Evolution, 57(12), 2003, pp. 2904–2910

CORRELATED EVOLUTION OF CONSPICUOUS COLORATION AND BODY SIZE IN POISON FROGS (DENDROBATIDAE)

MATTIAS HAGMAN AND ANDERS FORSMAN[1]
Department of Biology and Environmental Sciences, Kalmar University, SE-391 82 Kalmar, Sweden

Abstract.—Conspicuous coloration is often used in combination with chemical defenses to deter predators from attacking. Experimental studies have shown that the avoidance inducing effect of conspicuous prey coloration increases with increasing size of pattern elements and with increasing body size. Here we use a comparative approach to test the prediction from these findings, namely that conspicuous coloration will evolve in tandem with body size. In our analysis, we use a previously published mitochondrial DNA-based phylogeny and comparative analysis of independent contrasts to examine if evolutionary shifts in color pattern have been associated with evolutionary changes in body size in aposematic poison frogs (Anura: Dendrobatidae). Information on body size (snout to vent length) and coloration were obtained from the literature. Two different measures of conspicuousness were used, one based on rankings by human observers and the other based on computer analysis of digitized photographs. The results from comparative analyses using either measure of coloration indicated that avoidance inducing coloration and body size have evolved in concert in poison frogs. Results from reconstruction of character change further indicate that the correlated evolution of size and coloration has involved changes in both directions within each of the different clades of the phylogenetic tree. This finding is consistent with the hypothesis that selection imposed by visually guided predators has promoted the evolution of larger body size in species with conspicuous coloration, or enhanced evolution of conspicuous coloration in larger species.

Key words.—Aposematism, body size, coloration, Dendrobatidae, evolution, phylogeny, signaling.

Received June 17, 2003. Accepted July 3, 2003.

Animals that are distasteful, noxious, or otherwise dangerous typically possess bright colors (often red, yellow, or white in combination with black) and simple, conspicuous patterns, presumably to signal their unprofitable nature to potential predators (Bates 1862; Darwin 1871; Wallace 1878; Poulton 1890; Cott 1940; Edmunds 1974; Endler 1991). The received view of aposematism is that conspicuous coloration has evolved because it is easy for predators to detect, learn, recall, and associate with the defense (Gittleman and Harvey 1980; Leimar et al. 1986; Roper and Redstone 1987; Guilford 1988, 1990; Alatalo and Mappes 1996; Gamberale and Tullberg 1996; Rowe and Guilford 1996).

Recent findings suggest that the efficacy of warning coloration increases with increasing size of color pattern elements as well as with increasing body size. Thus, Gamberale and Tullberg (1996, 1998) experimentally presented naive domestic chicks different sized instars of live aposematic insects (*Tropidothorax leucopterus*) and found that the predator's unconditioned aversion increases towards larger sized prey. There is also experimental evidence, based on behavioral responses of domestic chicks to artificial butterfly wing displays, that the protective value of visual warning signals is increased by large pattern elements (Forsman and Merilaita 1999). Similarly, great tits have been shown to learn more rapidly to discriminate artificial signaling unpalatable prey from nonsignaling palatable prey if the signal has large rather than small pattern elements (Lindström et al. 1999). These findings suggest that prey species that have acquired warning coloration may be exposed to selection for larger body size and visual displays with large pattern elements (Forsman and Merilaita 1999). The positive effect of large body size on avoidance signaling also suggests that warning coloration may evolve more easily in already large, as opposed to small, prey species (Nilsson and Forsman 2003). Another reason to expect conspicuous avoidance-inducing signals to evolve more easily in larger animals is that large body size may impair the effectiveness of the alternative strategy camouflage, or cryptic coloration, which functions to decrease the risk of detection. If cryptic coloration is more difficult to achieve for large as compared to small species (Cott 1940), then this constraint on camouflage may enhance the evolution of conspicuous coloration by reducing the initial costs of such antipredator signals. All these three scenarios predict evolutionary increments in the degree of conspicuousness of color patterns to be correlated with evolutionary increments in body size. Here we use a comparative approach to test if conspicuousness has evolved in tandem with body size in the poison frogs (Anura: Dendrobatidae).

Poison frogs provide a good opportunity to test for correlated evolution of conspicuous coloration and body size. These anuran amphibians display a wide range of color patterns and toxicity, with some species being extremely conspicuously colored and containing some of the most toxic alkaloid compounds known (e.g., Daly and Myers 1967; Heselhaus 1992; Walls 1994; Daly 1995). There also is recent evidence that conspicuous coloration and toxicity has evolved in concert in poison frogs, a finding consistent with the notion that they are aposematic (Summers and Clough 2001). Although poison frogs are known for their relatively small size (15–50mm adult snout to vent length), variation in body size exists among different species (Heselhaus 1992; Walls 1994), such that an association between conspicuousness and body size is detectable, if present. Finally, a hypothesis of the phylogenetic relationships among different species of poison

---

[1] Corresponding author. E-mail: anders.forsman@hik.se.

frogs, based on mitochondrial DNA sequence variation, is available (Clough and Summers 2000). Such a phylogenetic hypothesis is a prerequisite for the reconstruction and analysis of evolutionary change, and allows separating associations among traits that are caused by shared ancestry from those that are caused by correlated evolutionary change (Felsenstein 1985; Harvey and Pagel 1991). The aim of this study is to use the hypothesis of evolutionary relationships in a comparative analysis of independent contrasts to investigate whether evolutionary shifts in coloration have been associated with evolutionary changes in body size, using data for 21 species of poison frogs. Because toxicity, coloration, and body size may interactively influence susceptibility to predation we also examine if changes in body size have been associated with shifts in toxicity.

MATERIALS AND METHODS

Data on Coloration and Body Size

Our dataset includes the same 21 species of poison frogs that were used in Summers and Clough (2001). We used two different measures of coloration, both of which were obtained from Summers and Clough (2001). The first measure was based on ratings made by 24 human observers presented with color photographs of the 21 species. Ratings of brightness and extent of coloration were then combined in a composite measure, and the mean value across observers was used for each species (for details see Summers and Clough 2001). Admittedly, any attempt to classify animal color patterns as either cryptic or conspicuous without taking into consideration the visual background in the natural habitat will be prone to error (Endler 1978). To obtain a second, independent, estimate of coloration, digitized color images of the animals were analyzed with a computer program to quantify the brightness of each of the three major color hues (red, blue, and green) for each species of frog. Species-specific measures of brightness were then contrasted against measures of brightness from a similar analysis carried out on photographs of leaf-litter. These computer-generated estimates thus yielded a measure of the overall brightness of coloration of each species relative to a leaf-littered visual background (Summers and Clough 2001). The scale of variation in coloration was 1–10 for both the human observer- and computer-generated measures. Both measures of coloration also showed substantial variation among species (see table 1 in Summers and Clough 2001) and were highly correlated across species ($r = 0.75$, $n = 21$, $P < 0.0001$). As for variation in coloration, individuals within populations generally look similar relative to differences between species. There is not a continuous gradient of color and pattern between different species in the field, and in most cases even closely related species look distinctly and consistently different in color and pattern (K. Summers, pers. comm). Intraspecific variation in coloration thus is unlikely to confound the results of the present study. Moreover, because the frogs in the photos used to measure coloration were all very similar in size and were not shown in their natural sizes, it is unlikely that size itself may have confounded the measurements of conspicuousness (K. Summers, pers. comm). Because birds, unlike humans, can perceive reflected light also in the UV range of the spectra it is possible that a species classified as relatively cryptic by a human observer appears conspicuous to avian predators. However, recent evidence suggests that color patterns that appear colorful to humans are also likely to appear colorful to birds (Vorobyev et al. 2000).

Data on minimum and maximum adult body size (snout to vent length) was obtained from the literature (Silverstone 1976; Heselhaus 1992; Haddad and Martins 1994; Walls 1994; Coloma 1995). Because both the largest and the smallest value was used for each species, our conclusions are not likely to be confounded by any sexual differences in body size.

Analyses

The hypothesis that conspicuous coloration is associated with large body size was tested using two types of analyses. First, each species was treated as an independent unit, to search for general associations between coloration and body size. Second, we computed phylogenetically independent contrasts (Felsenstein 1985) using computer program CAIC (Comparative Analysis by Independent Contrasts, version 2.6.8.b, Purvis and Rambaut 1995), which offers a means of testing for correlated evolution among different characters when data consists of continuous variables, and avoids the problem that associations across species may reflect phylogenetic inertia (Felsenstein 1985, Harvey and Pagel 1991; Purvis and Rambaut 1995).

In their test for correlated evolutionary change of coloration and toxicity in poison frogs, Summers and Clough (2001) used both the punctuational model of character evolution, assuming that all character change occurs at speciation events, and a gradual change model in which the amount of change is assumed proportional to the branch length, where branch length was measured as the genetic distance based on sequence divergence of mitochondrial DNA sequences. Their analyses yielded nearly identical results for these maximally distinctive models of character evolution. We nevertheless follow their approach and analyze the data using both models of character evolution. Information on branch lengths was provided by K. Summers, Biology Department, East Carolina University, Greenville, NC. Data on body size and coloration was square-root transformed prior to analyses to meet the statistical assumptions (Purvis and Rambaut 1995). To test the null hypothesis of no relationship between evolutionary changes in these two variables, we regressed contrasts for coloration on contrasts for body size, through the origin, and tested if the slope of the relationship differed significantly from zero (Harvey and Pagel 1991; Pagel 1993; Purvis and Rambaut 1995).

To obtain a visual representation of evolution of coloration and size we used the ‘‘squared-change’’ parsimony option for continuous characters to reconstruct character evolution using computer software Mac Clade 4, version 4.02 (Maddison and Maddison 2000). Data on coloration and size were not recoded as discrete characters but treated as continuous characters in their native form. The squared-change algorithm which minimizes the sum of the squared changes on the branches of the tree does not allow reconstruction of character evolution if the phylogeny contains soft polytomous nodes

TABLE 1. Statistics for the regression of the standardized contrasts of body size on coloration in poison frogs, under a punctuational and gradual model of character evolutionary change, using data on minimum and maximum body size, and observer- and computer-rated estimates of coloration.

Model of character evolution	Body size	Coloration	R^2	$F_{1,17}$	P
Punctuational	Maximum	Observer	0.24	5.24	0.035
Punctuational	Maximum	Computer	0.39	10.80	0.0044
Punctuational	Minimum	Observer	0.54	20.05	0.0003
Punctuational	Minimum	Computer	0.49	16.18	0.0009
Gradual	Maximum	Observer	0.22	4.80	0.043
Gradual	Maximum	Computer	0.41	11.59	0.0034
Gradual	Minimum	Observer	0.39	11.07	0.004
Gradual	Minimum	Computer	0.46	14.49	0.0014

that represent uncertainty of species relationships (Maddison and Maddison 2000 and references therein). We therefore resolved the two polytomies (*Colostethus talamance*, *C. marchesianus* and *Dendrobates pumilo*, *D. speciosus*, *D. histrionicus*) in the phylogeny of poison frogs proposed by Summers and Clough (2001). Examination of alternative dichotomous trees resolved from the two polytomies yielded very similar reconstructions of character evolution. We therefore present the results from only one of the alternative trees.

RESULTS

Minimum and maximum adult body size was highly correlated across the different species of poison frogs ($r = 0.83$, $n = 20$, $P < 0.001$). Coloration and maximum body size also was positively and significantly correlated across the different species (analysis based on human observer-ratings of coloration: $r = 0.48$, $n = 21$, $P = 0.029$; computer-generated ratings: $r = 0.54$, $n = 21$, $P = 0.011$). The results from the analysis of independent contrasts suggest that this pattern of increased degree of conspicuousness with increasing body size across species was not simply an epiphenomenon of shared ancestry. Thus, there was a significant correlation between evolutionary changes in maximum body size and evolutionary changes in coloration. This was the case both when using the measures of coloration as rated by human observers and the computer-generated measures (Table 1, Fig. 1). The correlation between evolutionary changes in body size and coloration was even stronger when analyses were based on data on minimum (rather than maximum) adult body size (Table 1). The association between the evolution of body size and conspicuousness was evident assuming either a punctuated or a gradual model of character evolution for these traits (Table 1). These results thus indicate that when coloration or adult body size has undergone an evolutionary change, the other variable generally also has changed in the

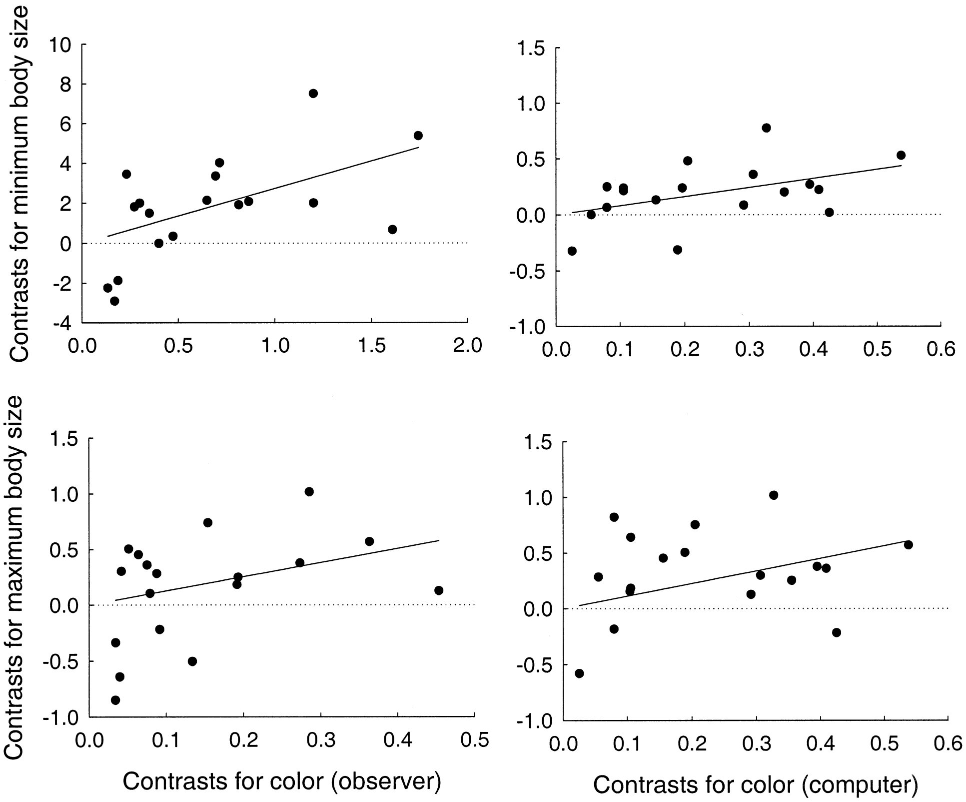

FIG. 1. Relationship between evolutionary shifts in coloration and body length in poison frogs as estimated by phylogenetically independent contrasts, using a punctuational model of evolutionary change in each character. The figure shows the standardized contrasts for minimum body size (top panels) and maximum body size (bottom panels) plotted against the standardized contrasts for coloration as measured by human observers (left) and coloration as measured with a computer-based analysis (right). Results were similar when a gradual change model was used. See text for details.

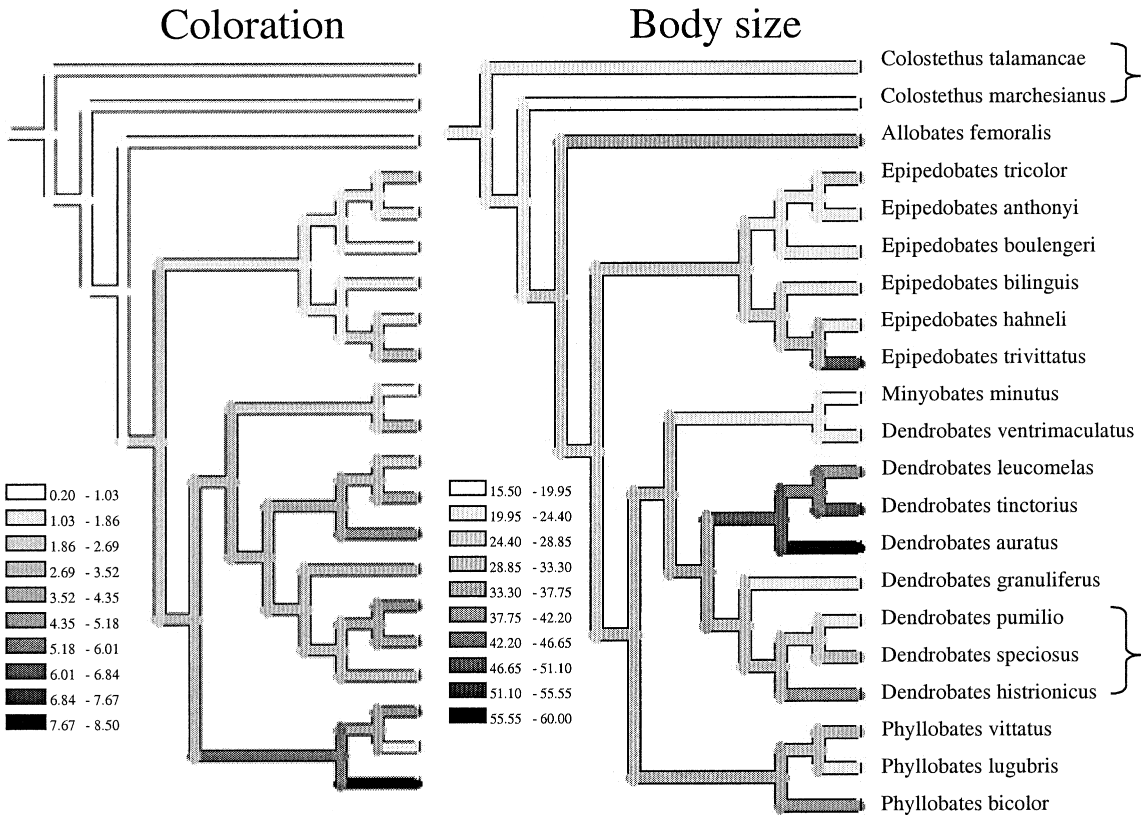

FIG. 2. Evolution of coloration (left) and body size (right) in poison frogs as reconstructed using the squared-change parsimony option for continuous characters in computer software MacClade version 4.02. Darker shadings of branches indicate more conspicuous coloration and larger body size respectively. The phyolgeny is a modified version of the one proposed by Summers and Clough (2001) which contained two polytomies (indicated by brackets on the right) that had to be resolved to allow reconstruction of continuous character change (see text for details).

same direction, that is, coloration and body size have evolved in tandem.

The evolution of coloration and maximum body size in poison frogs as reconstructed using the squared-change parsimony option for continuous characters is depicted separately for each character in Figure 2. Note, however, that the changes in the clade consisting of *Dendrobates pumilo, D. speciosus*, and *D. histrionicus* should be treated with caution because the true phylogenetic relationships of these species is uncertain (Summers and Clough 2001), but had to be resolved to allow reconstruction of the continuous characters (see above). A comparison of the two trees reveals that the overall pattern of correlated evolution of coloration and body size is evident within each of the different clades of the phylogeny. More importantly, this correlated evolution has involved character changes in both directions (Fig. 2 and Table 2). Thus, evolution of more conspicuous coloration has generally been accompanied by evolutionary increments in body size and evolution towards less conspicuous coloration has been generally associated with evolution of smaller body size, within each of the groups Epipedobates, Phyllobates and Dendrobates.

There was no significant correlation between evolutionary changes in body size and evolutionary changes in toxicity (a composite measure of the diversity, quantity, and toxicity of the toxins found in each species, as obtained from Summers and Clough 2001), neither when using data on minimum ($r^2 = 0.20$, $n = 18$, $P = 0.057$) or maximum adult body size ($r^2 = 0.19$, $n = 18$, $P = 0.059$).

TABLE 2. Cross-tabulation showing the association of evolutionary changes in maximum body size and coloration in poison frogs, as reconstructed using the squared-change parsimony option for continuous characters in computer software MacClade version 4.02 and illustrated in Figure 2.

Change in body size	Change in conspicuousness		
	Increase	Decrease	No change
Increase	9	0	6
Decrease	3	7	4
No change	2	2	7

DISCUSSION

Several factors have been proposed to favor the evolution of conspicuous prey coloration, including unprofitability (i.e., toxicity or ability to resist predation), kin selection, gregarious behavior, and neophobic reactions of predators (Coppinger 1969, 1970; Guilford 1988, 1990; Gittleman and Harvey 1980; Leimar et al. 1986; Roper and Redstone 1987; Alatalo and Mappes 1996; Gamberale and Tullberg 1996; Rowe and Guilford 1996). A central tenet of models of evolution of aposematism is that warning coloration is used by prey to signal their unprofitable nature to potential predators as a means of avoiding being attacked. If so, one would thus expect that conspicuous coloration will become correlated with unprofitability over evolutionary time, a scenario that received support in a recent comparative study of poison frogs (Summers and Clough 2001).

The results of the present study suggest that coloration in poison frogs has evolved in tandem not only with toxicity (Summers and Clough 2001) but also with body size (Figs. 1 and 2, Table 1). This finding is consistent with the hypothesis that evolution of conspicuous coloration enhances the evolution of larger body size, or, alternatively, that large body size promotes the evolution of more conspicuous coloration. Although the reconstruction of character evolution suggests that coloration and size have evolved in tandem within each of the different clades of the phylogeny (Fig. 2 and Table 2), it does not allow us to determine whether evolution of more conspicuous coloration has preceded the evolution of larger body size or vice versa. We are therefore unable to separate between the two competing hypotheses. However, given that body size covaries with several important physiological and life-history traits (e.g., Roff 1992), we consider it most plausible that changes in body size have preceded the shifts in coloration. Moreover, large body size may facilitate the evolution of conspicuous coloration not only by increasing the effectiveness of avoidance-inducing signals (Gamberale and Tullberg 1996, 1998) but also by constraining camouflage.

We are aware of only one previous test of the hypothesis addressed in this study. In a comparative analysis of data from butterflies, Nilsson and Forsman (2003) found no support for the hypothesis that evolutionary changes of larval coloration had been associated with evolutionary changes in larval body length. There are several possible explanations for the discrepancy between these two studies. First, in the butterfly study coloration was scored on a dichotomous scale (i.e., either cryptic or conspicuous). In the present study, however, coloration was scored on a scale from 1 to 10, resulting in higher statistical power. Second, the butterfly study was based on a relatively poorly resolved phylogenetic hypothesis with several polytomies and data on larval coloration and body size was not available for all species. Consequently, the probability of detecting correlated evolution between coloration and size, if present, was smaller in the analysis of butterflies, compared to the present study. Third, phylogenetic studies suggest that coloration mode in butterflies is dependent on lifestyle, with conspicuous coloration occurring primarily in species with gregarious larvae and cryptic coloration predominating among species with solitary larvae (Sillén-Tullberg 1988, 1993). This association between coloration and lifestyle in butterflies may have confounded the relationship between coloration and body size because evolutionary transitions in lifestyle were found to be correlated with evolutionary changes in larval body size, with group living being associated with smaller body size (Nilsson and Forsman 2003). Finally, because evolutionary increments in larval body length were accompanied by increments in adult wingspan the predicted association between coloration and body size in butterflies may have been confounded also by conflicting selection on body size in larvae and adults (Nilsson and Forsman 2003).

The finding that coloration is more conspicuous in larger species of poison frogs seems to be paralleled by the ontogeny of color pattern in some dendrobatid species. For instance, juveniles of the species *Phyllobates terribilis* and *P. bicolor* both are dark brown to black in ground color with two yellowish lateral bands but become almost uniform yellow as adults (Zimmermann 1986; Walls 1994). This change in coloration with increasing size and age is consistent with the notion that the protective value of a certain color pattern may change as a function of body size (Cott 1940; King 1992) or behavior (Brodie 1992; Forsman and Appelqvist 1998, 1999). Although our present results (Fig. 1) are consistent with the hypothesis that selection imposed by visually guided predators has promoted the evolution of larger body size in species with conspicuous coloration, or enhanced evolution of more conspicuous coloration in larger species, it is important to remember that correlation does not demonstrate causation. Information on the response of predators presented with conspicuous versus dull individuals of different size (Brodie 1993; Gamberale and Tullberg 1996, 1998) is required to further test the hypothesis of an interactive effect of coloration and body size on predator avoidance (King 1992) in poison frogs. Monitoring the survival in natural populations of individuals whose color patterns has been experimentally manipulated also is necessary to evaluate the role of predators for selection on coloration (Forsman and Appelqvist 1999).

Selective factors other than predation may have influenced the evolution of coloration and body size in these frogs, and there are alternative hypotheses for the correlated evolution of these two traits. For instance, sexual selection may favor the evolution of both large size and bright coloration (Andersson 1994). Experimental evidence suggests that female poison frogs use visual cues in mate choice, and that coloration may be such a cue (Summers et al. 1999). However, the fact that strong sexual selection occurs in inconspicuously colored species of the genus *Colostethus* as well as in conspicuous species of the genus *Dendrobates* (Summers 2000) argues against sexual selection being responsible for the joint evolution of coloration and size. Because frogs are ectothermic organisms, the bodily functions of which are strongly dependent upon body temperature (Huey and Kingsolver 1989), selection is likely to have influenced characters that affect the ability to achieve and maintain body temperatures that optimize performance (Huey and Hertz 1984; Peterson et al. 1993). Both coloration (e.g., De Jong et al. 1996) and body size (Stevenson 1985) significantly influence heat balance of ectotherms. However, behavioral observations of species of the genus *Colostethus* that occur sympatrically with more brightly colored dendrobatids suggest that effective temperature regulation by these frogs does not require conspicuous coloration (Summers 2000). We thus consider both sexual selection and selection for effective thermoregulation possible but less plausible alternative explanations for the correlated evolution of conspicuous coloration and body size in poison frogs. The role of body size in the evolution of conspicuous coloration and aposematism should be investigated also in other groups of organisms to evaluate the generality of our findings.

Acknowledgments

We are grateful to K. Summers for sharing his knowledge on poison frogs and providing data on branch lengths, and to J. Ahnesjö, M. Härlin, S. Merilaita, K. Summers, L. Trueb, and J. Wallin for discussion and comments that helped improve an earlier draft of the manuscript. The study was supported financially by The Swedish Research Council (grant to AF), Växjö University and Kalmar University.

Literature Cited

Alatalo, R. V., and J. Mappes. 1996. Tracking the evolution of warning signals. Nature 382:708–709.

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

Bates, W. H. 1862. Contributions to an insect fauna of the Amazon valley. Lepidoptera: Helicinidae. Trans. Linn. Soc. London 23: 495–566.

Brodie, E. D., III 1992. Corrleational selection for color pattern and antipredator behaviour in the garter snake *Thamnophis ordinoides*. Evolution 46:1284–1298.

———. 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa-Rica. Evolution 47: 227–235.

Clough, M., and K. Summers. 2000. Phylogenetic systematics and biogeography of the poison frogs: evidence from mitochondrial DNA sequences. Biol. J. Linn. Soc. 70:515–540.

Coppinger, R. P. 1969. The effect of experience and novelty on avian feeding behaviour with reference to the evolution of warning coloration in butterflies. I. Reactions of wild-caught adult blue-jays to novel insects. Behavior 35:4–60.

———. 1970. The effect of experience and novelty on avian feeding behaviour with reference to the evolution of warning coloration in butterflies. II. Reactions of the naïve birds to novel insects. Am. Nat. 104:323–335.

Coloma, A. 1995. Ecuadorian frogs of the genus Colostethus. Misc. Pub. Univ. Kansas Nat. Hist. Mus. 87:1–75.

Cott, H. B. 1940. Adaptive coloration in animals. Methuen, London.

Daly, J. 1995. The chemistry of poisons in amphibian skin. Proc. Natl. Acad. Sci. 92:9–13.

Daly, J. and C. Myers. 1967. Toxicity of Panamanian poison frogs (Dendrobates): some biological and chemical aspects. Science 156:970–973.

Darwin, C. 1871. The descent of man and selection in relation to sex. 2nd ed. John Murray. London.

DeJong, P., S. W. S. Gussekloo, and P. M. Brakefield. 1996. Differences in thermal balance, body temperature and activity between non-melanic and melanic two-spot ladybird beetles (*Adalia bipunctata*) under controlled conditions. J. Exper. Biol. 199: 2655–2666.

Edmunds, M. 1974. Defence in animals. Longman, Harlow, U.K.

Endler, J. A. 1978. A predators view of animal color patterns. Evol. Biol. 11:319–364.

———. 1991. Interactions between predators and prey. Pp. 169–196 *in* J.R. Krebs and N.B. Davies, eds. Behavioural ecology: an evolutionary approach. 3rd ed. Blackwell, Oxford, U.K.

Felsenstein, J. 1985. Phylogenies and the comparative method. Am. Nat. 125:1–15.

Forsman, A., and S. Appelqvist. 1998. Visual predators impose correlational selection on prey color pattern and behavior. Behav. Ecol. 9:409–413.

———. 1999. Experimental manipulation reveals differential effects of colour pattern on survival in male and female pygmy grasshoppers. J. Evol. Biol. 12:391–401.

Forsman, A., and S. Merilaita. 1999. Fearful symmetry: pattern size and asymmetry affects aposematic signal efficacy. Evol. Ecol. 13:131–140.

Gamberale, G., and B. S. Tullberg. 1996. Evidence for a peak-shift in predator generalization among aposematic prey. Proc. R. Soc. Lond. B. 263:1329–1334.

———. 1998. Aposematism and gregariousness: the combined effect of group size and coloration on signal repellence. Proc. R. Soc. Lond. B 265:889–894.

Gittleman, J. L., and P. H. Harvey. 1980. Why are distasteful prey not cryptic? Nature 286:149–150.

Guilford, T. 1988. The evolution of conspicuous coloration. Am. Nat. 131:7–21.

———. 1990. The evolution of aposematism. Pp. 23–61 *in* D. L. Evans and J. O. Schmidt, eds. Insect defence 1. State Univ. of New York Press, Albany, NY.

Haddad, C. F. B., and M. Martins. 1994. Four species of Brazilian poison frogs related to *Epipedobates pictus* (Dendrobatidae): Taxonomy and natural history observations. Herpetologica 50: 282–295.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford Univ. Press, Oxford, U.K.

Heselhaus, R. 1992. Poison arrow frogs. Ralph Curtis Books, Sanibel Island, FL.

Huey, R. B., and P. E. Hertz. 1984. Is a jack-of-all temperatures a master of none? Evolution 38:441–444.

Huey, R. B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends Ecol. Evol. 4: 131–135.

King, R. B. 1992. Lake Erie water snakes revisited: morph- and age-specific variation in relative crypsis. Evol. Ecol. 6:115–124.

Leimar, O., M. Enquist, and B. Sillén-Tullberg. 1986. Evolutionary stability of aposematic coloration and prey unprofitability: a theoretical analysis. Am. Nat. 128:468–490.

Lindström, L., R. V. Alatalo, J. Mappes, M. Riipi, and L. Vertainen. 1999. Can aposematic signals evolve by gradual change? Nature 397:249–251.

Maddison, D. R., and W. P. Maddison. 2000. MacClade 4. Vers. 4.02. Sinauer Associates, Sunderland, MA.

Nilsson, M., and A. Forsman. 2003. Evolution of conspicuous coloration, body size and gregariousness: a comparative analysis of lepidopteran larvae. Evol. Ecol. 17:51–66.

Pagel, M. 1993. Seeking the evolutionary regression coefficient: an analysis of what comparative methods measure. J. Theor. Biol. 164:191–205.

Peterson, C. R., A. R. Gibson, and M. E. Dorcas. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. Pp. 241–314 *in* R. A. Seigel and J. T. Collins, eds. Snakes—ecology and behavior. McGraw Hill, New York.

Poulton, E. B. 1890. The colour of animals: their meaning and use. Keagan Paul, Trench, Trubner, London.

Purvis, A. and A. Rambaut. 1995. Comparative analysis by independent contrasts (C.A.I.C.): an Apple Macintosh application for analyzing comparative data. Computer Appl. Biosciences 11: 247–251.

Roff, D. A. 1992. The evolution of life histories. Chapman and Hall, New York.

Roper, T. J., and S. Redstone. 1987. Conspicuousness of distasteful prey affects the strength and durability of one-trial avoidance learning. Anim. Behav. 35:739–747.

Rowe, C., and T. Guilford. 1996. Hidden colour aversions in domestic chicks triggered by pyrazine odours of insect warning displays. Nature 383:520–522.

Sillén-Tullberg, B. 1988. Evolution of gregariousness in aposematic butterfly larvae: a phylogenetic analysis. Evolution 42:293–305.

———. 1993. The effect of biased inclusion of taxa on the correlation between discrete characters in phylogenetic trees. Evolution 47:1182–1191.

Silverstone, P. 1976. A revision of the poison-arrow frogs of the genus Phyllobates Bibron in Sagra (Family Dendrobatidae). Nat. Hist. Mus. Los Angeles County Sci. Bull. 27:1–53.

Stevenson, R. D. 1985. Body size and limits to the daily range of body temperatures in terrestrial ectotherms. Am. Nat. 125: 102–117.

Summers, K. 2000. Mating and aggressive behaviour in dendrobatid frogs from Corcovado National Park, Costa Rica: a comparative study. Behavior 137:7–24.

Summers, K., and M. E. Clough. 2001. The evolution of coloration and toxicity in the poison frog family (Dendrobatidae). Proc. Natl. Acad. Sci. USA 98:6227–6232.

Summers, K., R. Symula, M. Clough, and T. Cronin. 1999. Visual mate choice in poison frogs. Porc. R. Soc. London, Series B. 266:2141–2145.

Vorobyev, M., J. Marshall, D. Osorio, N. De Ibarra, and R. Menzel. 2000. Colourful objects through animal eyes. Color Res. Appl. 26:S215–S217.

Wallace, A. R. 1878. Tropical nature and other essays. Macmillan, London.

Walls, J. G. 1994. Jewels of the rainforest. T. F. H. Publications, Neptune, NJ.

Zimmerman, E. 1986. Breeding terrarium animals. T. F. H. Publications, Neptune, NJ.

Corresponding Editor: P. Wainwright