Oecologia (1998) 116:113–119

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

Received: 18 December 1997 / Accepted: 23 March 1998

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.