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Ecological divergence among sympatric colour morphs in blood pythons, *Python brongersmai*

Abstract Blood pythons in northeastern Sumatra display a series of discrete colour morphs, even among hatchlings within a single clutch. The first step towards understanding the maintenance of this polymorphism is to test the null hypothesis that colour variation in this species has no major biological correlates. Data on > 2,000 blood pythons killed for the commercial leather industry enabled us to test, and reject, this hypothesis. The four colour morphs differed significantly in most of the traits that we measured, including temporal and spatial abundances, sex ratios, age structures, mean adult body sizes, body shapes (tail length and body mass relative to snout-vent length), energy stores, numbers of gut parasites, prey types, feeding frequencies and clutch sizes. The causal basis for these associations remains unclear, but is likely to involve three processes: direct effects of colour, linkages between genes for colour and other traits, and correlated spatial heterogeneity in colour, morphology and ecology. The colour polymorphism may be maintained by frequency-dependent selection and genotype-specific habitat selection, because these sedentary ambush predators are under strong selection for effective camouflage to hide them from both predators and potential prey. In support of this hypothesis, similar colour polymorphisms have evolved independently in several other snake taxa that rely upon ambush predation.

Key words Ecology · Life-history · Microevolution · Chromatic polymorphism · Reptile

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Introduction

Colour polymorphism is relatively common, but presents a challenge to simplistic evolutionary theory because a single "strategy" should prevail unless the morphs have exactly equal fitnesses, or possess a fitness advantage when they are rare. Hence, chromatic polymorphism has been a classic focus of microevolutionary research, with two of the earliest field studies on natural selection involving colour polymorphisms in snails and moths in the English countryside (Clarke and Murray 1962; Kettlewell 1973). Population genetics models suggest that longterm coexistence of alternative colour morphs within a panmictic population can occur only under certain restricted conditions, such as spatial or temporal variation in the relative fitnesses of the different morphs, correlational selection, heterozygote advantage, frequency-dependent selection, or genotype-specific habitat selection (e.g. Tilling 1983; Endler 1986; Hendrick 1986; Brodie 1992). In practice, the mechanisms maintaining intrapopulational polymorphisms are clearly understood in only a few cases (Futuyma 1986).

Many species of snakes display chromatic polymorphisms (e.g. Greene 1997), but the underlying microevolutionary causes for this phenomenon have attracted relatively little study. Colour polymorphisms in snakes may involve several phenomena. The number of different colour morphs within a single population may vary from two (e.g. *Acanthophis antarcticus*: Johnston 1996) to at least four (e.g. *Corallus hortulanus*: Henderson 1990; Stafford and Henderson 1996). The morphs may characterise different age groups (e.g. *Chondropython viridis*: Ross and Marzec 1990) or sexes (e.g. *Dispholidus typus*: see Shine 1993 for a review), or simply different individuals regardless of age or sex (e.g. *Crotalus horridus*: Brown 1991). Laboratory studies on snakes have clarified the genetic basis of this kind of variation (e.g. Zweifel 1981; King 1993a) and demonstrated genetic linkages between colour pattern and behaviour (Brodie 1989, 1992), but the adaptive significance of the polymorphisms has remained obscure.

The only type of colour polymorphism in snakes that has attracted substantive study in the field is melanism. A balance of selective forces seems to be involved in these cases; for example, darker colours may provide a thermoregulatory advantage but increase the snake's conspicuousness and thus vulnerability to predation (e.g. Gibson and Falls 1988; Lawson and King 1996). Alternatively, camouflage may be the primary selective force, with different habitats favouring different morphs (e.g. Ehrlich and Camin 1960; King 1987, 1993b; King and Lawson 1995). Different colour morphs may influence organismal fitness differently in the two sexes (Forsman 1995). Thus, the pressures influencing morph frequencies in snake populations seem to be complex, with important roles for gene flow between adjacent populations (e.g. Lawson and King 1996), as well as for thermal factors and camouflage. Here we document and examine chromatic polymorphism within a snake species that has hitherto attracted very little ecological study, living in a region where herpetofaunal research has been focussed almost exclusively on taxonomic rather than ecological questions (David and Vogel 1996).

Materials and methods

Study species

Blood pythons (*Python brongersmai*) are large (to 2.5 m total length), extremely heavy-bodied (to 15 kg) nonvenomous snakes distributed through eastern Sumatra and adjacent parts of Malaysia (David and Vogel 1996). They have generally been regarded as a subspecies of the short-tailed python (*P. curtus*), but recent phylogenetic analyses of morphology and DNA sequence data indicate that the two forms constitute separate species (S. Keogh, R. Shine and D. Barker, unpublished work). Many blood pythons are killed each year for the international leather industry, and data presented in this paper were gathered as part of a broader study on the ecological sustainability of this industry (Shine et al. 1998b). We emphasise that the animals we examined had been collected for the existing commercial trade; no snakes were killed for the purposes of our study.

We classified the snakes we examined into four types, based on their predominant dorsal colour: brown, orange, red or yellow. This allocation was generally straightforward; any intermediate-coloured animals were allocated to morphs by the same person (Mumpuni). In this area, all blood pythons are brown or orange-brown at hatching, and develop their adult colours gradually. Our analyses of DNA sequence data revealed no genetic differences between the colour morphs of *P. brongersmai* (S. Keogh et al., unpublished work). Studies of captive snakes indicate that all four colour morphs are interfertile and readily interbreed, with offspring from a single litter often developing into adults of two or three colour morphs (Barker and Barker 1996; D. and T. Barker, personal communication).

Study area and methods

We visited four locations in northern Sumatra (Medan, 3°35′N 98°39′E; Seisuka, 3°25′N 99°27′E; Rantauprapat, 2°05′N 99°46′E; Cikampak, 1°43′N 100°15′E) on each of four trips. The trips were evenly spaced throughout the year (March, June, August, December), to provide information on the seasonality of ecological processes in these tropical snakes. The climate in this area is characterised by consistently high mean temperatures (all months have mean temperatures > 26°C: Arakawa 1969) and high rainfall (mean annual precipitation > 2 000 mm: Arakawa 1969).

The pythons are collected in various parts of northern Sumatra, and are transported alive to the slaughterhouses. We could not reliably determine the origin of most specimens, but many of them (based on statements by the collectors) came from oil-palm plantations close to the slaughterhouses. We weighed and measured the snakes immediately after they were killed, and then dissected the freshly-skinned bodies to quantify aspects such as food habits and reproductive biology. Sex was determined by visual inspection of the gonads, and we recorded testis sizes in males, and the number and diameters of oviductal eggs, vitellogenic ovarian follicles and corpora lutea in adult females. Males were scored as adult if they had large turgid testes and/or opaque, thickened efferent ducts. Females were classed as mature if they had thickened muscular oviducts, vitellogenic follicles (> 10 mm diameter), corpora lutea, or oviductal eggs.

Prey items in the alimentary tract (usually, faecal material from the rectum) were removed. These samples were later examined microscopically to identify prey species using fur characteristics, in conjunction with a reference collection of fur from all of the common Sumatran mammal species (see Shine et al. 1998a for further details). Abdominal fat bodies were scored on a four-point scale to provide an index of energy stores. Ascarid nematodes in the stomach were counted to provide an index of parasite burdens.

Results

We obtained data from 2063 *P. brongersmai*, comprising four discrete morphs that differed in dorsal colouration (Table 1). The name given to each morph reflects its overall dorsal colour; all snakes also displayed darker blotches, similar in size and colour among the morphs. The red morph was the most common type (65% of the total sample), followed by yellow (26%), brown (5%) and orange (4%) snakes (see Table 1 for numbers).

Snakes of the four different morphs were similar in most aspects of their basic biology, as would be expected from their very close relatedness. Thus, for example, females exceeded males in average adult body length in each morph, and the seasonal reproductive cycle was highly synchronised in adult females. Commensal vertebrates (especially rats and chickens) were the most common prey items. However, more detailed analysis revealed many significant differences between snakes of the different colour morphs, as described below.

Relative abundance of the morphs

Contingency table analysis reveals that the relative numbers of brown, orange, red and yellow snakes differed among the four localities we visited (see Table 1; $\chi^2 = 493.5$, 9 *df*, $P < 0.0001$): for example, red snakes were disproportionately common in Rantauprapat. Similarly, the relative numbers of each morph changed through time, with fewer red snakes in the first trip than at other times (Table 1; $\chi^2 = 258.2$, 9 *df*, $P < 0.0001$).

Table 1 Relative numbers of blood pythons of each colour morph from each of the four locations and in each of the four months in which we examined specimens

	Number of snakes			
	Brown	Orange	Red	Yellow
Location				
Rantauprapat	75	27	762	135
Cikampak	13	47	462	151
Medan	18	0	10	113
Seisuka	6	5	100	139
Month				
March	34	5	194	209
June	9	0	453	148
August	56	41	361	106
December	13	33	326	75
Total number	112	79	1334	538

This temporal variation was not an indirect result of differing numbers of snakes coming from the four locations on each trip; the variation in relative numbers of each morph among trips was significant even if analysis was restricted to a single location (e.g. for Rantauprapat, $\chi^2 = 146.1$, 9 df, $P < 0.0001$; for Cikampak, $\chi^2 = 69.8$, 9 df, $P < 0.0001$).

Age structure and sex ratio of the sample

The relative numbers of adult and juvenile snakes that were killed at the slaughterhouses differed significantly among morphs ($\chi^2 = 33.3$, 3 df, $P < 0.0001$), ranging from 11.4% juveniles (red morph) to 20.3% juveniles (yellow morph). Restricting attention to the adults only, the sex ratio (proportion male) varied from 51% (brown morph) to 76% (orange morph). These proportions enable rejection of the null hypothesis of equal adult sex ratios among the four morphs ($\chi^2 = 10.45$, 3 df, $P < 0.02$).

Body sizes and morphology

The four colour morphs of *P. brongersmai* differed significantly in most of the traits that we measured. In both sexes, for example, red snakes were substantially larger and heavier than yellow snakes (Table 2). These differences in mean adult body sizes among the four morphs are not a byproduct of spatial differences in morph numbers. Even if analysis is restricted to snakes from a single slaughterhouse, the morphs differed significantly in body sizes (using two-factor ANOVAs with sex and morph type as the factors, main effect of morph for Rantauprapat snakes only, $F_{3,860} = 9.14$, $P < 0.0001$; for Cikampak only, $F_{3,665} = 7.64$, $P < 0.0001$).

The difference in mean body mass among morphs was not a simple consequence of the variation in average snout-vent lengths; the snakes also differed in body shape. Figure 1 shows that these differences in body proportions among the morphs were subtle but consistent. One-factor analysis of covariance (with morph as the factor, snout-vent length as the covariate, and ln body mass as the dependent variable) revealed significant differences among morphs in mass relative to body length in both females (slopes homogeneous, $F_{3,963} = 0.31$, $P = 0.82$; elevations differ, $F_{3,966} = 2.66$, $P < 0.05$) and males (slopes heterogeneous, $F_{3,1033} = 4.27$, $P < 0.006$). Similarly, tail length relative to snout-vent length showed significant differences among morphs (females – slopes homogeneous, $F_{3,980} = 1.39$, $P = 0.24$; elevations differ, $F_{3,983} = 4.91$, $P < 0.003$; males – slopes homogeneous, $F_{3,1050} = 1.63$, $P = 0.18$; elevations differ, $F_{3,1053} = 3.95$, $P < 0.01$).

Fat stores, food habits, and parasite numbers

The four morphs differed in all of these respects. For example, compared to yellow individuals, red snakes had fewer stomach parasites and larger energy stores (note from Table 2 that among-morph differences in fatbody scores did not attain statistical significance in tests within each sex, but a two-factor ANOVA on the combined data set, with sex and morph as the factors, revealed a highly significant difference among morphs in mean fatbody size: $F_{3,1757} = 3.42$, $P < 0.017$). Food habits also varied, with the proportion of snakes containing identifiable prey being significantly lower in red snakes than in the other morphs, and non-rodent mammalian prey (slow loris, banded civet, striped civet, tree shrew, yellow-throated marten) comprising a higher proportion of the diet in the brown morphs than in the other snakes (Table 2).

Reproductive biology

We detected relatively little variation among the four morphs in variables related to reproductive output. For example, egg sizes were similar, and approximately half of the adult female pythons were reproductive in the year in which they were collected (Table 2). Clutch sizes were significantly higher in red snakes than in the other morphs (Table 2), but further analysis revealed that this difference was entirely due to the larger body sizes of adult females of this morph. Single-factor analysis of covariance (with morph as the factor, maternal snout-vent length as the covariate, and clutch size as the dependent variable) showed that all morphs exhibited very similar relationships between clutch size and maternal body size (Fig. 2; slopes $F_{3,134} = 0.67$, $P = 0.57$; elevations $F_{3,137} = 1.95$, $P = 0.12$).

More variation was evident in the male reproductive cycle. Adult males of the four morphs differed in testicular volumes relative to body size on two of the four trips (using ANCOVA with colour morph as the factor, body mass as the covariate and testicular volume as the

females

males
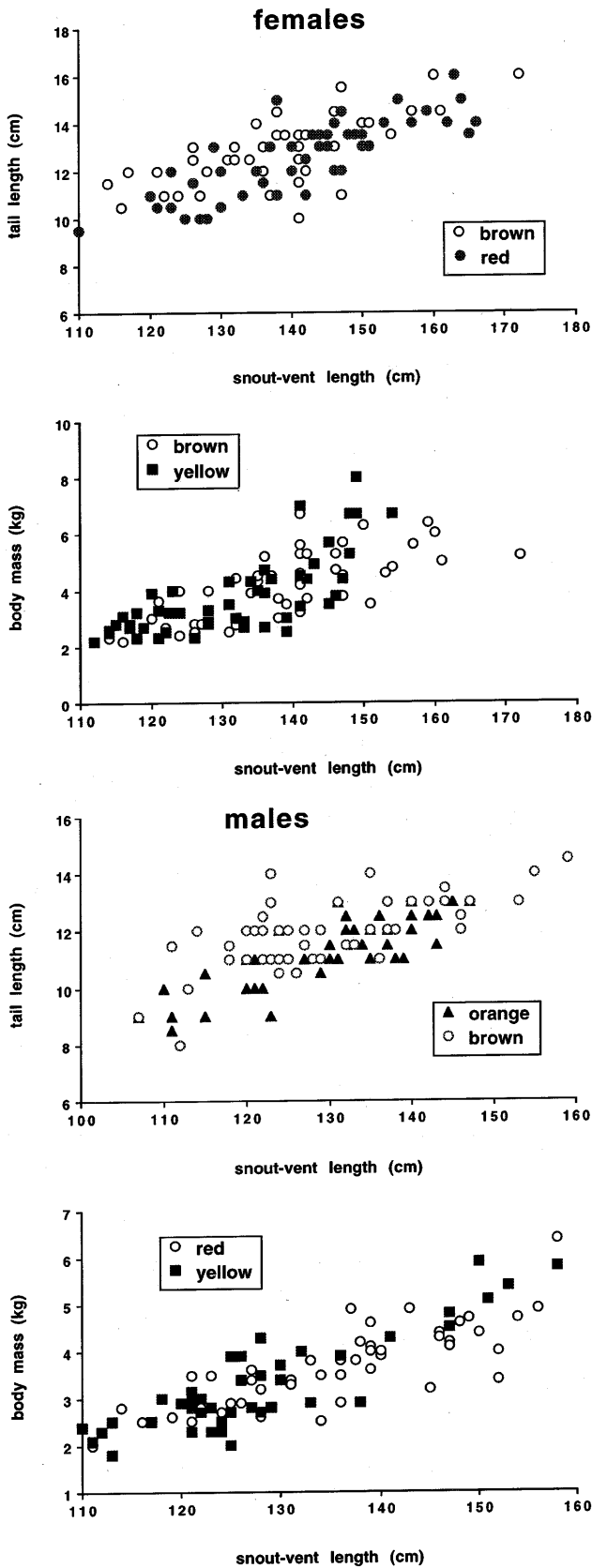
Fig. 1 Morphological divergence between blood pythons of different adult colour morphs. For simplicity, each graph shows only two colour morphs, the two that were most different in the trait of interest. See text for statistical analyses
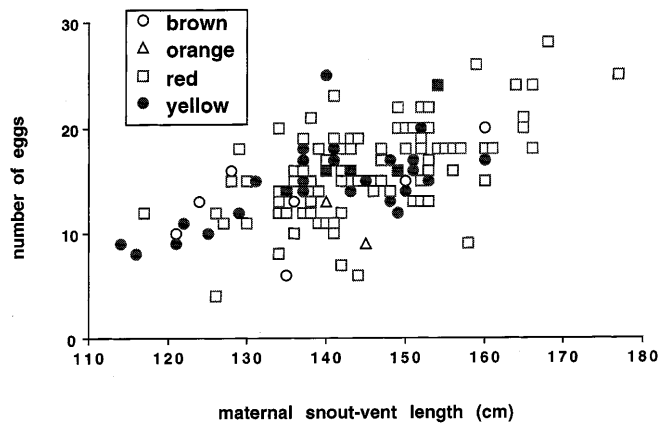
Fig. 2 Clutch sizes relative to maternal body size in four colour morphs of the blood python. Mean body sizes and mean clutch sizes differed among the morphs, but the relationship between these two variables was similar in all four morphs (see Table 2 for comparisons of means, and text for statistical analysis)

dependent variable, $P < 0.04$ for trips in March and August). Trends were similar, but not statistically significant, on the other two trips. We thus infer that the morphs differ in the seasonal timing of testicular enlargement and regression.

Discussion

Our data reveal strong morphological and ecological divergence among the four colour morphs of *P. brongersmai*, despite the fact that a single clutch of eggs may produce hatchlings of more than one colour morph. This is a surprising and highly counter-intuitive result. We began this study under the impression that colour morph was a trivial aspect of the biology of blood pythons, and that snakes of all four morphs were essentially the same kind of animal. Our data do not show that colour *per se* is important, but they indicate that dorsal colour is associated with a host of other traits involving size, shape and ecology. Other traits may also vary among the morphs; for example, Indonesian skin-traders report that skin quality is higher for the red morph than for the other types (Erdelen 1997). Of course, these associations with colour (Table 2) may not constitute independent effects. For example, the difference in mean clutch sizes is most parsimoniously interpreted as a secondary consequence of differences in the mean body sizes of adult females (Fig. 2). Other traits such as prey types, feeding frequencies, energy stores and parasite loads may also be functionally related, perhaps arising from divergence in a single aspect such as habitat selection.

In the following discussion, we first consider alternative explanations for the association of colour pattern with other aspects of the biology of blood pythons, before tackling the question posed at the beginning of this paper: what processes maintain chromatic polymorphism within this species?

Firstly, why does colour pattern correlate with so many other aspects of the biology of blood pythons (e.g. Table 2)? Extensive data from captive breeding indicate that the colour morphs have a genetic basis (D. Barker, personal communication), so we can rule out the possibility that the alternative morphs reflect developmental plasticity in response to different environments. Hence, it is not plausible to argue that the association of a trait with dorsal colour is due to the trait influencing development of the colour (as occurs in some insects: e.g. Goulson and Cory 1995; Matena 1995) rather than vice versa. Nonetheless, this still leaves us with three possible reasons why colour is associated with ecological and morphological characteristics:

1. Dorsal colour directly influences the other traits. Under this hypothesis, the morphological and ecological differences between the four morphs are a direct consequence of the colour difference. For example, colour might influence the effectiveness of camouflage, so that snakes of one colour are more likely to obtain prey (and thus, feed more frequently, perhaps on a different type of prey, and thus expose themselves to different risks of parasite transmission), thus lay down more fat stores, and thus grow larger and more heavy-bodied. Differences in mean adult body sizes between morphs might also reflect differences in survival (and thus, age structure), due to more effective camouflage in some morphs than in others. This type of explanation has been proposed for other cases of polychromatism in snakes (e.g. Gibson and Falls 1988; Monney et al. 1995, 1996).

2. The genes controlling colour morph are linked to other genes that influence morphological and ecological traits. This hypothesis suggests that snakes differing in colour pattern also differ in genes that affect a variety of significant traits – either directly (e.g. genes for growth rates, body shape, prey preference) or indirectly (e.g. genes for habitat selection, thus affecting prey availability : *cf*. Harris and Jones 1995). This genetic linkage

Table 2 Comparisons of morphological and ecological traits among four colour morphs of blood pythons from northern Sumatra. Table shows mean values (SD in parentheses), and the results of statistical tests of the null hypothesis of no significant differences among morphs in the trait of interest. *F* ratios are derived from one-factor ANOVAs (with morph as the factor), and χ^2 values from contingency tables (*n* sample size; note that sample sizes differ among traits e.g. because alimentary tracts of some snakes had been flushed with water and so we could not determine whether or not they had contained prey). The proportions of adult females that were reproductive is based only on trips in August and December, when reproductive condition could be established most reliably

Trait	Colour morph				Statistical tests
	Brown	Orange	Red	Yellow	
Adult males					
n	50	45	688	255	
Snout-vent length (cm)	129.5 (11.7)	130.2 (9.5)	134.9 (11.3)	126.8 (12.3)	$F_{3,1033} = 32.55, P < 0.0001$
Body mass (kg)	3.27 (0.76)	3.42 (0.88)	3.81 (1.00)	3.07 (0.91)	$F_{3,1033} = 38.80, P < 0.0001$
Fatbody scores	0.60 (0.64)	0.73 (0.78)	0.72 (1.00)	0.61 (0.61)	$F_{3,1033} = 1.13, P = 0.33$
Parasite numbers	0.10 (0.51)	0.00 (0)	0.00 (0)	0.01 (0.13)	$F_{3,1033} = 9.77, P < 0.0001$
Adult females					
n	49	14	493	174	
Snout-vent length (cm)	140.9 (11.6)	146.3 (8.9)	146.1 (11.3)	138.3 (11.5)	$F_{3,728} = 21.45, P < 0.0001$
Body mass (kg)	4.40 (1.12)	4.65 (1.20)	4.94 (1.54)	3.97 (1.27)	$F_{3,728} = 19.50, P < 0.0001$
Fatbody scores	1.31 (0.85)	1.64 (1.01)	1.34 (0.91)	1.16 (0.83)	$F_{3,728} = 2.51, P = 0.058$
Parasite numbers	0.00 (0)	0.00 (0)	0.01 (0.05)	0.23 (2.13)	$F_{3,728} = 2.12, P = 0.097$
Number of records of each major prey type					
Rats	60	46	751	285	
Other mammals	8	2	17	8	
Chickens	1	0	22	7	$\chi^2 = 22.1, 6\ df, P < 0.002$
Proportion of snakes containing prey					
n	108	74	1272	491	
Proportion with prey	74.1%	87.8%	70.1%	78.2%	$\chi^2 = 20.44, 3\ df, P < 0.0001$
Reproductive output Clutch size:					
n	10	2	97	33	
Mean (SD)	13.0 (3.9)	11.0 (2.8)	16.1 (4.4)	15.1 (3.7)	$F_{3,139} = 2.76, P < 0.05$
Egg mass (g)					
n	3	0	23	4	
Mean (SD)	74.8 (28.1)	–	84.8 (18.6)	81.0 (28.9)	$F_{2,27} = 0.33, P = 0.72$
Proportion of adult females reproductive					
n	31	14	239	50	
Proportion reproducing	48.4%	35.7%	50.6%	58.0%	$\chi^2 = 2.30, 3\ df, P = 0.51$

would thus explain the association between colour, morphology and ecology.

3. Some third factor generates the differences in morph colour and in the correlated traits. This hypothesis, like the one above, posits that there is no causal link between colour and the ecological/morphological divergences that we have documented. However, it goes a step further in suggesting that the correlation between these traits reflects some third factor rather than a mechanistic (genetic) link. A plausible candidate for such a third factor would be spatial heterogeneity. If various locations differ in morph frequencies as well as in both genetically-based and environmentally-determined traits of the snakes, this heterogeneity could generate associations between colour morph, morphology and ecology.

All three of these explanations are likely to be true to some extent. The first hypothesis is simple and plausible (*a priori*, it seems unlikely that the colour of a highly camouflaged "ambush" predator would have no effect on its foraging success or survival); the second is supported by colour-associated variation in a trait (relative tail length) that is likely to be under genetic control, and by previous work on polymorphic snakes documenting genetic linkages between colour pattern and behaviour (Brodie 1989); and the third by the documented existence of geographic and habitat-associated variation in morph frequencies within blood pythons (red snakes most common in oil palm plantations, brown snakes in rockier habitats: Groombridge and Luxmoore 1991). No single hypothesis is likely to provide a complete answer. For example, the "spatial heterogeneity" hypothesis is inconsistent with the observations that more than one colour morph can hatch from a single clutch of eggs, and that morph differences are seen even if analysis is restricted to a single slaughterhouse (and hence, presumably, a relatively small area). Further work to distentangle these effects would be of great interest. Field studies could clarify the spatial and habitat distributions of each morph, and radiotelemetric monitoring would reveal if different colour morphs select different microhabitats. Captive animals could be used to illuminate possible genetic links between colour and behaviour (e.g. Brodie 1989; Garrett and Smith 1994), as well as the mode of inheritance of body colour.

What processes maintain the polymorphism? Two different kinds of answers to this question are possible. Either the polymorphism is actively maintained by frequency-dependent selection, or by non-equilibrial factors such as spatial and temporal variation in fitnesses of the various morphs, or heterozygote advantage (Endler 1986). Comparative evidence supports the former answer, because chromatic polymorphisms very similar to those seen in *P. brongersmai* have evolved independently in a series of distantly related snake species in various parts of the world. The species involved all display a heavyset build and camouflage colouration, and most or all of them rely upon ambush predation. They include boids (e.g. *Corallus annulatus*, *C. hortulanus*: Henderson

1990; Garrett and Smith 1994), colubrids (e.g. *Cerberus rhynchops*, *Psammodynastes pulverentulus*: Rasmussen 1975; Shine 1991), elapids (e.g. *Acanthophis antarcticus*, *Echiopsis curta*: Cogger 1992; Johnston 1996), pythonids (*Chondropython viridis*, *Python brongersmai*: Ross and Marzec 1990; Barker and Barker 1996), and both crotaline and viperine viperids (e.g. *Agkistrodon halys*, *Atheris hispida*, *A. squamiger*, *Bothriechis schlegelii*, *Crotalus lepidus*, *C. horridus*, *Tropidolaemus wagleri*, *T. mcgregori*, *Trimeresurus flavoviridis*, *Vipera kaznakovi* complex: Neill 1963; Pitman 1974; Garrett and Smith 1994; Nilson et al. 1994; Nobusaka et al. 1994; Greene 1997). A pygopodid lizard that displays strong morphological, behavioural and ecological convergence with "ambush" snakes, also displays polychromatism (*Lialis burtonis*: Wilson and Knowles 1988).

The convergent evolution of polychromatism in heavy-bodied "ambush" predators of several reptile lineages, from several parts of the world, suggests that there is some underlying adaptive significance to the development of multiple colour morphs in these kinds of snakes. Frequency-dependent selection is a plausible explanation, with either prey or predators more liable to detect the more common morph. Alternatively, the fitnesses of different morphs may vary among habitat types, imposing strong selection for genotype-specific habitat selection. Thermal advantages of particular colour morphs may play a role in some cases, but are unlikely to be the primary factor in these tropical reptiles (e.g. Shine and Madsen 1996, but see Henderson 1990). Neither is a colour-associated diversity in predator-escape tactics (as in the studies of Brodie 1989, 1992) likely to be important, since most of these taxa rely on immobility and camouflage to evade predation. As in other systems involving colour polymorphism, multiple causal factors may be involved (e.g. Tilling 1983). Thus, a full understanding of the microevolutionary forces maintaining polymorphism will require information on each of these factors (Endler 1986).

In summary, the remarkable diversity of colour morphs in Sumatran blood pythons poses an intriguing biological puzzle. Our data do not enable us to solve that puzzle, but they are sufficient to dismiss one possible answer – that the variation is trivial, and hence might be due to stochastic processes (such as genetic drift) rather than resulting from adaptation. Such an interpretation would be inconsistent with two main facts. Firstly, the colour morphs of blood pythons differ in many biologically significant variables. Because the effect of dorsal colour on organismal fitness is thus unlikely to be trivial, we would expect genes coding for all but the "best" colour to be eliminated by natural selection unless there is some active process (such as frequency-dependent selection) maintaining the polymorphism. Secondly, the independent evolution of similar chromatic polymorphisms in several lineages of ecologically and morphologically convergent snake species strongly reinforces the hypothesis that the polychromatism has some underlying adaptive significance.

We need further studies, in the field as well as the laboratory, to clarify the processes involved in this phenomenon.

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