Secondary Sexual Traits and Individual Phenotype in Male Green Frogs (*Rana clamitans*)

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Abstract.—Secondary sexual characteristics are often under intense sexual selection as ornaments for attracting mates or as traits associated with male-male competition such as combat. Secondary sexual traits under sexual selection are predicted to be related to male phenotype, because only high-quality males should be capable of developing these costly and exaggerated traits. Therefore, high-quality males should have larger or more elaborate secondary sexual traits than poor-quality males. We used the Green Frog (*Rana clamitans*) to test this hypothesis using three sexually dimorphic traits (the enlarged forelimbs, enlarged tympanum, and yellow throat of the male Green Frog) and two measures of male phenotype (body condition and size). Forelimb size was condition-dependent—males with larger forelimbs were in better condition than males with small forelimbs. Males with an intermediate shade of yellow on their throat tended to be in better condition than males with dark and light yellow throats, but the degree of yellow was related to body size—males with a dark yellow throat were larger than males with a light yellow throat. There was no evidence of condition-dependence of tympanum diameter; although after correcting for body size, males with a large tympanum had large forelimbs suggesting that tympanum size reflected some other, unmeasured, indicator of male quality. These results are consistent with the hypothesis that males produce multiple signals and cues that reflect different aspects of male quality. Females can maximize the benefits of mate choice by using multiple traits to assess male quality.

Secondary sexual characteristics are often important determinants of the outcome of sexual selection (Andersson, 1994). Traits subjected to sexual selection are predicted to be correlated with male genetic quality and competitive ability because only high-quality males should be able to invest more energy into developing and maintaining these costly exaggerated traits (Andersson, 1994). This relationship between quality and costly traits is particularly important in good-genes models of sexual selection in which females assess males based on their genetic quality. Evidence is accumulating that structures associated with male-male combat (Côté and Festa-Bianchet, 2001; Festa-Bianchet et al., 2004; Bonduriansky and Rowe, 2005) and female mate choice (Keyser and Hill, 1999; Møller and Petrie, 2002; Cotton et al., 2004) are dependent on aspects of male quality such as body condition.

We used the Green Frog (*Rana clamitans*) to test the prediction that secondary sexual traits are correlated with male quality. Green Frogs are a particularly good species to examine the consequences of male quality because, like many frogs, Green Frogs show sex differences in morphology and behavior including body size and chorus behavior (Howard et al., 1994; Judge and Brooks, 2001). Nonetheless, the relationship between morphological secondary sexual traits and male quality in anurans has received little attention (but see Lee, 2001).

We focused on three secondary sexual traits—the tympanum, the forelimb including the thumb pad, and the coloration of the throat. We assumed that each of these traits was costly, whether the result of growth and development of enlarged tissues (tympanum/forelimbs), synthesis/acquisition of pigments (throat color), or the maintenance of enlarged structures (tympanum/forelimbs). Male Green Frogs have a relatively larger tympanum and larger forelimbs and thumb pads than females, and the male throat is yellow in the breeding season, compared with the white throat of the female (Harding, 1997). The large male tympanum is hypothesized to be an adaptation for male-male competition because it is particularly sensitive to sound frequencies produced by other male frogs (Hetherington, 1994), thus allowing individuals to determine the location of male rivals (Bosch and Marquez, 2000). Perhaps most important, the tympanum may be involved in sound production, and males with large tympana may be able to broadcast more powerful calls than males with small tympana (Purgue, 1997). The development of the enlarged forelimb and thumb pad of most male frogs is

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mediated by androgens (Emerson et al., 1997; Sidor and Blackburn, 1998) and is hypothesized to play a role in amplexus when a male must grasp a female with the forelimbs for prolonged periods until oviposition occurs (Peters and Aulner, 2000). Finally, the yellow throat of many ranid frogs may act as a sexual signal indicating male quality to females. Color in frogs has been found to be both a signal with respect to female mate choice (Summers et al., 1999; Vasquez and Pfennig, 2007) and a signal of genetic quality (Sheldon et al., 2003). In addition, males may use the yellow throat to display toward rival males as an act of male-male competition (Wells, 1978; Ryan, 1980). Rosenthal et al. (2004) concluded that, in the nocturnal Túngara Frog (*Physalaemus pustulosus*), the inflated throat may function as a visual cue based on video-playback behavioral experiments. Thus, because each of these traits is expected to be important in mating success and under sexual selection, we predicted that these traits reflect different aspects of male quality with respect to both female mate choice and male competitive ability. We examined these secondary sexual traits with respect to two phenotypic traits that can reflect male quality—body condition and body size. Both of these traits have been found to be independently correlated with mating success in male frogs (e.g., Wells, 1977; Dyson et al., 1998; Lee, 2001; Vasquez and Pfennig, 2007). Although the heritability of body condition has not been established in Green Frogs, body condition has been found to be heritable in other taxa (e.g. Merilä et al., 2001, Simmons and Kotiaho, 2002). Body condition also explains variation in fitness in other taxa (see Green, 2001; Schulte-Hostedde et al., 2005, and references therein).

MATERIALS AND METHODS

We sampled male Green Frogs from five ponds on and around the campus of Laurentian University, Sudbury, Ontario, early in the breeding season (late May to mid-June) 2004. By sampling in the early breeding season, we controlled for mass loss that may occur over the course of the entire breeding season. Frogs were captured from dusk into the night (the active period for male Green Frogs) by hand using smelt nets. All males were calling when sampled.

Upon capture, Green Frogs were sexed (males are smaller than females with a tympanum at least as large as the eye [Zug et al., 2001]), and a number of measurements taken. Snout–urostyle length (body size) was measured using callipers ($\pm$ 0.01 mm). Both the right and left side of the following traits were also measured—tympa-

num diameter, the length and maximum width of the forearm, nuptial thumb pad, and total thumb length. The dorsal-ventral diameter of the tympanum was measured for all frogs. Forearm length was measured from the distal end of the radial-ulna (interface of the radio-ulna and the carpals) to the proximal end of the humerus (at the interface between humerus and clavicle and scapula). Thumb length was measured from the base of the thumb to the tip. Frogs were blotted dry with a cloth and weighed on a portable balance ($\pm$ 0.01 g; PB-05, Salter Brecknell, Fairmont, MN).

To categorize the color of the throat, we used a Pantone Formula Guide (Carlstadt, NJ). This guide has been commonly used to quantify the color of bird feathers (Montgomerie, 2006). The yellow of the throat was matched to a color in the guide. One group of frogs had white under the throat (100), and the remaining frogs were classified according to four shades of yellow ranging from light to dark (106, 107, 108, 109). Although this method is subjective, we minimized the potential for bias by conducting all observations in the same conditions (in the field under a head lamp) and all observations were done by the same person (CS).

Statistical Analysis.—All morphological variables were $\log_{10}$-transformed prior to analysis to linearize all relationships. To quantify overall forelimb size, we calculated the mean between the right and left forelimb for each of the forelimb measurements—length and width of forelimb and thumb pad, and total thumb length. These measurements were entered into a principal components analysis and the scores from the first principal component were used as an index of overall forelimb size. To quantify the size of the tympanum, we used the mean of the right and left tympana in all analyses.

We used size-corrected mass to measure body condition using one of two techniques. First, where possible, we used multiple regressions to examine the effects of body mass and body length on secondary sexual traits. We interpreted the partial correlation coefficient of body mass as the independent effect of size-corrected body mass (body condition) on the size of the dimorphic structure. Where body condition was used as a dependent variable, we used the residuals from a regression of body mass on snout–urostyle length as an index of body of condition (Schulte-Hostedde et al., 2005). These approaches are statistically equivalent—both use regression to determine size-corrected mass (Schulte-Hostedde et al., 2005). We used multiple regression and fixed nonlinear regression to assess the relationship between secondary sexual traits and body size and condition. Means are given ± 1 SD.

TABLE 1. Descriptive statistics for measured morphological traits in male Green Frogs.

Trait	Mean	SD
Body mass (g)	47.93	13.49
Snout–urostyle length (mm)	74.25	7.03
Average tympanum diameter (mm)	10.84	1.30
Yellow throat score*		
(106, light to 109, dark)	107.38	1.02

* indicates the exclusion of frogs with no yellow throat color (i.e., white throat).

RESULTS

A total of 30 calling male Green Frogs was sampled (for descriptive statistics of measured traits see, Table 1 and 2). Body mass and snout–urostyle length were positively correlated ($F_{1,28}$ = 172.9, r^2 = 0.86, $P < 0.001$).

Traits associated with the forelimbs were all highly correlated. The first principal component (PC1) from the principal component analysis with these traits explained 73.7% of the variation in the data (eigenvalue = 3.686), and all five traits were highly correlated with PC1 (Table 2). PC2 only explained 10.8% of the variation in the forelimb traits (eigenvalue = 0.539). Thus PC1 was used as an index of forelimb size.

As predicted, males with large forelimbs were in good condition relative to males with small forelimbs ($F_{2,27}$ = 63.4, r^2 = 0.824, $P < 0.001$; length partial r = 0.094, P = 0.63; mass partial r = 0.585, $P < 0.001$; Fig. 1). Larger males did have larger forelimbs relative to small males ($F_{1,28}$ = 76.98, r^2 = 0.733, $P < 0.001$). Although together body size and body mass explained significant variation in tympanum diameter ($F_{2,27}$ = 29.06, r^2 = 0.68, $P < 0.001$), we found no evidence that condition (mass independent of body size) was related to tympanum diameter (mass partial r = 0.21, P = 0.27). However, larger males had larger tympana than small males ($F_{1,28}$ = 56.27, r^2 = 0.667, $P < 0.001$).

The five categories of throat coloration had variable sample size (100, N = 4; 106, N = 6; 107, N = 8; 108, N = 8; 109, N = 4). We compared males with yellow throat coloration (Pantone color scores 106–109) to those males with no yellow coloration (color score 100) with respect to size (snout–urostyle length) and condition (residual mass). Males with no yellow coloration were smaller than males with a yellow throat (t_{28} = −2.34, P = 0.026), and although males with no yellow coloration were in poorer condition (mean residual mass = −0.032 ± 0.021) than males with a yellow throat (mean residual mass = 0.005 ± 0.048), this difference was not significant (t_{28} = −1.49, P = 0.15). When we considered only those males with a yellow throat, large males had darker yellow throats compared to small males (r^2 = 0.15, df = 1,24, P = 0.047; Fig. 2). Although there was no linear relationship between body condition (residual mass) and throat color (r^2 = 0.002, N = 26, P = 0.8), a trend toward a curvilinear relationship was found between color and body condition when an outlier was removed (quadratic term P = 0.20 with outlier included). The quadratic term in the nonlinear regression between condition and throat color approached significance ($F_{2,22}$ = 1.67, N = 25, r^2 = 0.13, P = 0.21; quadratic term P = 0.08; Fig. 3).

Males of high quality may be able to produce large and costly dimorphic traits without producing trade-offs among these traits. Because all of the dimorphic traits were related to body size, we controlled for body size when comparing dimorphic traits. To compare tympanum diameter and forelimb size, we used the residuals from the regression of each dimorphic trait on snout–urostyle length to correct for body size in a correlation analysis. After correcting for size, males with large tympana had larger forelimbs (r = 0.356, P = 0.05; Fig. 4).

To determine whether throat color was related to forelimb size or tympanum diameter, we used general linear models with the throat color category and snout–urostyle length as independent variables and the residual (size-corrected) value of the dimorphic trait as the dependent variable. We found no evidence of a relationship between throat color and forelimb size or tympanum diameter ($P > 0.5$ for all analyses).

DISCUSSION

Secondary sexual traits may reflect various aspects of male quality, whether in the context

TABLE 2. Descriptive statistics for traits measured from forelimb, and factor loadings for each trait in principal components analysis. Proportion of variance explained = 73.7%.

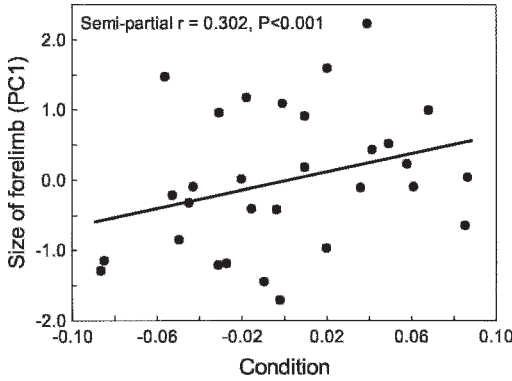| Trait	Mean	SD	Factor loading
Forelimb width (mm)	8.68	1.02	0.831
Forelimb length (mm)	23.05	2.47	0.837
Thumb pad width (mm)	4.60	0.57	0.890
Thumb pad length (mm)	8.14	1.04	0.872
Total thumb length (mm)	12.61	1.62	0.861

FIG. 1. Semipartial correlation between size of forelimb and condition (mass corrected for snout–urostyle length) for male green frogs ($N = 30$). Males in good condition had larger forelimbs than males in poor condition.

FIG. 3. Trend toward a curvilinear relationship between the degree of yellow and body condition. Color code 106 is palest yellow, 109 is darkest. The quadratic term approaches significance ($P = 0.08$). The open square is an outlier that was removed from the analysis.

of female mate choice (females choose high-quality males to mate with), or male-male competition (males of high quality are better competitors). We found evidence that male body size and condition were correlated with the size of three secondary sexual traits in Green Frogs, indicating that these traits may function as signals of male quality.

The observed condition dependence of forelimb size may be because of the apparent developmental and maintenance costs associated with these structures. Because the strength of condition dependence indicates the strength of sexual selection on a particular trait (Bonduriansky and Rowe, 2005), forelimb size is likely to be the most affected by sexual selection as compared to throat color and tympanum size. The cost associated with enlarged forelimbs
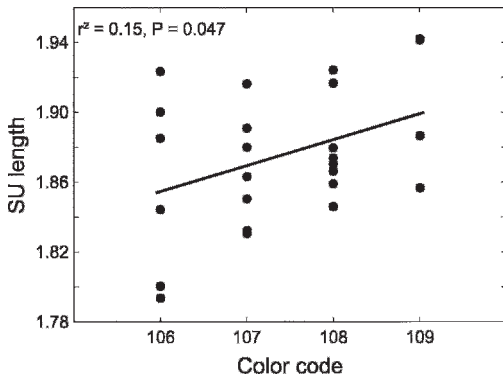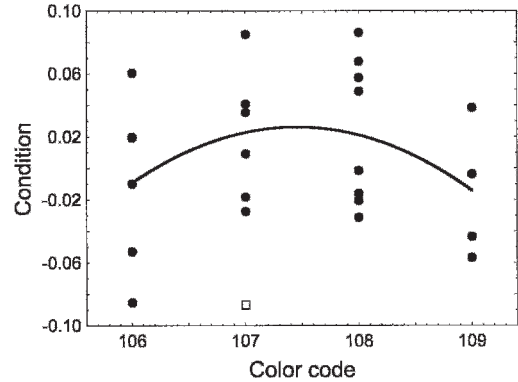
may be associated with the large amount of muscle that compose these grasping structures (Yekta and Blackburn, 1992; Peters and Aulner, 2000). The forelimbs are used for grasping the female for extended periods (amplexus) during mating. Maintaining this force during amplexus is likely an important component of reproductive success for male frogs because it reduces the possibility of other males fertilizing the eggs. The fitness consequences of large forelimbs have been observed in male Marine Toads (*Bufo marinus*), where males in amplexus have larger forelimbs than nonamplectant males (Lee, 2001). In addition, males use their forelimbs to wrestle for position when chorusing (Wells, 1977), suggesting that enlarged forelimbs would be advantageous in male-male combat.

FIG. 2. Regression between snout–urostyle length ($\log_{10}$-transformed) and color ($N = 26$; excludes males with white throats). Color code 106 is palest yellow, 109 is darkest. The open square represents an outlier removed from the analysis. Large males have darker yellow throats than small males.
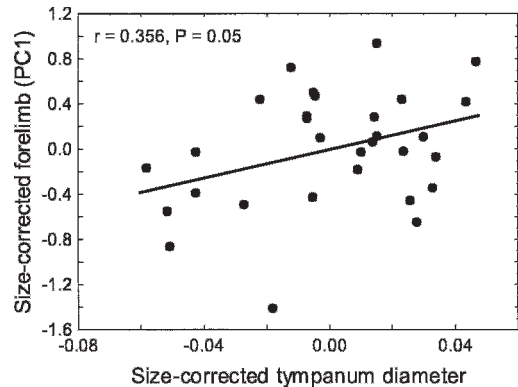

FIG. 4. Correlation between tympanum diameter and forelimb size. After correcting for size, males with large tympana had large forelimbs.

In the context of intersexual selection, there are two likely scenarios that could lead to the evolution of condition dependence in the forelimbs. First, females may resist amplexus and thus males in good condition can overcome female resistance. This may be an example of sexual conflict where the costs of mating are higher for females relative to males (Chapman et al., 2003) or females may use resistance to assess male quality (Cordero and Eberhard, 2003). In both cases, only males in good condition with large forelimbs may be capable of overcoming female resistance and successfully mating. Second, males may experience male-male competition during amplexus. In many frog species, males attempt to disrupt amplexus and take the place of the displaced male (Howard and Kluge, 1985). Males in good condition with large forelimbs may be better able to resist these attempts at disruption.

Coloration can have important fitness consequences, especially when used as a condition-dependent signal of male quality (Candolin, 1999; Keyser and Hill, 1999; Sheldon et al., 2003). The fitness benefits of color signals in amphibians has been demonstrated in the Moorfrog (*Rana arvalis*), where dark blue males produced more viable offspring than light blue males (Sheldon et al., 2003). Our results showed a nonsignificant trend that indicate that males with a low-quality signal (pale yellow throat) were in poor condition, and males with a high quality signal (dark yellow throat) tended to be in poor condition. Males in good condition tended to have an intermediate quality signal (medium yellow throat). This type of result may be a consequence of three scenarios. First, there may be a trade-off between trait quality and body condition—if a male is in poor condition, he may be unable to sustain a costly sexually selected trait, and if a male is sustaining a costly sexually selected trait, then he may be unable to maintain a high body condition. Second, males with a high-quality signal may represent a terminal investment strategy. A similar scenario has been invoked with respect to the nuptial red coloration of male Three-Spined Sticklebacks (*Gasterosteus aculeatus*) where males in both poor and good condition had larger red areas than males in intermediate condition (Candolin, 1999). Males with large red areas in poor condition either engaged in a terminal investment strategy, or were maintaining a high signalling effort for a long period of time (Candolin, 1999).

The degree of yellow in the throat, although not a reliable signal of body condition, reflected body size and, thus, age (because older males tend to be larger [Shirose and Brooks, 1995]). Large male frogs are often more successful at acquiring mates (Howard, 1988; Howard et al., 1994) and, thus, male size may play an important role in female mate choice. Males that are larger may be older and, thus, have enhanced survival and higher quality genes. The degree of yellow throat, thus, may serve as a signal of male size. This might be especially important in a species in which the male posture during courtship may prevent females from evaluating body size directly because males are partially submerged when attracting females. In addition, there is some evidence that males of the closely related American Bullfrog (*Rana catesbeina*) display their throats when interacting with rival males (Ryan, 1980).

The tympanum was not related to body condition, but it was related strongly to body size. It is difficult to determine whether the tympanum is large in large males because it is a signal of large body size or because of allometry. Nonetheless, the tympanum is an important trait with respect to sexual selection. Not only is the male tympanum attuned to sound frequencies emitted by other males (Hetherington, 1994), but it is critical for producing sound (Purgue, 1997) and locating rival males (Bosch and Marquez, 2000). Although the tympanum was not related to our measure of body condition, it was related to forelimb size independent of body size, indicating that, although tympanum diameter may not be related to body condition, it could be related to some other, unmeasured, index of male quality.

The sexually dimorphic structures of male Green Frogs reflected different aspects of male quality. These patterns are consistent with the view that sexual signals and traits associated with sexual selection are components of an overall signal that reflects different aspects of male quality (Badyaev et al., 2001; Møller and Petrie, 2002). In addition, secondary sexual traits that are important for male-male competition may also be used as cues, in that they may confer a mating advantage to males that have large traits (e.g., forelimbs) but may also signal male quality to females. Females may rely on multiple signals to uncover males that are cheating and displaying high-quality signals yet are of poor individual quality (Møller et al., 1998; Vasquez and Pfennig, 2007). In the context of ranid frogs, our results indicate that sexually dimorphic structures in male Green Frogs reflect both body condition and size, thus providing specific morphological traits that a female can use to evaluate male quality. Females may bias mate choice toward males that offer multiple signals of quality, including morphological traits. In addition, these signals

may be important in the assessment of rivals by males.

Future directions should examine the effects of the secondary sexual traits we examined on mating success, as well as any genetic benefits that females may accrue by mating with males of high quality. In addition, by assessing the developmental and maintenance costs of these secondary sexual traits, application of the handicap model of sexual selection may be possible, especially with respect to throat coloration.

LITERATURE CITED

ANDERSSON, M. 1994. Sexual Selection. Princeton University Press, Princeton, N.J.

BADYAEV, A. V., G. E. HILL, P. O. DUNN, AND J. C. GLEN. 2001. Plumage color as a composite trait: developmental and functional integration of sexual ornamentation. American Naturalist 158:221–235.

BONDURIANSKY, R., AND L. ROWE. 2005. Sexual selection, genetic architecture, and the condition dependence of body shape in the sexually dimorphic fly *Prochyliza xanthostoma* (Piophilidae). Evolution 59:138–151.

BOSCH, J., AND R. MARQUEZ. 2000. Tympanum fluctuating asymmetry, body size and mate choice in female Midwife Toads (*Alytes obstetricans*). Behavior 137:1211–1222.

CANDOLIN, U. 1999. The relationship between signal quality and physical condition: is sexual signalling honest in the Three-Spined Stickleback? Animal Behavior 58:1261–1267.

CHAPMAN, T., G. ARNQVIST, J. BANGHAM, AND L. ROWE. 2003. Sexual conflict. Trends in Ecology and Evolution 18:41–47.

CORDERO, C., AND W. G. EBERHARD. 2003. Female choice of sexually antagonistic male adaptations: a critical review of some current research. Journal of Evolutionary Biology 16:1–6.

CÔTÉ, S. D., AND M. FESTA-BIANCHET. 2001. Life-history correlates of horn asymmetry in mountain goats. Journal of Mammalogy 82:389–400.

COTTON, A., K. FOWLER, AND A. POMIANKOWSKI. 2004. Condition dependence of sexual ornament size and variation in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). Evolution 58:1038–1046.

DYSON, M. L., S. P. HENZI, T. R HALLIDAY, AND L. BARRETT. 1998. Success breeds success in mating male Reed Frogs (*Hyperolius marmoratus*). Proceedings of the Royal Society of London 265B:1417–1421.

EMERSON, S. B., L. CARROLL, AND D. L. HESS. 1997. Hormonal induction of thumb pads and the evolution of secondary sexual characteristics of the Southeast Asian Fanged Frog, *Rana blythii*. Journal of Experimental Zoology 279:587–596.

FESTA-BIANCHET, M., D. W. COLTMAN, L. TURELLI, AND J. T. JORGENSON. 2004. Relative allocation to horn and body growth in bighorn rams varies with resource availability. Behavioral Ecology 15:305–312.

GREEN, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? Ecology 82:1473–1483.

HARDING, J. 1997. Amphibians and Reptiles of the Great Lakes Region. University of Michigan Press, Ann Arbor.

HETHERINGTON, T. E. 1994. Sexual differences in the tympanic frequency responses of the American Bullfrog (*Rana catesbeiana*). Journal of the Acoustic Society of America 96:1186–1188.

HOWARD, R. D. 1988. Reproductive success in two species of anurans. *In* T. H. Clutton-Brock (ed.), Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems, pp. 99–113. University of Chicago Press, Chicago.

HOWARD, R. D., AND A. G. KLUGE. 1985. Proximate mechanisms of sexual selection in Wood Frogs. Evolution 39:260–277.

HOWARD, R. D., H. H. WHITEMAN, AND T. I. SCHUELLER. 1994. Sexual selection in American toads: a test of a good-genes hypothesis. Evolution 48:1286–1300.

JUDGE, K. A., AND R. J. BROOKS. 2001. Chorus participation by male Bullfrogs, *Rana catesbeiana*: a test of the energetic constraint hypothesis. Animal Behavior 62:849–861.

KEYSER, A. J., AND G. E. HILL. 1999. Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. Proceedings of the Royal Society of London 266B:771–777.

LEE, J. C. 2001. Evolution of a secondary sexual dimorphism in the toad, *Bufo marinus*. Copeia 2001:928–935.

MERILÄ, J., L. KRUUK, AND B. C. SHELDON. 2001. Natural selection on genetical component of variation in body condition index in a wild bird population. Journal of Evolutionary Biology 14:918–929.

MØLLER, A. P., AND M. PETRIE. 2002. Condition dependence, multiple sexual signals, and immunocompetence in peacocks. Behavioral Ecology 13:248–253.

MØLLER, A. P., N. SAINO, G. TARAMINO, P. GALEOTTIE, AND S. FERRARIO. 1998. Paternity and multiple signaling: effects of a secondary sexual character and song on paternity in the barn swallow. American Naturalist 151:236–242.

MONTGOMERIE, R. 2006. Analyzing colors. *In* G. E. Hill and K. J. McGraw (eds.), Bird Coloration: Methods and Mechanisms. Harvard University Press, Cambridge MA.

PETERS, S. E., AND D. A. AULNER. 2000. Sexual dimorphism in forelimb muscles of the Bullfrog *Rana catesbeiana*: a functional analysis of isometric contractile properties. Journal of Experimental Biology 203:3639–3654.

PURGUE, A. P. 1997. Tympanic sound radiation in the Bullfrog *Rana catesbeiana*. Journal of Comparative Physiology A 181:438–445.

ROSENTHAL, G. G., S. A. RAND, AND M. J. RYAN. 2004. The vocal sac as a visual cue in anuran communication: an experimental analysis using video playback. Animal Behavior 68:55–58.

RYAN, M. J. 1980. The reproductive behavior of the Bullfrog (*Rana catesbeiana*). Copiea 1980:108–114.

SCHULTE-HOSTEDDE, A. I., B. ZINNER, J. S. MILLAR, AND G. J. HICKLING. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology 86:155–163.

SHELDON, B. C., H. ARPONEN, A. LAURILA, P.-A. CROCHET, AND J.Merilä. 2003. Sire coloration influences offspring survival under predation risk in the Moorfrog. Journal of Evolutionary Biology 16:1288–1295.

SHIROSE, L. J., AND R. J. BROOKS. 1995. Growth rate and age at maturity in syntopic populations on *Rana clamitans* and *Rana septentrionalis* in central Ontario. Canadian Journal of Zoology 73:1468–1473.

SIDOR, C. A., AND D. G. BLACKBURN. 1998. Effects of testosterone administration and castration on the forelimb musculature of male Leopard Frogs, *Rana pipiens*. Journal of Experimental Zoology 280:28–37.

SIMMONS, L. W., AND J. S. KOTIAHO. 2002. Evolution of ejaculates: patterns of phenotypic and genotypic variation and condition dependence in sperm competition traits. Evolution 56:1622–1631.

SUMMERS, K., R. SYMULA, M. CLOUGH, AND T. W. CRONIN. 1999. Visual mate choice in poison frogs. Proceedings of the Royal Society of London 266B:2141–2145.

VÁSQUEZ, T., AND K. S. PFENNIG. 2007. Looking on the bright side: females prefer coloration indicative of male size and condition in the sexually dichromatic Spadefoot Toad, *Scaphiopus couchii*. Behavioral Ecology and Sociobiology 62:127–135.

WELLS, K. D. 1977. Territoriality and male mating success in the Green Frog (*Rana clamitans*). Ecology 58:750–762.

———. 1978. Territoriality in the Green Frog (*Rana clamitans*): vocalizations and agonistic behavior. Animal Behavior 26:1051–1063.

YEKTA, N., AND D. BLACKBURN. 1992. Sexual dimorphism in mass and protein content of the forelimb muscles of the northern Leopard Frog *Rana pipiens*. Canadian Journal of Zoology 70:670–674.

ZUG, G. R., L. J. VITT, AND J. P. CALDWELL. 2001. Herpetology. Academic Press, San Diego, CA.