Biological Journal of the Linnean Society (2000), *70:* 633–665

doi: 10.1006/bijl.1999.0421, available online at http://www.idealibrary.com on IDEAL®

A review of colour and pattern polymorphisms in anurans

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Received 16 February 1999; accepted for publication 30 October 1999

Species that exhibit polymorphism, the simultaneous occurrence of two or more discrete, genetically-based phenotypes in a population, are ideal for studying the microevolutionary forces that maintain genetic variation in nature. Many anuran species exhibit striking colour or dorsal pattern polymorphisms, and so provide an excellent system in which to study questions pertaining to the evolution and maintenance of polymorphisms. Despite the wide occurrence of pattern or colour polymorphisms in anurans (current records cite at least 225 species representing 35 genera and 11 families) surprisingly little conclusive work has been done on the inheritance and selective maintenance of this variation. The mode of inheritance has been investigated in 26 species, but conclusively demonstrated in only two. Forty-six species have been described as undergoing ontogenetic change, and 32 species have been described as sexually dimorphic. That anuran polymorphisms are under some sort of selection has been inferred from the large number of polymorphic species, from putative cases of apparent convergent evolution and the existence of identical polymorphisms in closely related species, from cyclical fluctuations in morph frequencies, and from a few observations of non-random survival during bouts of stress. The selective mechanisms maintaining these polymorphisms have been investigated in only 19 species. Most studies looked for physiological traits correlated with the polymorphism, rather than studying the most obvious mechanism, selective predation on colour/pattern itself. Thus, anuran polymorphisms remain a rich but largely unexploited system for studying the evolution of phenotypic variation in nature.

ADDITIONAL KEY WORDS:—amphibian – chromatophore – frog – evolution – inheritance – ontogenetic change – selection – sexual dimorphism – toad.

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0024–4066/00/080633+33 $35.00/0

INTRODUCTION

Polymorphism can be defined as the simultaneous occurrence of two or more discrete, genetically-based phenotypes in a population, in which the frequency of the rarest type is higher than can be maintained by recurrent mutation (Ford, 1975; e.g. greater than 1% given reasonable values for selection and mutation rates in finite populations; Hartl & Clark, 1997; Hedrick, 1985). Species that exhibit visible polymorphisms are ideal for examining the microevolutionary forces that maintain genetic variation in nature. This is because phenotypes are easily scored, and because colour or pattern polymorphisms often have simple Mendelian inheritance. Classic examples include studies of the peppered moth, *Biston betalaria* (Kettelwell, 1961), and the land snail, *Cepaea* sp. (Jones, Leith & Rawlings, 1977).

Many anuran species exhibit striking colour or dorsal pattern polymorphisms, and so provide an excellent system in which to study questions pertaining to the evolution and maintenance of polymorphisms. Nevertheless, surprisingly little conclusive work has been done on the inheritance and selective maintenance of anuran polymorphisms, so the system remains largely unexploited. Here we review the literature on anuran colour or pattern (hereafter CP) polymorphisms by focusing on five main topics: proximate basis of colour or pattern variation, colour change, sexual dimorphism, modes of inheritance, and evidence for natural selection. Our goals in this review are to identify major gaps in the understanding of anuran polymorphisms, and to highlight the potential of this system for future work on the evolution and maintenance of genetic variation in nature.

TYPES OF VARIATION AND TAXONOMIC DISTRIBUTION

Published accounts describe discrete CP polymorphisms in 11/23 (48%) anuran families (Table 1). Thirty-five genera are represented within these 11 families, and at least 225 different species are known to be polymorphic. Interestingly, over one third of these are *Eleutherodactylus* species, and *Phrynobatrachus* and *Hyperolius* represent one fourth of the species (Table 2). All three of these genera are extremely speciose, and *Eleutherodactylus* and *Phrynobatrachus* are poorly studied. Anuran polymorphisms manifest as variation in body colour or in dorsal pattern. The presence or absence of dark stripes or spots on the dorsum is a common polymorphism in many families of anurans (Table 1). Colour variation can involve the entire body, or just parts of the dorsum. Polymorphism for red, green or brown/grey dorsal colour is a common motif. Some species exhibit a combination of the above designs; for example, variation in *Hyla regilla* includes presence/absence of dorsal stripes as well as an array of body colours (Resnick & Jameson, 1963).

Despite the abundance of polymorphic species, surprisingly little is actually known about these polymorphisms. For most species, all we have are brief descriptions or anecdotal observations of a polymorphism (e.g. most *Eleutherodactylus* species, as well as the species listed in Laurent, 1950, 1957; Glaw & Vences, 1992; Stewart, 1974;

TABLE 1. Species for which there is a record of colour or pattern variation. Species are categorized into families as listed by Frost (1985)

Family	Species	Type of polymorphism	Reference
Arthroleptidae	*Arthroleptis adolfifriederici* Nieden	Dorsal colour variation: grey, tan, or green	Stewart, 1967
Bufonidae	*Bufo arenarium* Hensel	Presence/absence of yellow spots	Cei, 1959
	Bufo canorus Camp	Females: black spots on grey or brown. Males: uniform yellow-green to olive	Karlstrom, 1973
	Bufo houstonensis Sanders	Ontogenetic colour change from beige to white	Mays & Freed, 1985
	Bufo periglenes Savage	Females are olive/black. Males are orange	Savage, 1966
	Bufo raddei Strauch	Sexual dimorphism noted, but not described	Savage, 1966
	Bufo regularis Reuss	Presence/absence of vertebral stripe	Stewart, 1967
	Bufo spinulosus Wiegmann	Presence/absence of yellow spots	Cei, 1959
	Bufo taitanus Peters	Males: middorsal pattern of 3 dark blotches. Females: light reddish-brown dorsum with dark flanks	Stewart, 1967
	Bufo typhonius Linnaeus	Body pattern and colour variation	Jones, 1963
Dendrobatidae	*Colostethus pulchellus* Jimenez de la Espada	Dorsal stripe variations	Edwards, 1974
	Dendrobates histrionicus Berthold	Extremely variable in colour pattern	Myers & Daly, 1976
	Dendrobates leucomelas Steindachner	Born with yellow bands around waist, black spots develop within yellow band as they mature	Mattison, 1998
	Dendrobates pumilio O. Schmidt	Dorsal pattern variation	Myers & Daly, 1983
Discoglossidae	*Bombina orientalis* Boulenger	Rare pale morph	Ellinger, 1980
	Discoglossus pictus Otth	Stripe and spot pattern variation	Bruce & Parkes, 1947; Lantz, 1947

continued

TABLE 1—*continued*

Family	Species	Type of polymorphism	Reference
Hylidae	*Acris crepitans* Baird, *Acris gryllus* LeConte	Grey, green, or red vertebral stripe	Pyburn, 1961a, b; Wendelken, 1968; Isaacs, 1971; Gray, 1972, 1977, 1978, 1983; Nevo, 1973; Gorman, 1986
	Agalychnis callidryas Cope	Development of spotting pattern	Starret, 1960; Duellman, 1983
	Amphignathodon guentheri Boulenger	Tan, dark brown, or uniform green	Duellman & Ruiz-C, 1986
	Gastrotheca andaquiensis Ruiz & Hernandez	Males are brown and females are green	Lynch, pers. comm.
	Gastrotheca aureomaculata Cochran & Goin	Brown to black with gold spots, or green with no spots	Duellman & Ruiz-C, 1986; Duellman, 1983; Titus, Hillis, & Duellman, 1989
	Gastrotheca griswoldi Shreve	Young juveniles are green, old juveniles are brown to grey	Duellman & Ruiz-C, 1986
	Gastrotheca helenae Dunn	Juveniles are always light tan, adults are tan to dark brown	Duellman & Ruiz-C, 1986
	Gastrotheca peruana Boulenger	Dorsal pattern variation	Duellman & Fritts, 1972
	Hyla bokermanni Goin	Female: 2 dorso-lateral stripes, males: diffusely spotted or speckled	Rivero, 1969
	Hyla leucophyllata Beireis	Colour pattern, variation not described	Titus *et al.*, 1989
	Hyla luteocellata Roux	Female: 2 dorso-lateral stripes, males: diffusely spotted or uniform	Rivero, 1969
	Hyla parviceps group Boulenger	Variation noted but not described	Duellman & Crump, 1974; Rivero, 1969; Duellman & Trueb, 1989
	Hyla regilla Baird and Girard	Red, green, brown, or grey colour morphs	Test, 1898; Brattstrom & Warren, 1955; Resnick & Jameson, 1963; Jameson & Pequegnat, 1971; Schuab & Larson, 1978; Morey, 1990
	Hyla triangulum Gunther	Dorsal spotting variation	Duellman, 1974
	Phrynohyas venulosa Laurenti	Dorsal striping variation	Duellman, 1971
	Pseudacris ornata Holbrook	Brown, red, green, and green spot colour morphs	Travis & Trexler, 1984; Harkey & Semlitsch, 1988; Blouin, 1989a, b
	Pseudacris triseriata Wied-Neuwied	Brown, grey, red, or green colour morphs	Mathews & Pettus, 1966; Tordoff & Pettus, 1977; Mathews, 1971; Tordoff, 1980; Hoppe & Pettus, 1984
		Albino morphs in high frequency	Corn, 1986
	Smilisca baudinii Dumeril & Bibroon	Variation noted but not described	Duellman & Trueb, 1966

continued

TABLE 1—*continued*

Family	Species	Type of polymorphism	Reference
Hyperoliidae	*Afrixalus fornasini* Bianconi	Presence/absence of middorsal stripe	Schiotz, 1975
	Afrixalus fulvovittatus Peters	Juveniles have uniform dark coloration, adults develop dorsal and lateral stripes	Laurent, 1950
	Afrixalus orophilus Laurent	Juveniles have uniform dark coloration, adults develop dorsal and lateral stripes	Laurent, 1950
	Heterixalus variabilis Ahl	Males are without conspicuous coloration, females are beige to yellow with large black markings	Glaw & Vences, 1992
	Hyperolius alborufus Laurent	Dorsal pattern polymorphism	Schiotz, 1971
	Hyperolius argentovittis Ahl	Dorsal pattern polymorphism	Schiotz, 1971
	Hyperolius argus Peters	Males and juveniles: pale green. Females: pale to dark brown with white spots	Stewart, 1967; Schiotz, 1975; Hayes, 1997; Hayes & Menendez, 1999
	Hyperolius castanus Ahl	Juveniles have white dorso-lateral stripe that is generally retained in males, but not so in females. Males and females possess many patterns of stripes and spots	Laurent, 1950
	Hyperolius cinnamomeoventris Bocage	Males and juveniles: brown or green with dorso-lateral stripe. Females: uniform green	Laurent, 1950; Laurent, 1957; Schiotz, 1975
	Hyperolius cystocandicans Richards & Schiotz	Juveniles are pale green with gold/white stripe, adults are continuous to mottled with yellow, orange or brown	Richards & Schiotz, 1977
	Hyperolius discodactylus Ahl	White stripe on sides and back of males, not present in females	Laurent, 1950
	Hyperolius glandicolour Peters	Juveniles are hourglass patterned, females are dark dorsum with white spots	Schiotz, 1971
	Hyperolius granulatus Boulenger	Juveniles four stripes on dorsum that fade with age (no stripes in adults)	Laurent, 1957
	Hyperolius huillensis Bocage	Dorsal pattern polymorphism	Schiotz, 1971
	Hyperolius karisimbiensis Ahl	Juveniles have dorsal pattern that completely disappears in females and disappears in some males	Laurent, 1950
	Hyperolius kibarae Laurent	Juveniles have dorso-lateral stripes that fade with age (no stripes in adults)	Laurent, 1957

continued

TABLE 1—*continued*

Family	Species	Type of polymorphism	Reference
Hyperoliidae *continued*	*Hyperolius kivuensis* Ahl	Juveniles have three dorso-lateral stripes. These stripes are sometimes retained in adult males and seldom retained in adult females. Also, green to brown ontogenetic change	Laurent, 1950; Laurent, 1950, 1957; Schiotz, 1975
	Hyperolius lateralis Laurent	Juveniles are green, females are dark green with a broad cream lateral stripe	Schiotz, 1975
	Hyperolius langi Noble	Two discrete pattern groups in males, too few females have been investigated to see if same polymorphism exists	Laurent, 1950
	Hyperolius mariae Barbour & Loveridge	Juveniles are hourglass patterned, females are uniform yellow or brown	Schiotz, 1971
	Hyperolius marmoratus Rapp	Juveniles are brown with hourglass pattern, females are uniform yellow or brown with four dark stripes	Stewart, 1967; Passmore & Carruthers, 1979; Mattison, 1998
	Hyperolius mitchelli Loveridge	Juveniles are brown with dark spots, females are brown with white dorso-lateral stripe	Schiotz, 1975
	Hyperolius nasutus Gunther	Juveniles and some males have dorso-median and doro-lateral stripes. Other males and all females lack all three stripes	Laurent, 1950
	Hyperolius nitidulus aureus Perret	Presence/absence of dorsal spots	Schiotz, 1971
	Hyperolius nyassae Ahl	Juveniles are hourglass patterned, females are uniform yellow with black spots	Schiotz, 1971
	Hyperolius ocelatus Ahl	Females have small black spots and males do not	Laurent, 1950
	Hyperolius parallelus Gunther	Juveniles are hourglass patterned, females are dark with middorsal stripe	Schiotz, 1975
	Hyperolius pictus Ahl	Juveniles are brown with three green stripes, adults are green & brown with stripes and spots	Stewart, 1967
	Hyperolius platyceps Boulenger	Juveniles have hourglass pattern, adults have dorso-lateral stripes	Laurent, 1957
	Hyperolius pleurospilus Laurent	Males and females differ in coloration, but not described	Laurent, 1950
	Hyperolius pusillus Cope	Presence/absence of black dorsal stripes and spots	Passmore & Carruthers, 1979

continued

TABLE 1—*continued*

Family	Species	Type of polymorphism	Reference
Hyperoliidae *continued*	*Hyperolius puncticulatus* Pfeffer	Juveniles are brown with diffuse mottling, females are red-brown with spots	Schiotz, 1975
	Hyperolius quinquevittatus Bocage	Juveniles have longitudinal black stripes. In adult, males have golden/brown dorsum with stripes, females have green dorsum with lateral stripes	Laurent, 1957; Schiotz, 1975
	Hyperolius rubrovermiculatus Schiotz	Juveniles are brown with dark spots, females are dark with red spots	Schiotz, 1975
	Hyperolius spatzi Ahl	Juveniles are white, females are light grey with black spots	Schiotz, 1971
	Hyperolius spingularis Stevens	Pattern polymorphism: light triangle on snout or dorso-lateral stripes	Schiotz, 1975
	Hyperolius tuberculatus Laurent	Juveniles are hourglass patterned, females are grey with black spots	Schiotz, 1971
	Hyperolius tuberilinguis Smith	Juveniles have brown or mottled green dorsum, females are bright green	Stewart, 1967; Passmore & Carruthers, 1979
	Hyperolius v. viridiflavus Dumeril & Bibroon	Juveniles are brown, females are green, many pattern variations	Laurent, 1950; Schiotz, 1971; Richards, 1976, 1982; Hayes & Menendez, 1999
	Leptopelis natalensis Smith	Dorsal pattern polymorphism	Passmore & Carruthers, 1979
	Leptopelis concolor Poynton	Juveniles are green, females are tan to dark brown	Passmore & Carruthers, 1979
	Leptopolis flavomaculatus Gunther	Green/brown colour polymorphism	Stewart, 1967; Schiotz, 1975
	Leptopolis vermiculatus Boulenger	Green/brown colour polymorphism	Schiotz, 1975
	Taychynemis seychellensis Dumeril & Bibron	In some populations males are brown, females are green	Nussbaum & Wu 1995
Leptodactylidae	*Eleutherodactylus* sp. Dumeril & Bibroon	Dorsal stripe pattern variation	See Table 2
Microhylidae	*Breviceps poweri* Parker	Presence/absence of vertebral stripe	Stewart, 1967
	Cophyla phyllodactyla Boettger	Presence/absence of beige vertebral stripe	Glaw & Vinces, 1992
	Scaphiophryne calcarata Mocquard	Dorsum is light brown or light green	Glaw & Vinces, 1992

continued

TABLE 1—*continued*

Family	Species	Type of polymorphism	Reference
Myobatrachidae	*Crinia georgiana* Tschudi, *C. glauerti* Loveridge	Dorsal pattern variation	Main, 1965, 1968; Bull, 1975
	Crinia insignifera Moore, *C. pseudoinsignifera* Main	Dorsal pattern variation	Main, 1961, 1965, 1968; Bull, 1975, 1977
	C. (Ranidella) parinsignifera Main, *C. signifera* Girard, *C. subinsignifera* Littlejohn, *C. tinnula* Straughan & Main	Dorsal pattern variation	Bull, 1975
Ranidae	*Cacosternum boettgeri* Boulenger	Green/brown colour polymorphism	Passmore & Carruthers, 1979
	Hildebrantia sp. Nieden	Pattern polymorphism—variation not described	Stewart, 1974
	Limnonectes tigerinus Daudin	Green/brown colour polymorphism	Glaw & Vinces, 1992
	Mantella aurantiaca Mocquard	Uniform yellow, orange, or red	Glaw & Vinces, 1992
	Mantella crocea Pintak & Bohme	Yellow/orange/green colour polymorphism, and presence/absence of reticulation	Glaw & Vinces, 1992
	Mantidactylus aerumnalis Peracca	Green/brown colour polymorphism and presence/absence of light vertebral stripe	Glaw & Vinces, 1992
	Mantidactylus depressiceps Boulenger	Dorsum is uniform grey, brown, or black	Glaw & Vinces, 1992
	Mantidactylus granulatus Boettger	Presence/absence of dark spots on dorsum	Glaw & Vinces, 1992
	Mantidactylus guttulatas Boulenger	Presence/absence of small yellow spots on dorsum	Glaw & Vinces, 1992
	Mantidactylus liber Peracca	Red/green/grey colour polymorphism and presence/absence of light vertebral stripe	Glaw & Vinces, 1992
	Mantidactylus lugubris Dumeril	Brown, black, or green coloration	Glaw & Vinces, 1992
	Mantidactylus peraccae Boulenger	Green/brown colour polymorphism	Glaw & Vinces, 1992

continued

TABLE 1—*continued*

Family	Species	Type of polymorphism	Reference
Ranidae *continued*	*Phrynobatrachus accraensis* Ahl, *P. acridoides* Cope, *P. cryptotis* Schmidt & Inger, *P. francisci* Boulenger, *P. graueri* Nieden, *P. keniensis* Barbour & Loveridge, *P. minutus* Boulenger, *P. natalensis* Smith, *P. ogoensis* Boulenger, *P. parkeri* Witte, *P. parvulus* Boulenger, *P. tokba* Chabanaud, *P. ukingensis* Loveridge, *P. werneri* Nieden	Dorsal pattern variation and presence/absence of dorsal stripe	Stewart, 1967, 1974
	Phrynobatrachus alleni Parker, *P. bequaerti* Barbour & Loveridge, *P. calcaratus* Peters, *P. cricogaster* Perret, *P. dendrobates* Boulenger, *P. fraterculus* Chabanaud, *P. kinangopensis* Angel, *P. parogoensis*, *P. perpalmatus* Boulenger, *P. petropeditoides* Ahl, *P. rungwensis* Loveridge, *P. versicolour* Ahl	Presence/absence of vertebral stripe	Stewart, 1974
	Ptychadena mascareniensis Dumeril & Bibron	Dark pigment variant	Richards & Nace, 1983
		Green/brown colour polymorphism and presence/absence of vertebral stripe	Glaw & Vinces, 1992
	Pyxicephalus sp. Tschudi	Pattern polymorphism—variation not described	Stewart, 1974
	Rana arvalis Nilsson	Presence/absence of dorsal stripe	Ishchenko & Shchupak, 1974; Ishchenko, 1994
	Rana clamitans Latreille	Rare blue variant	Berns & Narayan, 1970
		Dark pigment variant	Richards & Nace, 1983
	Rana limnocharis Boie	Presence/absence of yellow dorso-median stripe	Moriwaki, 1953
	Rana macrocnemis Boulenger	Variation noted but not described	Ishchencko, 1940
	Rana nigromaculata Hallowell	Presence/absence of dorso-median stripe and ventral markings	Moriya, 1952

continued

TABLE 1—*continued*

Family	Species	Type of polymorphism	Reference
Ranidae *continued*	*Rana pipiens* Schreber	Spot pattern variation	Browder & Davison, 1964; Merrell & Rodell, 1968; Moore, 1942, 1943; Volpe, 1955, 1956, 1960, 1961a, 1961b, 1963, 1970, Volpe & Dasgupta, 1962a, b; Anderson & Volpe, 1958; Davison, 1961, 1963, 1964; McKinnell, 1962; Merrell, 1965, 1972; Underhill, 1968; Gill and Nace, 1969; Gill, 1970; Schueller 1979
		Green and brown colour morphs	Fogleman *et al*., 1980; Corn, 1982
		Dark pigment variant/Albanism	Richards & Nace, 1983; Browder, 1972
	Rana septentrionalis Baird	Colour (tan-green) and dorsal spotting variation	Kramek & Stewart, 1980
	Rana sphenocephala Cope	Presence/absence of spotting pattern	Brown & Funk, 1977
	Rana sylvatica Leconte	Presence/absence of white dorsal stripe	Martof & Humphries, 1959; Browder *et al*., 1966; Fishbeck & Underhill, 1971; Schueler & Cook, 1980
		Dark pigment variant	Richards & Nace, 1983
Rhacophoridae	*Aglyptodatylus madagascariensis* Dumeril	Presence/absence of vertebral stripe	Glaw & Vinces, 1992
	Boophis mandrake Bloomers-Schlosser	Presence/absence of large yellow spots on dorsum	Glaw & Vinces, 1992
	Boophis microtympanum Boettger	Males are green, females are yellow-green	Glaw & Vinces, 1992
	Boophis pauliani Guibe	Males are green, females are brown	Glaw & Vinces, 1992
	Boophis tephraeomystax Dumeril	Presence/absence of large brown spots and markings	Glaw & Vinces, 1992
	Polypedates (Rhacophorus) leucomystax Gravenhorst	Brown, green, grey colour morphs and spotted or striped pattern	Church, 1963

TABLE 2. *Eleutherodactylus* sp. exhibiting pattern polymorphism

Species	Reference
E. achatinus	Lynch & Duellman, 1997
E. actinolaimus	Lynch & Rueda, 1998a
E. affinis	Cochran & Goin, 1970
E. agusti	Mattison, 1998
E. alticola	Lynn, 1940
E. amadeus	Hedges, Thomas & Franz, 1987
E. antillensis	Schmidt, 1920; Schmidt, 1928
E. apiculatus	Lynch & Duellman, 1997
E. auriculatus	Schmidt, 1920
E. bicolor	Rueda & Lynch, 1983
E. bicumulus	Lynch & LaMarca, 1993
E. binotatus	Heyer *et al.*, 1990
E. biporcatus	A. Crawford, pers. comm.
E. bogotensis	Cochran & Goin, 1970
E. bransfordii	Savage & Emerson, 1970
E. brevifrons	Lynch, 1998
E. brittoni	Schmidt, 1928
E. calcaratus	Cochran & Goin, 1970
E. carmelitae	Cochran & Goin, 1970
E. carvalhoi	Rodríguez & Duellman, 1994
E. caryophyllaceus	A. Crawford, pers. comm.
E. colodactylus	Lynch, 1979
E. cundalli	Lynn, 1940
E. elassodiscus	Lynch, 1973
E. erythropleura	Lynch, 1992
E. factiosus	Lynch & Rueda, 1998a
E. fitzingeri	A. Crawford, pers. comm.
E. gossei	Goin, 1954
E. griphus	Crombie, 1986
E. gryllus	Schmidt, 1928
E. guentheri	Heyer *et al.*, 1990
E. gularis	Cochran & Goin, 1970
E. hamiotae	Flores, 1993
E. junori	Goin, 1954
E. laticeps	Savage, 1987
E. laticlavius	Lynch & Duellman, 1997
E. latidiscus	Lynch & Duellman, 1997
E. lauraster	Savage, McCranie & Espinal, 1996
E. llojsintuta	Kohler & Lotters, 1999
E. luteolus	Lynn, 1940
E. megalops	Lynch & Ruíz-Carranza, 1985
E. mexicanus	Lynch, 1966
E. nasutus	Goin, 1950
E. nasutus	Lynn & Lutz, 1947
E. nubicola	Goin, 1950; Lynn, 1940
E. nubicola	Goin, 1960
E. nyctophylax	Lynch & Duellman, 1997
E. ockendeni	Lynch, 1974a
E. orcutti	Lynn, 1940; Goin, 1950
E. orpacobates	Lynch, Ruiz & Ardila, 1994
E. pantoni	Goin, 1950; Lynn, 1940
E. parvillus	Lynch & Duellman, 1997
E. parvus	Heyer *et al.*, 1990
E. permixtus	Lynch, Ruíz-Carranza & Ardila-Robayo, 1994
E. phoxocephalus	Lynch, 1979; Lynch & Duellman, 1997
E. podiciferus	Lynch, 1965
E. polychrus	Ruiz, Lynch & Ardila, 1997
E. portoricensis	Schmidt, 1928
E. proserpens	Lynch, 1979
E. pygmaeus	Lynch, 1966

continued

TABLE 2—*continued*

Species	Reference
E. pyrrhomerus	Lynch & Duellman, 1997
E. randorum	Heyer *et al.*, 1990
E. rhodopis	Lynch, 1966
E. ricordii	Goin, 1947; Lynn, 1940
E. ridens	A. Crawford, pers. comm.
E. riveti	Lynch, 1979
E. rosadoi	Lynch & Duellman, 1997
E. sanguineus	Lynch, 1998
E. sanctaemartae	Lynch & Ruíz-Carranza, 1985
E. stejnegerianus	Scott, 1983; A. Crawford pers. comm.
E. suetus	Lynch & Rueda, 1998b
E. taeniatus	Lynch, 1980
E. tayrona	Lynch & Ruiz, 1985
E. uranobates	Lynch, 1995
E. versicolor	Lynch, 1979
E. vertebralis	Lynch & Duellman, 1997
E. vidua	Lynch, 1979
E. vocator	A. Crawford, pers. comm.
E. walkeri	Lynch, 1974b
E. w-nigrum	Lynch & Duellman, 1997

Duellman & Crump, 1974; Jones, 1963; Savage, 1966; Karlstrom, 1973; Martof & Humphries, 1959; Edwards, 1974). As we will illustrate below, conclusive data on modes of inheritance are available for only a handful of species, and studies on the selective maintenance of anuran polymorphisms are still in their infancy. We begin by reviewing the proximate physiological and morphological causes of CP variation.

PROXIMATE BASIS OF THE PHENOTYPIC VARIATION

Colour and pattern in anurans are primarily controlled by two cell types: melanophores, which contain melanin,and chromatophores, which contain coloured pigments. The melanin within melanophores is contained in organelles called melanosomes. Melanophores lie below the chromatophores, but have extensive cellular processes that extend up and over the chromatophores. When the skin appears light in colour, the melanosomes within the melanophore are concentrated in the cell body. When the skin darkens, the melanosomes spread out into the processes of the melanophore covering the chromatophores, thus obscuring the bright colours (Frost-Mason, Morrison & Mason, 1994). Factors that affect movement of the pigment include temperature, light, and humidity. Warm and dry conditions result in contraction of the pigment granules, making the frog pale; cold and damp conditions facilitate the dispersal of pigment, making the frog appear darker. Because a dark-coloured frog will lose heat quicker when its temperature is higher than the surroundings, or absorb more heat when exposed to the sun than will a light-coloured frog, some frogs thermoregulate via changing colour (Passmore & Carruthers, 1979). Dispersal of the pigment granules is controlled by the pituitary gland, which produces melanophore-stimulating hormone (MSH) in response to various stimuli, including visual cues (Bagnara, 1976; Heatwole, 1994). In the case of *Rana pipiens*, spots or

stripes are created by increased concentrations of melanin per melanophore, rather than by an increase in number of melanophores per unit area (Baker, 1951). Similarly, the pale morph in *Bombina orientalis* results from a reduction in melanin concentration per melanophore, rather than from a reduced density of melanophores (Ellinger, 1980). Nevertheless, not all pale and/or dark variants are caused directly by increasing or decreasing melanin concentration. Dark variants of *Ptychadena mascrareniensis*, *Rana clamitans*, and *R. pipiens* primarily result from a lack of iridophores, whch are a type of chromatophore (Richards & Nace, 1983).

Chromatophores are divided into two main categories: non-reflecting and reflecting. Non-reflecting chromatophores that contain carotenoids, pteridines, and flavins are called xanthophores when predominantly yellow, and erythrophores when predominantly red. Reflecting chromatophores that contain the purines guanine, hypoxanthine, and adenine are called iridophores (Bagnara, 1966; Heatwole, 1994). These cell types work together to cause the colours found in anuran skin. For example, green in at least two anurans (*Hyla cinerea* and *R. pipiens*) is not caused by a green pigment (Lyerla & Jameson, 1968; Browder, 1968). Rather, a yellow xanthophore lies above an iridophore, and the two are above cup-shaped melanophores. Some of the incoming light is scattered into the blue wavelength by the iridophore, and the remaining light is absorbed by the melanophores. The blue light that is reflected back must first pass through a layer of yellow xanthophores, which makes the frog appear green. Bagnara, Taylor & Hadley (1968) produced blue coloured skin by leaching out the xanthophore pigments with alcohol.

Berns and Narayan (1970) used solvent extractions and absorption spectrophotometry to compare blue and green areas of skin on variant blue frogs of *Rana clamitans*. They found carotenoids were greatly reduced, and xanthophores were either absent, or present but lacking carotenoid vesicles in blue areas of the skin. Nishioka and Ueda (1985) report a remarkable occurrence in *Rhacophorus schlegelii*. Some albinos of this species are green. Green colour can develop because certain xanthophores sink down into spaces below iridophores and turn into violet-black violophores. This allows the iridophores to reflect blue and the frog to appear green, despite the absence of melanin. Lyerla and Jameson (1968) found no noticeable difference in the arrangement cell types in brown and grey skin, but xanthophores were much less abundant in grey than in brown skin.

COLOUR CHANGE

Although all frogs can lighten or darken existing skin tones, actual colour change (e.g. from uniform green to brown) is uncommon. During the culture of xanthophores and iridophores from *Rana catesbeiana*, Ide (1974; 1978) recognized the appearance of melanophores and thus demonstrated *in vitro* plasticity of pigment cells. The extent to which this change happens *in vivo* is unknown. Colour change observed in nature is usually age-related and in one direction. The exceptions are *Hyla regilla* and *Acris crepitans*. In *H. regilla,* individuals have been observed to change from brown to green, or vice versa, over periods of weeks to months under laboratory conditions (pers. obs.; Mackey, 1958; Haugen, 1992). Colour change is reversible in some individuals under some environmental conditions (W. Wente, pers. comm.). In *A. crepitans*, individuals have been observed to change from green stripe to grey stripe or vice versa over a six month period (Pyburn, 1961b).

Age-related (ontogenetic), directional changes in CP have been observed in at least 39 species (Table 3), over half of which belong to the genus *Hyperolius*. Examples include *Amphignathodon guentheri*, which are uniformly green as juveniles and tan or dark brown-grey as adults (Duellman & Ruiz-C, 1986), and *Gastrotheca aureomaculata*, which are uniformly green as juveniles, and become brown/olive and spotted as adults (Duellman, 1983; Duellman & Ruiz-C, 1986). The most studied (and perhaps most interesting) anurans that undergo ontogenetic change are species in the genus *Hyperolius*. Several species in this genus undergo a characteristic ontogenetic change from a juvenile morph into an adult. Sometimes only adult females change colour [e.g. *Hyperolius v. viridiflavus* metamorphs have a tan dorsum with darker tan stripes, while all females and some males develop into bright green frogs with yellow spots (Richards, 1976)]. Richards (1982) treated *H. v. viridiflavus* tadpoles with daily estrogen or testosterone baths and found that all treated tadpoles metamorphosed with the adult green phenotype. Hayes and Menendez (1999) compared development in, and affects of exogenous steroid hormones on, two species, *H. v. viridiflavus* (which is sexually monomorphic) and *H. argus* (which is sexually dimorphic). Although their results for *H. v. viridiflavus* were identical to those of Richards (1982), they found that in *H. argus*, only oestrogen treatments induced adult coloration in metamorphs. Testosterone treatments had no effect. Hayes and Menendez (1999) conclude that sexual dichromatism may evolve by two mechanisms, depending on the state of the ancestral condition. If monomorphism is ancestral, then dichromatism may evolve with a loss of responsiveness to testosterone, so that males no longer change colour. If dichromatism is ancestral, then ontogenetic change in both sexes may result from the acquisition of the ability to respond to androgens as well as estrogens. Finally, many anurans tend to darken with age and/or size (e.g. *P. mascareniensis*, *R. pipiens*, and *R. clamitans*-Richards and Nace, 1983; *R. septentrionalis*-Kramek & Stewart, 1980), although this is not colour change *per se*. In the case of *R. septentrionalis*, age-related darkening is caused by a relative increase in spot size rather than by an increase in spot number (Kramek & Stewart, 1980).

The data on colour change suggest the following research priorities. First, although it is likely that hormonal changes control ontogenetic change in many species, few details have been worked out (Richards, 1982; Hayes & Menendez, 1999). The endocrinology of anuran colour development and/or change appears to be a wide-open area of research. Second, changes between green and brown states seem to be a particularly common transition (*A. guentheri*, *G. aureomaculata*, *G. griswoldi*, *Hyperolius viridiflavus*, *Hyla regilla*). More work on the proximate environmental and physiological control of green-brown polymorphisms would shed light on the opportunity for adaptive plasticities, and on potential limits to the heritability of these polymorphisms. Finally, there has been no work on whether ontogenetic colour change is adaptive in any anuran species.

SEXUAL DIMORPHISM

There are 25 examples of anurans that are sexually dimorphic for colour or pattern (Table 4). Not surprising, the literature does little more than describe the nature of the polymorphism for the majority of these species . *Bufo periglenes* provides a dramatic example of sexual dimorphism in anurans, with bright orange males and

TABLE 3. Species for which there is a record of ontogenetic change in colour or pattern

Species	Description	Reference
Acris crepitans	Grey stripe in metamorphs may change to red or green	Gray, 1972
Agalychnis callidryas	Spotted coloration does not develop until several weeks after metamorphosis	Starret, 1960; Duellman 1983
Amphignathodon guentheri	Juveniles are always uniform green, adults are tan or dark brown-grey	Duellman & Ruiz-C, 1986
Bufo houstonensis	Juveniles are beige, adults are grey/white	Mays & Reed, 1985
Dendrobates leucomelas	Born with yellow bands around waist, black spots develop within yellow band as they mature	Mattison, 1998
Eleutherodactylus polychrus	Juveniles have orange-red colours on the hidden parts of the legs and a yellow venter. Adult females have black-grey on the hidden parts of the legs and a black-grey venter	Ruiz *et al.*, 1997
Gastrotheca aureomaculata	Juveniles are always uniform green, adults are brown or olive to green. Additionally, spotted coloration does not develop until several weeks after metamorphosis	Duellman, 1983; Duellman & Ruiz-C, 1986
Gastrotheca griswoldi	Young juveniles are uniform green, old juveniles are uniform brown to grey	Duellman & Ruiz-C, 1986
Gastrotheca helenae	Juveniles are always light tan, adults are tan to dark brown	Duellman & Ruiz-C, 1986
Hyla regilla	Some individuals have the ability to change completely from brown to green, or vice versa	Mackey, 1958; Pers. obs.
Hylactophryne augusti	Born with white bands around body, these bands fade over time	Mattison, 1998
Hyperolius sp	A general pattern of ontogenetic pattern is present in many *Hyperolius* species (see Table 1 for descriptions)	See Table 1
Leptopelis concolor	Juveniles are green, females are tan to dark brown	Passmore & Carruthers, 1979
Pseudacris ornata	After metamorphosis many juveniles were copper in colour, later on they developed into other colours	Harkey & Semlitsch, 1988
Ptychadena mascrareniensis	Increase in pigmentation over time may lead to dark variants	Richards & Nace, 1983
Rana clamitans	Increase in pigmentation over time may lead to dark variants	Richards & Nace, 1983
Rana pipiens	Increase in pigmentation over time may lead to dark variants	Richards & Nace, 1983
Rana septentrionalis	Always an increase of dark pigmentation over time	Kramek & Stewart, 1980

TABLE 4. Species for which there is a record of sexual dimorphism in colour or pattern polymorphism

Species	Description	Reference
Boophis microtympanum	Males are green, females are yellow-green	Glaw & Vinces, 1992
Boophis pauliani	Males are green, females are brown	Glaw & Vinces, 1992
Bufo canorus	Male: uniform dorsal yellow-green to olive. Female: gray, tan, or brown, with black spots	Karlstrom, 1973
Bufo periglenes	Male: uniform bright orange. Female: olive to black with red spots	Savage, 1966
Bufo taitanus	Males: mid-dorsal pattern of 3 dark blotches. Females: light reddish-brown dorsum with dark flanks	Stewart, 1967
Eleutherodactylus bicolor	Males: red colour on hidden parts of legs. Females: yellow colour on hidden parts of legs	Rueda & Lynch, 1983
Eleutherodactylus erythropleura	Males: hidden area of legs with yellow spots. Females: hidden area of legs with orange-pink spots	Lynch, 1992
Eleutherodactylus factiosus	Males: hidden area of legs with yellow spots. Females: hidden area of legs with orange-pink spots	Lynch & Rueda, 1998a
Gastrotheca andaquiensis	Males are brown, females are green	JD Lynch, pers. comm.
Heterixalus variabilis	Males are without conspicuous coloration, females are beige to yellow with large black markings	Glaw & Vinces, 1992
Hyla bokermanni	Male: lateral markings. Female: dorso-lateral striped	Rivero, 1969
Hyla luteocellata	Male: lateral markings. Female: dorso-lateral striped	Rivero, 1969
Hyperolius argus, *H. castanus*, *H. cinnamomeoventris*, *H. discodactylus*, *H. glandicolor*, *H. karissimbiensis*, *H. kivuensis*, *H. mariae*, *H. marmoratus*, *H. nasutus*, *H. ocellatus*, *H. pleurosphilus*, *H. quinquevittatus*, *H. spatzi*, *H. tuberculatus*, *H. tuberilinguis*, *H. v. viridiflavus*	For descriptions see Table 1	See Table 1
Leptopelis concolor	Juveniles are green, females are tan to dark brown. Males occur as both phenotypes	Passmore & Carruthers, 1979
Rana septentrionalis	Females have dark pigmentation in a reticulate pattern that males do not have	Kramek & Stewart, 1980
Taychynemis seychellensis	In some populations males are brown, females are green	Nussbaum & Wu, 1995

females that are a cryptic olive/black with red spots (Savage, 1966). Unfortunately, this species is probably now extinct (Pounds & Crump, 1994). The most well studied taxon having sexually dimorphic species is the genus *Hyperolius*. Examples are described above.

Although few have speculated on the advantages of sexual dimorphism in anurans, one interesting hypothesis for *Hyla luteocellata* (Rivero, 1969) is that when a pair is in amplexus the different striping patterns meld to form the illusion of one large frog. A more general hypothesis is that sexual niche-partitioning exists (Shine, 1989). Hayes (1997) suggested that sexual dimorphism may exist in *Hyperolius argus* because males are at greater risk in breeding ponds where they vocalize to attract females, therefore green colour may provide better camouflage at the breeding sites. One interesting question is why sexual dimorphism in colour or pattern appears to be less common in anurans than in other vertebrates, such as birds. The most obvious explanation is that most anurans breed at night, which reduces the opportunity for sexual selection on CP traits. Interestingly, *B. periglenes* and *B. canorus* may breed during the day. Nevertheless, there have been no studies comparing the ecology or behaviour of dimorphic and non-dimorphic species.

MODES OF INHERITANCE

The inheritance of CP polymorphisms has been investigated in 26 species (Table 5), but conclusive data on the mode of inheritance are available for only a handful of these. Although there are numerous species in which extremely rare variants have been found or created by irradiation, this section is limited to true polymorphisms as defined in the Introduction. Studies on the inheritance of anuran CP polymorphisms fall into three main categories, which we can list in order of increasing strength of inference:

(1) Most studies have examined morph ratios in offspring from single generation clutches that were either field-collected (Lynn & Lutz, 1947; Ishchenko & Shchupak, 1974; Church, 1963) or produced via deliberate crosses between wild-caught animals (Pyburn, 1961a; Resnick & Jameson, 1963; Main, 1965; Bruce & Parkes, 1947; Travis & Trexler, 1984; Mathews & Pettus, 1966; Goin, 1947; Moriya, 1952; Moore, 1942; Volpe, 1955; Browder, Underhill & Merrell, 1966; Browder, 1968; Corn, 1986). Such data are useful for generating hypotheses about inheritance. However, many of these studies went on to use the same data to test those hypotheses, which is an obvious violation of statistical inference. Even more surprising is how uncritically subsequent authors have accepted the conclusions of many of these studies. For example, Lyerla and Jameson (1968) stated that for *Hyla regilla*, "Green has been shown to be the result of a pair of dominant genes (O__G__) in enzyme sequence, while non-green results if either locus is homozygous recessive (oo or gg)". This statement has been repeated in the literature for years. However, if one examines the original data (Resnick & Jameson, 1963), one can only conclude that colour is heritable (i.e. green parents tend to give green offspring, brown tend to give brown) and that one can rule out a single locus with green dominant (e.g. brown x brown crosses sometimes give green offspring).

(2) Much stronger inference is achieved in studies that used one set of crosses to

TABLE 5. Species for which the inheritance and/or genetic mechanisms of a colour polymorphism have been investigated. See text for explanation of categories of inference 1, 2, and 3; O = Other types of inference used to determine genetic basis of polymorphism

Species	Category of Inference	Hypothesized mode of inheritance (where applicable)	Reference
Acris crepitans	1	Green stripe is dominant to lack of stripe	Pyburn, 1961a
Acris crepitans	2	Red is permanent; green may change to grey; green is dominant to grey; red is dominant to grey	Pyburn, 1961b
Bombina orientalis	3	Pale is recessive to wild type	Ellinger, 1980
Crinia georgiana, glauerti, insignifera, pseudoinsignifera	1	*Same for all 4 species*: One locus, 2 alleles; Ridged = Homozygous Lyrate = Heterozygous Weak Lyrate = Homozygous	Main, 1965
Crinia (Ranidella) glauerti, insignifera, pseudoinsignifera	2	*Same for all 3 species* One locus, 2 alleles Lyrate = dominant Ridged = recessive	Bull, 1975
Discoglossus pictus	1	One locus, striped allele dominant to spotted allele	Bruce & Parkes, 1947
	3	One locus, striped allele dominant to spotted allele	Lantz, 1947
Eleutherodactylus alticola	2	Inheritance of mid-dorsal stripe is unclear; dorso-lateral stripe presence is dominant to absence	Goin, 1950
Eleutherodactylus bransfordii	O	One locus, ridging is caused by 3 alleles (parallel and U-shaped are recessive, and scattered is dominant)	Savage & Emerson, 1970
Eleutherodactylus nasutus	2	One locus, dorso-lateral stripe is dominant to non-stripe	Goin, 1950
Eleutherodactylus nubicola	O	Dorso-lateral stripe and mid-dorsal stripe are dominant to absence	Goin, 1960
Eleutherodactylus pantoni	2	Dorso-lateral stripe and mid-dorsal stripe are dominant to absence	Goin, 1950
Hyla regilla	2	Red allele recessive to brown at one locus; green colour may be controlled by dominant alleles at two other loci. One can rule out a single locus with green dominant	Resnick & Jameson, 1963

continued

TABLE 5—*continued*

Species	Category of Inference	Hypothesized mode of inheritance (where applicable)	Reference
Pseudacris ornata	1	Genetic basis to colour, but also environmental effects on determination of brown vs grey	Travis & Trexler, 1984
	O	Alteration of temperature in the larval environment may explain some variation in brown vs grey morph frequency	Harkey & Semlitsch, 1988
	2	Green is controlled by single dominant allele over brown/grey	Blouin, 1989b
Pseudacris triseriata	1	3 loci, with all red and green dominant to recessive brown	Mathews & Pettus, 1966
	1	One locus, albinism recessive	Corn, 1986
Ptychadena mascareniensis	O	Dark variant is caused by dominant gene	Richards & Nace, 1983
Rana arvalis	1	One locus, stripe (striata) is dominant to spotted (maculata)	Ishchenko & Shchupak, 1974
Rana clamitans	O	Dark variant is caused by dominant gene	Richards & Nace, 1983
Rana limnocharis	2	One locus, with allele for dorso-median stripe dominant to non-striped	Moriwaki, 1953
Rana nigromaculata	1	One locus, white ventral skin is dominant to dark markings on ventral skin	Moriya 1952
Rana pipiens	1	One locus, burnsi dominant to wild-type	Moore, 1942
	2	One locus, burnsi dominant to wild-type	Moore, 1943
	1	One locus, kandiyohi dominant to wild-type	Volpe, 1955
	2	Kandiyohi and burnsi are simple dominant to normal spot pattern but lack dominance with respect to each other. Double dominant gives mottled burnsi	Volpe, 1960
	1	One locus, kandiyohi mutation is incompletely dominant with variable expression	Browder, 1968
	2	One locus, green dominant to brown	Fogleman *et al.*, 1980
	O	Dark variant is caused by dominant gene	Richards & Nace, 1983
Rana sylvatica	1	One locus, striped dominant to unstriped	Browder *et al.*, 1966
	O	Dark variant is caused by dominant gene, but penetrance is low so in many cases looks recessive	Richards & Nace, 1983
Rhacophorus leucomystax	1	Inheritance is controlled by multiple genes	Church, 1963

generate hypotheses, and a second, *independent* set of wild crosses to test those hypotheses (Moriwaki, 1953; Fogleman, Corn & Pettus, 1980; Blouin 1989b; in some cases the tested hypotheses were posed by other authors: Pyburn, 1961b; Bull, 1975; Goin, 1950; Moore, 1943). Nevertheless, these studies all involve a single generation of offspring.

(3) Multigeneration breeding studies are necessary to prove a mode of inheritance absolutely because complicated modes of inheritance, such as quantitative threshold traits (Wright, 1934), can mimic simple Mendelian ratios in the F1 generation. Mode of inheritance has been demonstrated via multigeneration breeding studies in only two species, *Discoglossus pictus* and *Rana pipiens*. Lantz (1947) conducted eight crosses between various combinations of striped and spotted *D. pictus*, and then conducted five F1 backcrosses to prove that the striped pattern is controlled by a dominant allele at a single locus. Many investigators have studied the inheritance of spotting patterns in the common laboratory frog, *R. pipiens* (Table 5). Initially, the *R. pipiens* complex was thought to consist of three distinct species based on back pattern: *R. pipiens* (spotted), *R. burnsi* (unspotted), and *R. kandiyohi* (mottled; Weed, 1922). Eventually it was demonstrated that dominant alleles at each of two unlinked loci control the rare burnsi and kandiyohi phenotypes in a single species (e.g. Volpe, 1956, 1961a; Anderson & Volpe, 1958). Further work suggested that modifier loci and environmental effects influence the expression of the burnsi allele (Volpe, 1961a; Davison, 1964; Browder & Davison, 1964). There also appears to be an interaction between the dominant alleles at the two loci because there is a deficiency in kandiyohi progeny when eggs produced by burnsi females are fertilized by sperm from kandiyohi males (Nace, Richards & Asher, 1970; Merrell, 1972). Finally, a recessive allele at a third locus alters the differentiation of iridophores and xanthophores so that homozygous frogs are melanistic dorsally and transparent ventrally (Richards, Tartof & Nace, 1969). However, this morph is rarely found in nature.

Despite the lack of conclusive data on inheritance in most species, most of the above studies at least suggest that CP variation is highly heritable. If one takes the conclusions of the above studies at face value, then some interesting patterns emerge. First, in species that exhibit a rare morph, the allele causing the rare morph is usually dominant (*A. crepitans*, *Eleutherodactylus* sp., *Pseudacris ornata*, *P. triseriata*, *Rana pipiens*, and *R. sylvatica*) (also noted in Duellman & Trueb, 1986). Second, the presence of the middorsal stripe is usually caused by a dominant gene (*A. crepitans*, *D. pictus*, *P. ornata*, *Eleutherodactylus nasutus*, *E. nubicola*, *E. pantoni*, *Rana arvalis*, *R. limnocharis*, and *R. sylvatica*). Third, in four of the five species where green morph inheritance has been investigated, the green colour appears dominant to the grey/brown colour (*A. crepitans*, *H. regilla*, *P. ornata*, *R. pipiens*, but not *P. triseriata*). Fourth, light coloured or albinistic morphs are caused by a recessive allele in six of the seven species investigated, as is typical for other vertebrates (*B. orientalis*, *Ptychadena mascareniensis*, *R. clamitans*, *R. pipiens*, *R. sylvatica, P. triseriata*, but not *R. nigromaculata*). Finally, a gross environmental effect has only been demonstrated in two species (spot number in *R. pipiens*: Browder & Davison, 1964; Davison, 1964; Cassler, 1967; brown/grey ratio in *P. ornata*: Travis & Trexler, 1984; Harkey & Semlitsch, 1988), although few studies have tested for it. Thus, data on modes of inheritance of CP polymorphisms in

more species of anurans are needed. This step is necessary before meaningful studies on selective maintenance of these polymorphisms can be conducted.

SELECTIVE MAINTENANCE

Evidence for selection

There have been no direct demonstrations of selection on an anuran CP polymorphism in the wild using marked individuals followed over time. That polymorphisms are under selection has been inferred from three types of observations:

(1) Seasonal fluctuations in morph frequencies have been invoked as evidence for selection. For example, Mathews (1971) found that, for three years in a row, the percentage of green-spotted morph in breeding adult *P. triseriata* was higher than in their offspring at metamorphosis. Similarly, Jameson and Pequegnat (1971) found that the percentage of green *H. regilla* increased over the breeding season in two of three years. A similar class of studies infers selection from the observation that age classes in a static sample differ in morph frequency (Ishchenko, 1994). Of course, ontogenetic colour change (Table 3) or change in response to environment (known to occur for green/brown polymorphisms in *H. regilla* and *A. crepitans*), could seriously affect these sorts of studies. One must also consider the effective number of breeders, Nb, each generation, which can be substantially smaller than the number of males and females (e.g. Scribner, Antzen & Burke, 1997). Small Nb could cause large variation in allele frequencies between age classes.

(2) Examples of non-random survival of morphs during episodes of high mortality provide much more compelling evidence of selection. For example, when disease swept through three tanks holding *A. crepitans*, the grey morph survived best in all three tanks (Nevo, 1973). Here sample sizes were large and each tank held animals from a different population, so any confounding variables are hard to pinpoint. Similarly, Merrell and Rodell (1968) observed a higher proportion of burnsi *Rana pipiens* among living than dead frogs in the field after an episode of winter mortality. That % burnsi was higher in a spring sample of frogs than in a sample from the previous autumn is also consistent with higher burnsi overwintering survival. In a separate incident, Dapkus (1976) was overwintering 1598 *R.pipiens* in outdoor containers when a bout of warm weather killed one third of them. Again, burnsi morphs were over represented in the survivors. As compelling as these data appear, however, they are not the result of planned experiments. It is surprising that no one has tested these observations with planned experiments using marked individuals and insuring that no other variables, such as family, are confounded with morph type. Nevertheless, that anuran CP polymorphisms are under some sort of balancing selection seems likely. There are so many polymorphic species that it is hard to believe each is simply in a transition between fixation of alternate neutral alleles.

(3) Another way selection has been inferred is from apparent convergent evolution between distantly related species (Volpe, 1957; Milstead, Rand & Stewart, 1974; Richards & Nace, 1983; Blouin, 1989a). Here the argument is that similar selection pressures have caused the evolution of similar but non-homologous

polymorphisms in unrelated species. For example, the dorsal pattern polymorphisms of *D. pictus*, *R. limnocharis*, and *R. nigromaculata* are very similar, as are the spotting patterns of *R. pipiens* and *E. ricordii* (Volpe, 1957). Milstead *et al.* (1974) suggested that five genera of anurans, each on a different continent, fill the same niche and exhibit similar polymorphisms, thus supposedly showing the convergence of a selectively beneficial trait. A green/brown/grey polymorphism also appears to be a common cross-taxon phenomenon. At least 22 species from 14 different genera exhibit this striking colour polymorphism (including: *Acris crepitans*, *A. gryllus*, *Arthroleptis adolfifriederici*, *Cacosternum boettgeri*, *Hyla regilla*, *Hyperolius argus*, *H. v. viridiflavus*, *Leptopelis flavomaculatus*, *L. vermiculatus*, *Limnonectes tigerinus*, *Mantidactylus peraccae*, *Pseudacris ornata*, *P. triseriata*, *Rana pipiens*, *R. septentrionalis*, *Rhacophorus leucomystax*). The existence of this similar polymorphism in such a wide array of species suggests that both homology and convergence may influence this phenotypic character. The occurrence of identical polymorphisms in closely related species raises the intriguing possibility that ancestral polymorphisms have been maintained by selection for thousands or millions of years (Bull, 1975). For example, Main (1965) and Bull (1975) demonstrated, via interspecific crosses, that pattern polymorphism in different species of *Crinia* is controlled by homologous loci. Homology has not been tested in other cases of identical polymorphisms (e.g. Milstead *et al.*, 1974; Cei, 1959; Volpe, 1957; Goin, 1954; Lynch, 1966; Goin, 1950; Stewart, 1974; Blouin, 1989a; Brown & Funk, 1977; Richards & Nace, 1983) thus convergent evolution cannot be ruled out.

Mechanisms of selection

The most plausible mechanisms for maintaining a balanced polymorphism in nature are heterozygote advantage, frequency dependent selection, and spatial variation in selection pressure (Hartl & Clark, 1997; Hedrick, Ginevan & Ewing, 1976; Hedrick, 1986). Discussions of the maintenance of anuran polymorphisms invoke either selection directly on CP itself, or selection on traits genetically correlated with CP. These studies generally take one of the following approaches (Table 6):

(1) A common approach has been to observe a correlation between spatial or temporal variation in some environmental variable and variation in morph frequencies. For example, variation in morph frequencies among populations has been found to correlate with the colour and/or pattern of substrate and vegetation at pond edges (*Acris* sp.-Nevo, 1973; *Eleutherodactylus bransfordii*-Savage & Emerson, 1970; *Hyla regilla*-Test, 1898; Haugen, 1992; *Phrynobatrachus* sp.-Stewart, 1974; *Pseudacris triseriata*-Tordoff, Pettus & Mathews, 1976; Tordoff & Pettus, 1977; *R. pipiens*-Bresler, 1963; *R. septentrionalis*-Kramek & Stewart, 1980; *R. sylvatica*-Fishbeck & Underhill, 1971; Schueler & Cook, 1980). Similarly, short term changes in morph frequencies within a site have been hypothesized to be caused by changing vegetation cover (*A. crepitans*-Pyburn, 1961b; Isaacs, 1971; *Crinia* sp.-Main, 1968; *H. regilla*-Schaub & Larson, 1978; *P. triseriata*-Mathews, 1971; *Rana arvalis*-Ishchenko, 1994; *R. pipiens*-Merrell, 1965). Here the inferred mechanism is fluctuating selection by visual predators directly on CP (caused by changing substrate colour). For example, Fishbeck and Underhill (1971) found a clinal change in dorsal stripe frequency in *R. sylvatica*. They hypothesized that the striped phenotype has a selective advantage in coniferous forested areas and

TABLE 6. Species for which selective mechanisms maintaining a polymorphism were investigated. See text for description of codes of the approaches used to detect selection

Species	Approach used to detect selection	Data and/or hypothesized results	Reference
Acris crepitans	1	Red-stripe and green-stripe morphs favoured in wet season, grey morph favoured during dry season	Pyburn, 1961b
	3	No differential predation by birds on different colour morphs; lab test	Wendelken, 1968
	1	Difference in phenotypic frequencies was stable over a 12 week time period (summer to fall)	Isaacs, 1971
	1,2	Correlation between morph and substrate colour	Nevo, 1973
	2	Measured various physiological factors and found no differences between morphs	Gray, 1977
	3	No difference of predation on, and substrate preference of red, green, grey, stripped morphs	Gray, 1978
	2	Annual and geographic differences in frequency, but no seasonal differences	Gray, 1983
Acris gryllus	1,2	Correlation between morph colour and ecological variables. Differences between morphs in disease resistance	Nevo, 1973
Crinia georgiana, *glauerti*, *insignifera*, *pseudoinsignifera*	1,2	*Same for all 4 species*: All populations show a decline in frequency of the lyrate morph between March and November. Conclude: Cold season—lyrate favoured Warm season—ridged favoured	Main, 1968
Crinia (Ranidella) insignifera	2	During maturation to adulthood, higher proportions of lyrate morphs survived cool summers	Main, 1961
Crinia (Ranidella) insignifera	2	Measured heat tolerance and water loss and concluded that ridged animals have an advantage under warm conditions	Walker, 1966
Crinia (Ranidella) insignifera, *pseudoinsignifera*	2	*Same for both species*: Ridged morphs metamorphose faster than lyrate morphs	Bull, 1977
Eleutherodactylus bransfordii	1	Morph frequency is correlated with latitude. Different morph frequencies are correlated with amount of light on forest floor	Savage & Emerson, 1970
Hyla regilla	2	Predictable variation in colour frequencies within a year; also suggest difference in fecundity between morphs	Jameson & Pequegnat, 1971
	1	Frequency of green morphs highest in the spring	Schaub & Larson, 1978
	3	Higher predation on morphs that did not match substrate in lab	Morey, 1990

continued

TABLE 6—*continued*

Species	Approach used to detect selection	Data and/or hypothesized results	Reference
Phrynobatrachus acridoides, *natalensis*, *ukingensis*	1	*Same for all 3 species*: Geographic variation in morph frequency	Stewart, 1974
Pseudacris ornata	2	No difference between colour morphs in larval period, size at metamorphosis, size at day 46, or adult size	Travis & Trexler, 1984
	2	No difference between colour morphs in larval or juvenile fitness correlates	Blouin, 1989a
Pseudacris triseriata	2	Suggest individuals with brown spot have better survival in aquatic phase; green spot have better survival in terrestrial stage. Green metamorphose earlier	Mathews, 1971
	1	Spatial variation in morph frequency across 7 ponds	Tordoff *et al.*, 1976
	1	No significant fluctuations in dorsal colour frequencies occurred over five years; lab study	Tordoff & Pettus, 1977
	3	Jays selectively preyed upon frogs that did not match substrate	Tordoff, 1980
	2	Measured many fitness correlates and concluded that differences in rate of development existed between colour morphs in later juvenile stages	Hoppe & Pettus, 1984
Rana arvalis	2	Larval growth rates are same for both morphs, but maculata adults breed earlier and therefore their offspring emerge first	Ishchenko & Shchupak, 1974
Rana pipiens	1	Observed a large geographic range distribution of the burnsi morph	Bresler, 1963
	2	Suggests that burnsi adults are better able to survive winter than normal	Merrell & Rodell, 1968
	2	Found that B/+heterozygotes may have advantage over +/+ in survival	Gill, 1970
	2	Kandiyohi larvae have more rapid development than wild type	Merrell, 1972
	2	Observed differential morph survival when captive frogs died due to unusually warm temperature	Dapkus, 1976
	2	Rough estimate of larval period suggested that brown morphs matured quicker	Corn, 1981
Rana septentrionalis	1	Observed correlation between colour and habitat choice	Kramek & Stewart, 1980
Rana sylvatica	1	Observed a southeast to northwest gradient in dorsal stripe, with lowest frequencies in southeast	Fishbeck & Underhill, 1971

ponds with emergent vegetation because both of these variables correlated with the westerly increase in stripe frequency.

(2) A second approach has been to simply look for fitness-related traits that are correlated with CP polymorphisms. Various correlates of CP have been proposed or tested, including susceptibility to desiccation, stress resistance, emergence of adults, disease, fecundity, mating preference, length of larval period, size at metamorphosis, juvenile size, adult size, tadpole growth rate, and survival during different seasons (*Acris* sp.-Nevo, 1973; Gray, 1977, 1983; *Crinia* sp.-Main, 1961, 1968; Walker, 1966; Bull, 1977; *H. regilla*-Jameson & Pequegnat, 1971; *P. ornata*-Travis & Trexler, 1984; Blouin 1989a; *P. triseriata*-Mathews, 1971; Hoppe & Pettus, 1984; *Rana arvalis*-Ishchenko & Shchupak, 1974; *R. pipiens*-Merrell, 1965; Merrell & Rodell, 1967; Gill, 1970; Merrell, 1972; Dapkus, 1976; Corn, 1981). Most of these studies found no correlation between morph and trait, were anecdotal in nature, or were so flawed in experimental design that the results are difficult to evaluate. Additionally, one study (Hoppe & Pettus, 1984) measured nine variables and found two statistically significant correlations, but these disappear when a correction for multiple comparisons is made. Nevertheless, a few compelling examples of fitness traits correlated with CP morph exist. The survival difference between *R. pipiens* morphs suggests a correlation with some tolerance for physiological stress (Merrell & Rodell, 1968; Dapkus, 1976). Similarly, Nevo's (1973) data suggest a correlation with disease resistance in *A. crepitans*. There appears to be a correlation between decreased length of larval period and the ridged morph in *Crinia* sp. (Bull, 1977; Walker, 1966; Main, 1965). Although none of these three studies on *Crinia* provide conclusive evidence for a genetic correlation on their own, it is suggestive that all three independently found the same result. Finally, Merrell (1972) conducted three independent crosses of kandiyohi heterozygotes with wild type *R. pipiens* and found that kandiyohi heterozygotes always had a decreased larval period.

(3) Only four studies used an experimental approach to test for direct selection on the polymorphism itself. Wendelken (1968) allowed adult great-tailed grackles, *Cassidix mexicanus*, to prey upon green, grey, and red morphs of *A. crepitans* on a background of grass and soil. Gray (1978) tested predation susceptibility of *A. crepitans* in a 20 gallon aquarium with different substrates. He used juvenile bullfrogs (*R. catesbeiana*), garter snakes (*Thamnophis sirtalis* and *T. radix*), and northern water snakes (*Nerodia sipedon*) as predators. Tordoff (1980) tested whether or not grey jays, *Perisoreus canadensis*, would prey differentially on brown or green morphs of *P. triseriata* depending on background colour (dyed terrycloth). Finally, Morey (1990) used a setup similar to Tordoff's (1980) to test whether garter snakes (*T. elegans*) preferentially attack *H. regilla* morphs that do not match the substrate colour. Of these four studies, two found that predators preferentially ate non-matching morphs (Tordoff, 1980; Morey, 1990). All four of these experiments were conducted in a laboratory setting.

So what general conclusions can one draw about the form of natural selection maintaining these polymorphisms? First, there have been no direct tests of heterozygote advantage. In most species for which the inheritance of the polymorphism is understood, heterozygotes are indistinguishable from homozygous dominants, so any heterozygote advantage would obviously have to be expressed in a correlated trait. Second, one of the most frequently invoked mechanisms to maintain anuran

polymorphism is temporal variation in selection pressures (e.g. morph 'A' favoured as tadpole, morph 'B' favoured as adult). Unfortunately, the conditions necessary for a polymorphism to be maintained in such a manner would rarely be met (Hedrick *et al.*, 1976; Hedrick, 1986). Third, selection on correlated traits is plausible, but a large number of studies and traits have turned up little evidence. Also, these 'correlated trait' explanations are very ad hoc. At least two other problems emerge from the correlational data. First, correlational data do not show causation, which is sometimes assumed. Second, the presence of unrecognized species may account for the correlation between phenotypic variation and an environmental variable such as habitat locality or time of emergence (J. Lynch, pers. comm., e.g. Mathews, 1971; Savage & Emerson, 1970; Bresler, 1963; Cochran & Goin, 1970). There are so many species of anurans sporting striking CP polymorphisms, that it seems unlikely there is a common correlate of CP, such as desiccation tolerance or larval development rate. It seems even less plausible that a different correlated trait maintains the polymorphism in each species. Thus, direct selection on CP itself by visually oriented predators still seems the most likely explanation given anurans' position at the bottom of the vertebrate food chain. For species with apostatic predators (predators that prey differentially upon more common phenotypes), polymorphism reduces the overall predation risk for any one individual (Allen, 1988). For example, an apostatic predator may switch to an entirely different monomorphic species because the alternate prey appears more common (Endler, 1991). Nevertheless, there have been few experimental tests of the selective predation hypothesis, and none were conducted in the field. Most of the data on selection on anuran CP polymorphisms remains correlative or anecdotal, and even for the most well-studied species there is little consensus on how the polymorphisms are maintained.

SUMMARY

There are at least 225 species representing 35 genera and 11 families of anurans that exhibit a colour or pattern polymorphism. These include several apparent cases of parallel polymorphism or convergent evolution. This diversity provides an excellent system in which to study polymorphism.

The mode of inheritance has been investigated in 26 species. Although most studies indicate that CP is highly heritable, simple Mendelian inheritance has been conclusively demonstrated for CP polymorphisms in only two species (not counting albinos and other variants that are too rare to qualify as polymorphisms). There is an obvious need for more genetic studies.

Forty-six species have been described as undergoing ontogenetic change, and 32 have been described as sexually dimorphic. An interesting area of research would be on the adaptive benefits of ontogenetic change, and on why anurans are sexually dimorphic. That anuran CP polymorphisms are under some sort of selection has been inferred by the large number of polymorphic species, the occurrence of apparent convergent evolution and the existence of identical polymorphisms in closely related species, the observation of consistent cyclical fluctuation in frequencies of morphs over short (seasonal) or long (annual) periods of time, and a few fortuitous cases of non-random survival (*A. crepitans*, and *R. pipiens*).

The mechanisms behind the selective maintenance of colour and/or pattern polymorphism have been investigated in 19 species. Most of these studies attempted to determine if some fitness-related trait was correlated with morph type, and were mostly inconclusive. Although only four studies investigated direct selection by predators on CP polymorphism itself, two of these demonstrated differential selection (albeit in the laboratory). We believe that the simplest explanation for the maintenance of CP polymorphisms is indeed direct selection by visually-oriented predators. Well-designed studies are needed on the effects of predation on morph frequencies in the field. Although such studies are difficult to conduct, they are likely to be much more fruitful than yet more searching for correlated physiological traits. This remains a wide open and potentially rewarding area of study.

ACKNOWLEDGEMENTS

Thanks to A. Crawford, W. Wente, W. Duellman, J. Savage, T. Hayes, and J. Lynch for helping us compile the list of species that exhibit polymorphisms. Additional thanks to A. Crawford, K. Monsen, J. Lynch and two anonymous reviewers for helpful suggestions or comments on earlier drafts. Thanks also to I. Moore for help in translating French journals to obtain species descriptions. There are so many polymorphic anurans that we have undoubtedly missed some. We would be interested in hearing from readers who have additional information on any topic covered in this review.

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