producing variation in abdominal coloration is variation in the presence of melanin in the melanophores within the dermal layer of skin, we used light microscopy to compare melanin density of five species of phrynosomatid lizards with ancestral and derived abdominal coloration. Our results show that the skin of adults with blue abdominal coloration has more dermal melanin than white skin regardless of species or sex. We experimentally tested this relationship by examining the dermal melanin in skin from female *Sceloporus undulatus consobrinus* with exogenously elevated levels of testosterone or 5α-dihydrotestosterone. These females displayed malelike abdominal coloration and malelike melanin density. Our results suggest that melanin density plays a role in the presence of blue abdominal coloration in these phrynosomatid lizards.

STUDIES of sexual selection have focused on understanding the origin and maintenance of conspicuous secondary sex characteristics of males and female responses to male signals (Andersson, 1994), and fewer have focused on losses of these traits (Quinn and Hews, 2000; Wiens, 2001). We are engaged in a comprehensive research program applying an integrative approach to the study of sexual selection in the context of communication systems (Hews and Quinn, 2003). This approach involves investigating signal production, physiological control of both production (Quinn, 2001) and reception of signals, and transmission constraints imposed by the environment, in addition to more typical approaches of studying behavioral responses to signals (Quinn and Hews, 2000; Quinn, 2001). It is our intent to integrate these aspects of the communication system within a phylogenetic context to provide a more complete picture of the pattern of evolution of sexually selected traits and communication systems. As part of an integrative study of visual signals in *Sceloporus* lizards, we report here an examination of the relationship of dermal melanin density and blue abdominal coloration in five phrynosomatid lizards, *Sceloporus undulatus consobrinus*, *Sceloporus virgatus*, *Sceloporus jarrovii jarrovii*, *Urosaurus ornatus*, and *Uta stansburiana*.

Blue abdominal coloration is an aggressive visual signal in the sexually dimorphic *S. u. consobrinus* (Cooper and Burns, 1987; Quinn, 2001) and the sexually monomorphic-white *S. virgatus* (Quinn and Hews, 2000). However, female *S. u. consobrinus* and *S. virgatus* do not respond to blue abdominal coloration (Quinn, 2001). Thus, male-male competition may be a more important factor in the sexual selection of these species (Quinn, 2001).

A well-corroborated phylogeny, based on molecular and morphological traits, exists for phrynosomatid lizards (Reeder and Wiens, 1996; Wiens and Reeder, 1997) and Wiens (1999) studied the phylogenetic distribution of abdominal coloration in this family. This work suggests that the ancestral character state of the family is sexual monomorphism, in which both males and females have entirely white abdomens. Two genera (*Urosaurus* and *Sceloporus*) within this family have evolved blue abdominal coloration. Parsimony analysis of the phylogenetic distribution of abdominal coloration in these two genera supports the hypothesis that the ancestral character state is sexual dimorphism, in which males have blue abdominal coloration (Wiens, 1999). Two derived character states also exist: the loss of abdominal coloration in males (e.g., *S. virgatus*), which has occurred independently in at least nine different species or clades, and gain of coloration in females (e.g., *S. j. jarrovii*), which has occurred independently in at least 11 different species (Wiens, 1999).

The production of color in ectothermic vertebrates is the result of a combination of pigmentary colors (i.e., carotenoids, pteridines, and melanin) and structural colors located in specialized dermal chromatophores (Fox, 1976). The chromatophore type in the most superficial layer of reptilian skin is the xanthophore (Bagnara et al., 1968). Xanthophores can contain

pterinosomes (which contain pteridines) and carotenoid vesicles (which contain carotenoids). The next layer contains iridophores that reflect and scatter short wavelengths of light. These cells typically contain guanine platelets, which are responsible for the scattering of light. The deepest layer contains the melanophores, which contain melanin (e.g., Morrison et al., 1995 and references therein). Pigments (pteridines, carotenoids, and melanin) selectively absorb different wavelengths of light to produce different colors, whereas iridophores contribute to skin coloration through the production of structural colors (Alexander and Fahrenbach, 1969).

Variation in abdominal coloration among species and between sexes of phyronosomatid lizards may result from variation in the position, abundance, and density of these chromatophore types. The current model describing the production of blue abdominal coloration is that blue color is produced by the reflectance of short wavelengths of light by the iridophore layer and the absorption of all other wavelengths of light by the melanin layer in the underlying layer of melanophores (reviewed in Morrison et al., 1995). White skin is produced when there is little or no melanin (or potentially melanophores) and reflectance of all the remaining wavelengths (that were not scattered by the iridophore layer) by an underlying layer of highly reflective collagen fibers. A prediction of this model is that blue patches of skin will have higher concentrations of melanin, either by increasing the density of melanophores or by increasing the number of melanophores.

We performed five sets of comparisons to test predictions of this model using both observational and experimental analyses that quantified dermal melanin density in five species of phrynosomatid lizards. First, we compared dermal melanin density of abdominal skin of males and females of the sexually dimorphic species (*S. u. consobrinus* and *Urosaurus ornatus*) to examine the relationship between sex differences in abdominal coloration and sex differences in melanin density. Second, we compared melanin density in two monomorphic-white species (*S. virgatus* and *U. stansburiana*) and a monomorphic-blue species (*S. j. jarrovii*) to examine the relationship between melanin density and abdominal coloration in monomorphic blue and monomorphic white species. Next, we compared the melanin density of lizards with blue abdominal coloration (regardless of species or sex) to examine the relationship between blue abdominal coloration and melanin density of these species. Finally, we compared the melanin density of the skin of lizards with white abdominal coloration (regardless of species or sex) to examine the relationship between white abdominal coloration and the lack of melanin density within this family.

We further tested predictions of this model by experimentally manipulating abdominal coloration and subsequently measuring melanin. To this end, we manipulated the phenotype of female *S. u. consobrinus* with malelike abdominal coloration by elevating hatchling levels of androgens (Quinn, 2001); skin samples from these females were compared to skin samples from unmanipulated male conspecifics. Sex steroid hormones have pleiotriopic effects, including behavioral, morphological, physiological, and life-history traits (Sinervo et al., 2000a,b). In particular, sex steroid hormones play a role in controlling the expression of sexual dimorphism (e.g., Becker et al., 1992) and the expression of secondary sexual characteristics in vertebrates (Ketterson et al., 1992; Hews and Moore, 1995).

Materials and Methods

Data collection.—Adult male and female *U. stansburiana* (monomorphic-white), *Urosaurus ornatus* (dimorphic), *S. u. consobrinus* (dimorphic), *S. virgatus* (monomorphic-white), and *S. j. jarrovii* (monomorphic-blue) were sacrificed within one week of capture in 1997. *Uta stansburiana* were collected on Hwy. 80, between Rodeo and Road Forks, New Mexico, approximately nine miles south of Road Forks in 1997. *Urosaurus ornatus* were collected along U.S. Hwy. 80 between Rodeo, New Mexico, and intersection of 80 with New Mexico State Road 9 in 1997. *Sceloporus undulatus consobrinus* were collected along New Mexico State Road 533 in 1997. The collection locations of *S. u. consobrinus* were made within the generalized range for this subspecies in the United States (Smith et al., 1999; Lemos-Espinal et al., 1999; Leache and Reeder, 2002) in 1997. *Sceloporus virgatus* and *S. j. jarrovii* (Wiens et al., 1999) were collected in Cochise County, Arizona, near the Southwestern Research Station of the American Museum of Natural History in 1997.

Buffered 10% formalin was injected into a 1 cm incision in the abdomen and the whole body was immersed in buffered 10% formalin for fixation. After 1–3 months, specimens were soaked for 24 h in distilled water and were then stored in 40% isopropyl alcohol. A small (approximately 1 cm^2) patch of skin was removed from the center of the blue patch (or from the same location if the lizard had white abdominal coloration) and stored in 40% isopropyl alco-

hol. The skin sample was removed from male (n = 4) and female (n = 4) *S. j. jarrovii*, male *S. u. consobrinus* (n = 9) and male *U. ornatus* (n = 3) and from the same location in male (n = 3) and female (n = 3) *U. stansburiana*, male (n = 6) and female (n = 5) *S. virgatus*, female *S. u. consobrinus* (n = 8) and female *U. ornatus* (n = 3). To facilitate sectioning through scales, skin samples were soaked in Fisher decalcification fluid for 24 h and rinsed for 3–4 h in running reverse-osmosis water. Samples were processed routinely for paraffin embedding (Presnell and Schreibman, 1997) and cross-sections were cut at 7 μm. Sections were mounted on microscope slides, dried at 65 C for 1–3 h, deparaffinized in xylenes, rehydrated in a graded series of ethanol solutions, and stained with Harris modified hematoxylin and eosin (Presnell and Schreibman, 1997).

For each lizard, the amount of melanin was quantified in one randomly chosen histological section of skin, viewed at 10× (Fox, 1976). We determined the area of stained melanin and the total area of the dermal layer of skin using the software program "tpsDig," Version 1.28 by measuring the outlines of the cells. These values are measured in pixels. Melanin density was calculated as area of stained melanin/total area and is reported as a percentage.

Hormone manipulations.—Hatchling female *S. u. consobrinus* were assigned to testosterone (n = 14), 5α-dihydrotestosterone (n = 15), or blank-implanted groups (n = 15) and implanted 20 days posthatching. Dow Corning Silastic tubing implants (0.058″ i.d., 0.077″ o.d.) were packed with 0.5 mm crystalline testosterone or 5α-dihydrotestosterone, and sealed with silicon. Blank implants were filled with silicon and cut to the same total length. Implants were placed intraperitonally into hypothermically anesthetized animals through a small ventral incision. Implants remained in the animal for 180 days. Similar-sized implants are known to deliver androgens within the range of adult male levels (DKH, unpubl. data; Lovern et al., 2001).

Statistical analysis.—Data were arcsine transformed to meet assumptions for parametric analysis. Differences between sexes and among species were compared using Univariate Analysis of Variance (SPSS Statistical Software, vers. 10.0). To maintain an overall $\alpha = 0.05$, reported P-values were adjusted using the sequential Bonferroni correction (Rice, 1989).

Results

Cellular structure of melanophores.—Dermal melanophores conform to description of melanophores of other lizard species (von Geldern, 1921). In general, all lizards had at least some melanin in the dermal layer of skin (Fig. 1) but differed considerably in melanin density.

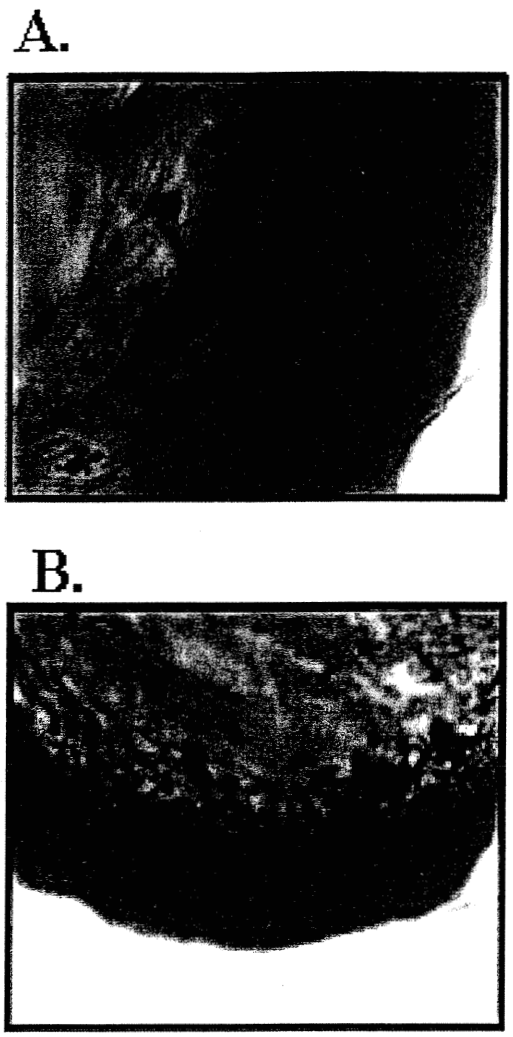

Fig. 1. A melanophore from a female *Sceloporus jarrovii jarrovii*. (A) In this orientation, the classic stellate nature of the cell is readily apparent. (B) Processes of the melanophore can be seen extending up from the more basal dermal layer into more superficial layers.

Figure 1 shows two cross-sectional views of a dermal melanophore from adult female *S. j. jarrovii* (monomorphic-blue). These melanophores

Melanin Density

Comparison 1. Are there sex differences in melanin

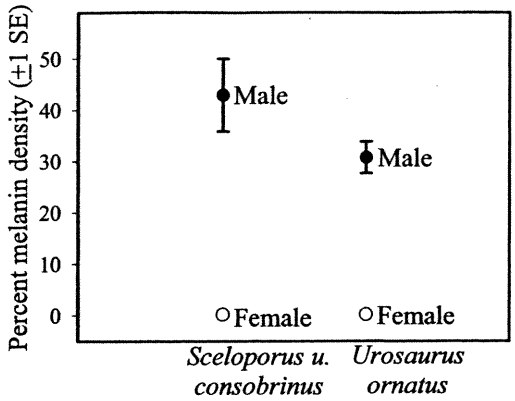

Fig. 2. *Comparison 1. Are there sex differences in melanin density in sexually dimorphic species?* Males with blue abdominal coloration have a higher density of melanin than female lizards with white abdominal coloration.

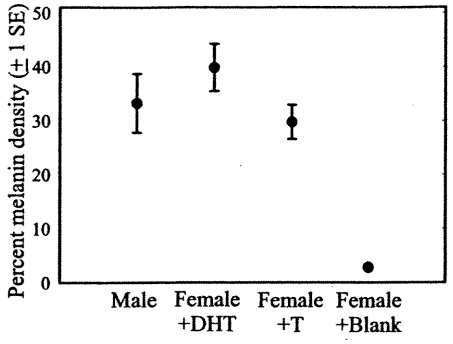

Fig. 4. *Comparison 5. Do mascinulized females have the same melanin density as males?* Female *Sceloporus undulatus consobrinus* implanted with either testosterone or DHT have similar levels of melanin compared to nonmanipulated male *S. u. consobrinus* and differ from female *S. u. consobrinus* implanted with a blank.

melanin density of the blue abdominal skin from males of *S. u. consobrinus* (dimorphic) and males of *U. ornatus* (dimorphic) did not differ significantly (Fig. 2; $F_{1,10} = 2.600$; $P = 0.126$). Because we did not detect a difference in melanin density, we combined these data. Similarly, the melanin density of white abdominal skin from females of *S. u. consobrinus* and females of *U. ornatus* did not differ (Fig. 2; $F_{1,9} = 0.031$; $P = 0.863$), and we combined these data. Using these combined datasets, we compared the melanin density of blue abdominal skin from males to the melanin density of white abdominal skin from females. The blue abdominal skin from male lizards had a higher density of melanin than the white abdominal skin from female lizards (Fig. 2; $F_{1,21} = 38.687$; $P < 0.001$).

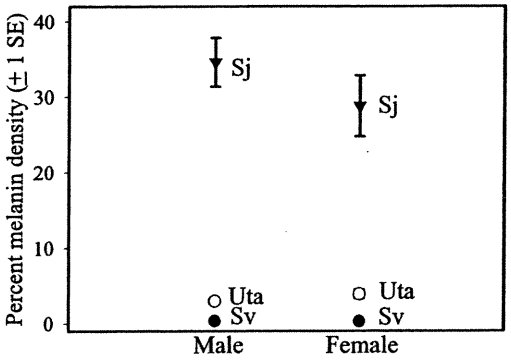

Fig. 3. *Comparisons 3 and 4. Are there within species differences in melanin density?* No difference in melanin density was detected when males and females were compared in the monomorphic-blue species (*Sceloporus jarrovii jarrovii*) or the monomorphic-white species (*Sceloporus virgatus* or *Uta stansburiana*).

Comparison 2. Are there within-species differences in melanin density?—Blue abdominal skin from male and female *S. j. jarrovii* (monomorphic-blue) did not differ in melanin density (Fig. 3; $F_{1,6} = 1.236$; $P = 0.309$). There was no difference in white abdominal skin from male and female *U. stansburiana* (monomorphic-white; Fig. 3; $F_{1,4} = 2.502$; $P = 0.189$) or male and female *S. virgatus* (monomorphic-white; Fig. 3; $F_{1,9} = 0.972$; $P = 0.972$).

Comparisons 3 and 4. Are there between-species differences in melanin density?—Blue abdominal skin from male and female *S. j. jarrovii*, male *S. u. consobrinus*, and male *U. ornatus* had similar densities of melanin ($F_{3,18} = 1.40$; $P = 0.269$; filled circles in Figs. 2–3). We compared the percent melanin density of white abdominal skin from male and female *S. virgatus*, *U. stansburiana*, female *U. ornatus*, and female *S. u. consobrinus*. All of the patches of white skin examined had similar densities of melanin ($F_{5,26} = 0.695$; $P = 0.633$; open circles in Figs. 2–3).

Comparison 5. Are there differences in melanin density between males and masculinized females?—Female *S. u. consobrinus* expressed blue abdominal coloration when implanted with either testosterone or 5α-dihydrotestosterone. The expression of blue abdominal coloration is almost identical to that of male abdominal coloration (Quinn, 2001). Lizards with blue abdominal coloration (females with a testosterone or 5α-dihydrotestosterone implant and males) have higher levels of melanin compared to unmanipulated female *S. u. consobrinus* given a blank (empty) implant ($F_{3,51} = 1.574$; $P = 0.238$; Figs. 4–5).

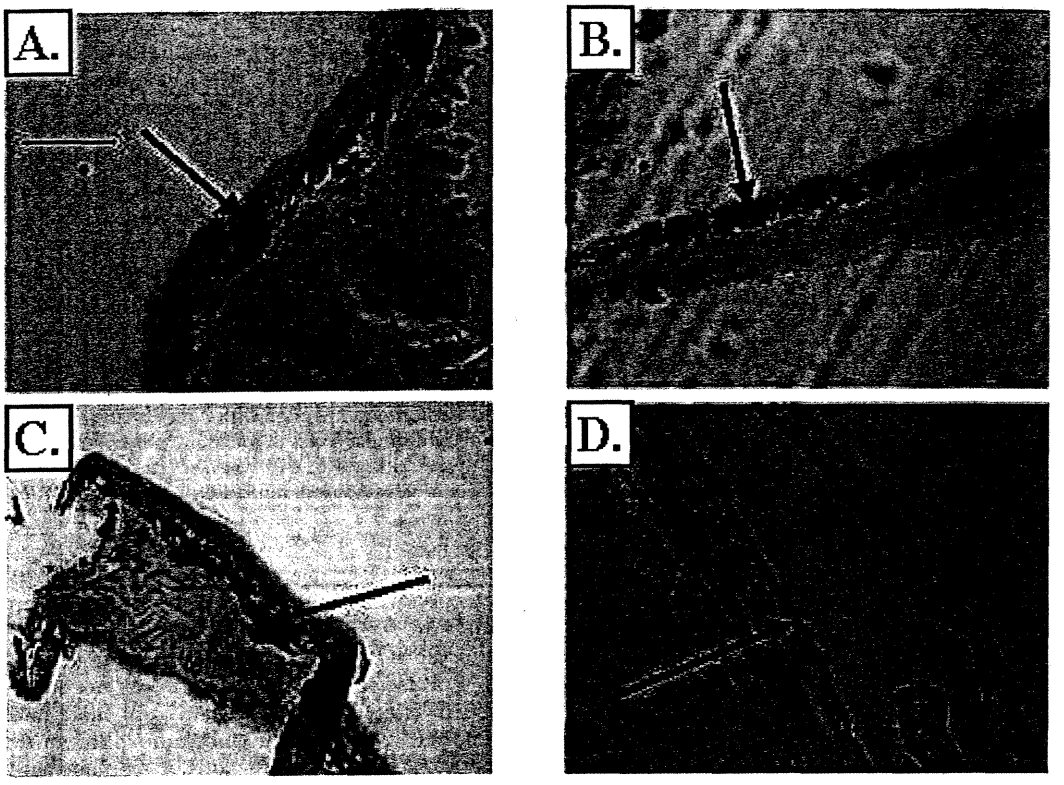

Fig. 5. *Comparison 5. Do masculinized females have the same melanin density as males?* Images were photographed at 40×. The arrow is pointing to the melanin layer in male *Sceloporus undulatus consobrinus* (A) and female *S. u. consobrinus* implanted with testosterone (B) or 5α-dihydrotestosterone (C), and to the lack of melanin in female *S. u. consobrinus* (D). The scale bar is 50 μm.

Discussion

This study and work by Macedonia et al. (2000) describe histological correlates of color differences between sexes and among closely related species, and both report that, within closely related species, the production of coloration may involve similar cellular components. The current model of skin color production suggests that blue abdominal coloration is produced by the reflectance of short wavelengths of light by the iridophore layer and the absorption of other wavelengths by an underlying melanin layer. This model predicts that blue abdominal skin will have more melanin then white skin and observational and experimental data reported herein support this model. Lizards with blue abdominal coloration have a higher density of melanin than lizards with white abdominal coloration. This relationship between melanin density and blue abdominal coloration is similar within these representatives of phrynosomatid lizards and should be examined in other lizard species. Our work provides the first experimental test of this model, and results from androgen-manipulated and control females strongly support this hypothesis.

Descriptive studies suggest that small changes in the cellular architecture can dramatically change the coloration of ectothermic vertebrates, including differences between the red-backed and lead-backed morph of *Plethodon cinereus* salamanders (Bagnara and Taylor, 1970), between albino and normally colored *Ambystoma mexicanum* salamanders (DuShane, 1935), and coloration differences between two species of *Bothriechis* vipers (Gosner, 1989). There are three dewlap color morphs of *Sceloporus undulatus erythrocheilus* lizards (orange, blue, and melanized) and qualitative and quantitative differences in the cellular mechanisms of color production have been shown, including differences in the presence of xanthophores, iridophores, and melanophores (Morrison et al., 1995). Shifts in the availability of metabolic precursors or in enzymes important in the biosynthetic pathways may account for the different pigments present (Morrison et al., 1995).

Variation in melanin production is only one of several possible mechanisms that could contribute to sex and species variation in abdominal coloration of *Sceloporus*. The importance of the iridophore layer in the production of abdominal coloration was not addressed in this study. Lizards lacking blue abdominal coloration could lack iridophores or some element of the iridophore. Horned Lizards (*Phrynosoma molestum*) have entirely white abdominal surfaces and possess guanine platelets located in the iridophore, but the intracellular arrangement of the guanine platelets is not highly organized (Sherbrooke and Frost, 1989). One hypothesis to explain the loss of blue in *S. virgatus* is that there could be an altered organization of guanine platelets. Tentative rejection of this hypothesis is suggested by transmission electron microscopy, which revealed that male *S. virgatus* (monomorphic-white) have iridophores and platelets (which presumably are guanine platelets) within the iridophores (Hews and Quinn, 2003). Furthermore, the platelet spacing appears comparable to that seen in blue skin of male *S. undulatus* (dimorphic; Morrison et al., 1995). Quantifying features of this layer will be required to more vigorously assess this hypothesis.

Another unresolved question is, how do hormones control coloration within *Sceloporus*? The seasonal production of orange facial coloration in *S. u. erythrocheilus* may be caused by the hormonal activation of xanthophores and initiation of the synthesis of pteridines in facial tissue by testosterone (Morrison et al., 1995). The subsequent decline of testosterone is consistent with a decline in colored pteridines and the orange facial coloration. The pattern of testosterone fluctuation in *S. u. erythrocheilus* is consistent with observed patterns of pteridine biosynthesis (Rand, 1992). In contrast to the facial coloration, abdominal coloration in *Sceloporus* is a permanent trait and is, at least in part, organized by the presence of elevated levels of testosterone or 5α-dihydrotestosterone in *S. u. consobrinus* (dimorphic; Quinn, 2001). What specific action these androgens have on potential target chromatophores (melanophores, iridophores) in the *Sceloporus* blue abdominal coloration awaits further study.

Results reported here show a strong relationship between abdominal coloration and melanin density and represent a first step in understanding the mechanisms responsible for color variation within and between phrynosomatid species. Future work will focus on understanding the molecular mechanisms responsible for color differences, the importance of the iridophore layer, and the role of hormones in the production of coloration in lizards.

Acknowledgments

We thank C. J. Amlaner, S. L. Lima, E. Tuttle, J. Wiens, M. Wikelski, and an anonymous reviewer for comments on this manuscript. The National Science Foundation Dissertation Improvement Grant (IBN: 0073203), Indiana Academy of Science, Indiana State University, Southwestern Research Station Graduate Student Fund, and the American Museum of Natural History, Theodore Roosevelt Fund (to VSQ) and National Science Foundation (to DKH; IBN-9629783) funded this research. This experiment was approved by Indiana State University Animal Care and Use Committee (Protocol 99–3:DH). Permits were obtained from Arizona (AZ-2655) and New Mexico (NM-1967).

Literature Cited

Alexander, N. J., and W. H. Fahrenbach. 1969. The dermal chromatophores of *Anolis carolinensis* (Reptilia, Iguanidae). Am. J. Anat. 126:41–56.

Andersson, M. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.

Bagnara, J. T., and J. D. Taylor. 1970. Differences in pigment-containing organelles between color forms of the red-backed salamander, *Plethodon cinereus*. Z. Zellforsch. 106:412–417.

———, ———, and M. E. Hadley. 1968. The dermal chromatophore unit. J. Cell Biol. 38:67–79.

Becker, J. B., S. M. Breedlove, and D. Crews. 1992. Behavioral endocrinology. MIT Press, Cambridge, MA.

Cooper Jr., W. E., and N. Burns. 1987. Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. Anim. Behav. 35:526–532.

Dushane, G. P. 1935. An experimental study of the origin of pigment cells in Amphibia. J. Exp. Zool. 72:1–31.

Fox, D. L. 1976. Animal biochromes and structural colors. Univ. of California Press, Berkeley.

von Geldern, C. E. 1921. Color changes and structure of the skin of *Anolis carolinensis*. Proc. Calif. Acad. Sci. 10:77–117.

Gosner, K. L. 1989. Histological notes on the green coloration of arboreal pit vipers; genus *Bothrops*. J. Herpetol. 23:318–320.

Hews, D. K., and M. C. Moore. 1995. Influence of androgens on differentiation of secondary sex characters in tree lizards, *Urosaurus ornatus*. Gen. Comp. Endocrin. 97:86–102.

———, and V. S. Quinn. 2003. Endocrinology of species differences in sexually dimorphic signals and aggression: using the organization and activation model in a phylogenetic framework, p. 253–277. *In:* Lizard social behavior. S. F. Fox, T. A. Baird, and J. K. McCoy (eds.). Johns Hopkins Univ. Press, Baltimore, MD.

KETTERSON, E., V. NOLAN, L. WOLF, AND C. ZIEGENFUS. 1992. Testosterone and avian life histories: effects of experimentally elevated testosterone on behavior and correlates of fitness in the dark-eyed junco (*Junco hyemalis*). Am. Nat. 140:980–999.

LEACHE, A. D., AND T. W. REEDER. 2002. Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. Syst. Biol. 51:44–68.

LEMOS-ESPINAL, J. A., D. CHISZAR, H. M. SMITH, AND C. HENKE. 1999. The known distribution in 1998 of the members of the *undulatus* group of the lizard genus *Sceloporus* in Chihuahua, Mexico. Bull. Maryland Herpetol. Soc. 35:152–163.

LOVERN, M. B., F. M. A. MCNABB, AND T. A. JENSSEN. 2001. Developmental effects of testosterone on behavior in male and female Green Anoles (*Anolis carolinensis*). Horm. Behav. 39:131–143.

MACEDONIA, J. M., S. JAMES, L. W. WITTLE, AND D. L. CLARK. 2000. Skin pigments and coloration in the Jamaican radiation of *Anolis* lizards. J. Herpetol. 34: 99–109.

MORRISON, R. L., M. D. RAND, AND S. K. FROST-MASON. 1995. Cellular basis of color differences in three morphs of the lizard *Sceloporus undulatus erythrocheilus*. Copeia 1995:397–408.

PRESNELL, J. K., AND M. P. SCHREIBMAN. 1997. Humason's animal tissue techniques. 5th ed. Johns Hopkins Univ. Press, Baltimore, MD.

QUINN, V. S. 2001. Proximate and ultimate factors leading to the loss of a sexually dimorphic trait in *Sceloporus* lizards. Unpubl. Ph.D. diss., Indiana State Univ., Terre Haute.

———, AND D. K. HEWS. 2000. Signal and behavioral response to the signal are not evolutionarily coupled in males: aggression affected by replacement of an evolutionarily lost color signal. Proc. R. Soc. Lond. B Biol. Sci. 267:755–758.

RAND, M. S. 1992. Hormonal control of polymorphic and sexually dimorphic coloration in the lizard *Sceloporus undulatus erythrocheilus*. Gen. Comp. Endocrinol. 88:461–468.

REEDER, T. W., AND J. J. WIENS. 1996. Evolution of the lizard family Phrynosomatidae as inferred from diverse types of data. Herpetol. Monogr. 10:43–84.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 46:223–225.

SHERBROOKE, W. C., AND S. K. FROST. 1989. Integumental chromatophores of a color-change, thermoregulating lizard, *Phrynosoma modestum* (Iguanidae; Reptilia). Am. Mus. Novit. 2943:1–14.

SINERVO, B., D. B. MILES, W. A. FRANKINO, M. KLUKOWSKI, AND D. F. DENARDO. 2000a. Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. Horm. Behav. 38:222–233.

———, E. SVENSSON, AND T. COMENDANT. 2000b. Density cycles and an offspring quantity and quality game driven by natural selection. Nature 406:985–988.

SMITH, H. M., D. CHISZAR, AND F. VAN BREUKELEN. 1999. The challenge of the Plateau and Prairie lizards (*Sceloporus undulatus*) of New Mexico. Bull. Maryland Herpetol. Soc. 35:143–151.

WIENS, J. J. 1999. Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards. Proc. R. Soc. Lond. B Biol. Sci. 266: 1529–1536.

———. 2001. Widespread loss of sexually selected traits: how the peacock lost its spots. Trends Ecol. Evol. 16:517–523.

———, AND T. W. REEDER. 1997. Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. Herpetol. Monogr. 11:1–101.

———, ———, AND A. N. MONTES DE OCA. 1999. Molecular phylogenetics and evolution of sexual dichromatism among populations of the Yarrow's Spiny Lizards (*Sceloporus jarrovii*). Evolution 53: 1884–1897.

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