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Variable coloration is associated with more northerly geographic range limits and larger range sizes in North American lizards and snakes

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ABSTRACT

Question: Is variable coloration associated with geographic distribution limits?

Hypothesis: The co-existence of two or more alternative colour variants is associated with more northerly geographic range limits and with larger range sizes.

Organisms: Lizards (77 species, 9 genera) and snakes (60 species, 8 genera) with either variable or non-variable colour patterns.

Study area: North America.

Methods: We performed pair-wise comparisons of northern distribution limits and range sizes for species with variable versus non-variable coloration.

Conclusions: Species with variable colour patterns had geographic distribution ranges that extended further north and covered much larger areas than those of congeneric species with non-variable colour patterns. Our results are consistent both with the hypothesis that species with variable colour patterns have experienced a faster rate of post-glacial range expansions, and with the competing hypothesis that species of large range that experience divergent selection more readily evolve variable colour patterns.

Keywords: biogeography, colour polymorphism, environmental variability, macro-ecology, population variability, range boundaries, reptiles.

INTRODUCTION

Ecological studies indicate that species geographic distribution boundaries are influenced by an array of environmental factors, such as direct and indirect effects of climate, competition, predation, and resource availability (Hoffman and Blows, 1994; Crozier, 2004; Guisan and Thuiller, 2005; Hastings *et al.*, 2005; Gilman, 2006; Sanford *et al.*, 2006). Studies of natural populations have demonstrated that the strength and direction of selection vary among populations and through time within populations due to environmental change (Wade and Kalisz, 1990). Taken together, this suggests that colonization events and establishment in novel environments responsible for range expansions may require rapid changes in many different characters

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and be facilitated by a high degree of genetic variability of the propagule (Garcia-Ramos and Rodrigues, 2002; Lockwood *et al.*, 2005; Forsman *et al.*, 2008). It has also been proposed that genetically more variable populations and species may be less susceptible to local extinctions and range contractions, due to decreasing effects of detrimental variants and an increased potential for adaptive modifications in response to temporal change (Ferrière *et al.*, 2004; Kolbe *et al.*, 2004; Forsman *et al.*, 2008).

Developing an understanding of how the interactive effects of ecological and evolutionary factors and processes influence the dynamics of species range boundaries is crucial for successful protection and restoration of biological diversity, and may shed light on the long-standing issue of whether biological invasions are best viewed as random phenomena, or if characteristics exist that predispose certain species to become invasive (Ferrière *et al.*, 2004; Lockwood *et al.*, 2005). We are concerned here with the proposition that variable coloration and polymorphism may promote the ecological success of populations and species and facilitate geographic range expansions (Dobzhansky, 1951; Fisher, 1958; Forsman and Åberg, 2008; Forsman *et al.*, 2008).

Animal colour patterns have a long tradition as a model system in empirical studies and in generating and testing theories central to ecology and evolutionary biology (Darwin, 1859; Poulton, 1890). An important reason for this is that colour pattern may influence the performance and fitness of individuals, for instance by serving as a visual signal in mate choice (Andersson, 1994) or by providing protection from predators (Ruxton *et al.*, 2004). In ectothermic animals such as reptiles and insects that rely on external radiant energy for body temperature regulation, coloration may influence heating rates and body temperature, body temperature may influence energy budgets and locomotion, and locomotion may influence the capacity to escape predation or to compete with conspecifics for access to mates (Porter, 1967; Stevenson, 1985; Peterson *et al.*, 1993).

Colour pattern may also influence fitness interactively with other traits. Studies of colour polymorphic populations have uncovered that natural selection favours certain combinations of coloration and behavioural, morphological, and physiological traits, at the expense of other trait–value combinations, rather than operating only on coloration *per se* (King, 1987; Brodie, 1992; Forsman, 1995; Forsman and Appelqvist, 1998). Such correlational selection will promote the evolution of genetic rearrangements that result in physical integration and associations of colour pattern with other traits (Jackson *et al.*, 1976; Brodie, 1989; Endler, 1995; Forsman *et al.*, 2002). Colour polymorphisms that have reached this stage lend themselves admirably to the adaptive landscape metaphor (Arnold *et al.*, 2001), with the fitness peaks representing alternative trait–value combinations displayed by different morphs. It has therefore been proposed (Forsman and Åberg, 2008; Forsman *et al.*, 2008) that populations that consist of two or more alternative colour morphs with co-adapted suites of characters and that occupy on average different niches will utilize more diverse resources, and display higher rates of colonization success, population persistence, and range expansions, while being less vulnerable to range contractions and extinctions, compared with monomorphic populations.

In this study, we perform a comparative analysis based on literature data for lizards and snakes of North America to determine whether species with variable colour patterns have geographic distribution ranges that extend further north and cover larger areas than those of species with non-variable coloration. During the Pleistocene epoch period of glaciations of North America, glaciers from the Rocky Mountains and north-central Canada met each other in the centre of the continent and created ice sheets and mountain glaciers that stretched from the Pacific to the Atlantic ocean (Pielou, 1992). At their greatest extent, the ice sheets of North America covered most of Canada and extended into the United States to a latitude of about 40°N, but mountain glaciers extended even further south. The areas south of the ice consisted of tundra and steppe biomes that were probably unsuitable for most reptiles. The most recent period of glaciations ended around 10,000 years ago and current geographic distributions of fauna and flora partially reflect differences among species in their ability to colonize new areas. We do not imply that colour patterns have remained unchanged since the Pleistocene. For the purpose of the present study, however, we have chosen to rely on information on current states, because assigning colour patterns to species that are different from those seen today would require a more complicated set of assumptions.

By testing for an association of variable coloration with contemporary northern distribution limits of North American reptiles, we can evaluate the proposition (Forsman *et al.*, 2008) that the co-existence within a population of alternative colour variants will increase the probability of colonization and establishment in novel environments and lead to a faster rate of post-glacial range expansions in polymorphic compared with monomorphic populations. Because our approach is based on correlative data, we are unable to separate cause from effect. For instance, a positive outcome of our analysis would be consistent also with the competing hypothesis that species of large range that experience divergent selection more readily evolve variable colour patterns. To our knowledge, however, our study is the first attempt to investigate if variable coloration is associated with northern geographic range limits. Despite the weakness of our present approach, it may provide an indication of whether future investigations of an experimental nature to explore causal mechanisms are likely to be fruitful.

METHODS

Reptiles lend themselves admirably to comparative investigations of ecological correlates of colour pattern variation. Chromatic polymorphism has evolved and been lost independently in a series of distantly related lineages of lizards and snakes in various parts of the world (Greer, 1989; Wolf and Werner, 1994; Greene, 1997). Because reptiles are ectothermic, coloration may not only influence survival and reproduction directly; indirect effects of coloration on fitness mediated via body temperature may also be important (Peterson *et al.*, 1993). Associations of coloration with morphology, behaviour, and life history other than sexual dimorphism have been documented in several species of lizards and snakes (Jackson *et al.*, 1976; King, 1987; Brodie, 1989; Forsman, 1995; Forsman and Shine, 1995; Shine *et al.*, 1998; Sinervo *et al.*, 2000), suggesting that the sympatric occurrence of two or more alternative ecomorphs is relatively common in this group of animals. Extensive information on the ecology of lizards and snakes emanating from the work of dedicated herpetologists has been compiled in readily available sources.

Sources of information

We classified species as being either variable or non-variable with regard to colour pattern based on the descriptions in published field guides to reptiles and amphibians of North America (Conant and Collins, 1998; Ernst and Ernst, 2003; Stebbins, 2003). Polymorphisms are not necessarily stable over time but may undergo evolutionary dynamics and transitions; a population may change from a polychromatic to a monochromatic state through elimination of phenotypes and genotypes by selection and drift, develop into geographic variation, serve as a precursor to the evolution of sexual dichromatism, or constitute an intermediate stage in the formation of new species (Hedrick, 2006; Forsman *et al.*, 2008). We therefore made no distinction between species described as exhibiting true within-population polymorphism and species displaying geographic variation in colour pattern; both were classified as variable coloration. It also was not always possible to discriminate within-population polymorphism from geographic variation based on the information in the field guides. (We comment on potential problems of this approach in the Discussion.) We classified sexually dichromatic species as having variable coloration only if it was evident from the description that polymorphism or geographic variation occurred within one or both sexes, otherwise they were considered non-variable. Species exhibiting ontogenetic change in coloration were classified as variable only if polymorphism or geographic variation occurred among adults.

To evaluate the hypothesis that evolutionary transitions between non-variable and variable coloration have been associated with changes in geographic distribution, we used a modified version (Forsman and Åberg, 2008) of the pair-wise comparative method (Felsenstein, 1985; Møller and Birkhead, 1992; Maddison, 2000). Comparative analyses should ideally be performed using methods based on highly resolved phylogenies that contain information on branch lengths, such that the direction and order of state transitions can be determined (Pagel and Meade, 2006). Unfortunately, such phylogenies are available only for a subset of North American reptiles. The pair-wise approach is suitable for situations where a phylogenetic hypothesis of the species under investigation is unavailable or poorly resolved and it does not rely heavily on assumptions about ancestral states, branch lengths or elaborate models of evolution (Felsenstein, 1985). It is based on comparisons between matched pairs of congeneric species that differ with regard to the trait of interest (in our case, variable vs. non-variable coloration) but are otherwise similar (Møller and Birkhead, 1992). It may be difficult, however, to decide which species constitute the most appropriate match, particularly for groups that contain poorly studied species. To circumvent this problem, we included in our analysis data for *all* species that we could reliably classify as either variable or non-variable based on the descriptions in the field guides. We then performed analyses based on pair-wise comparisons of generic means for species with variable versus non-variable coloration, as explained below. To normalize the data, northern range limits and range sizes were log-transformed before statistical analysis.

Because our approach is based on matched paired comparisons, we included in our analyses only those genera that contain species classified as having variable coloration and species in the same genera that were classified as non-variable. Those genera in which all species were either variable or non-variable were omitted. It might be argued that species for which the significance of variable coloration is not immediately obvious (e.g. species with a nocturnal or fossorial lifestyle) should be excluded from the data set. However, because it is difficult to identify species for which coloration (or other characteristics correlated with coloration) is unimportant, we chose the route of broad comparisons in our search for general patterns.

Do species with variable colour patterns have more northerly range limits?

To evaluate the hypothesis that species with variable colour patterns have experienced a faster rate of post-glacial range expansions, we compared northern range limits (degrees of latitude) between species with variable versus non-variable coloration. Because theory predicts variable coloration to enhance the rate of expansions (Forsman *et al.*, 2008), we compared northern range limits rather than current mean temperatures at the range limit. We obtained information on northern range limits for the species in our data set from the distribution maps in the field guides (Conant and Collins, 1998; Stebbins, 2003). To avoid pseudoreplication, we computed for each genus the mean (if more than one species; if there was only one species we used that value) northern distribution limit for species with variable coloration and the mean northern distribution range limit for species with non-variable coloration. We then performed the statistical analysis based on paired comparisons of generic means, using repeated-measures multivariate analysis of variance (MANOVA), and treating the mean range size of variable and non-variable species within each genus as a repeated measure (Forsman and Åberg, 2008). Because the northern distribution limit may differ between lizards and snakes, we included order (Sauria or Serpentes) as an independent class variable in the model. We implemented the analyses using procedure GLM in SAS, and sigma (type III) sums of squares were used to test hypotheses (SAS Institute Inc., 2004). This approach enabled us to test for a difference in northern distribution limit between species with variable and non-variable coloration in a single analysis (rather than performing two separate analyses) while controlling statistically for overall differences in northern distribution limit between lizards and snakes. We also performed separate analyses of data for lizards and snakes using non-parametric paired comparisons.

Do species with variable colour patterns have larger geographic ranges?

To determine range sizes for the species in our data set, we first digitized the distribution maps in the field guides (Conant and Collins, 1998; Stebbins, 2003) using a scanner and then performed measurements on the digitized images using an image process and analysis program (Scion Image, Release Beta 4.0.2.). We calibrated the program based on a known distance between two fixed locations on the map such that range sizes were expressed in square kilometres. To test for a difference in range size between species with variable versus non-variable coloration, we analysed the data using the same statistical approach as described above for northern distribution limit.

RESULTS

We obtained data for 137 species of North American reptiles distributed among lizards (77 species, 9 genera) and snakes (60 species, 8 genera). Summary statistics of the pair-wise comparisons of northern distribution limits and range sizes based on within-generic means are presented in Table 1. Overall, our analyses uncovered large and statistically significant differences in northern geographic distribution limits and in range sizes between species with variable versus non-variable colour patterns (Table 1, Fig. 1).

Variable coloration is associated with more northerly geographic range limits

Species with variable coloration have an average northern distribution limit of 42.1°N (95%CI = 39.3–44.9°, least squares means and 95% confidence interval as obtained from a two-factor ANOVA with colour and order as independent class variables), which is more than 6 degrees of latitude further north than the corresponding value for species with

Table 1. Pair-wise comparison of northern distribution limits and range sizes for North American species of lizards and snakes with variable or non-variable colour patterns

	Coloration variable			Coloration non-variable		
Taxon	*N*	Range (10^3 km^2)	Latitude (°N)	*N*	Range (10^3 km^2)	Latitude (°N)
Lizards						
Coleonyx	2	319	35	2	271	31.5
Crotaphytus	1	1830	40	5	158	34.4
Holbrookia	1	1797	44	2	149	31
Sceloporus	2	2684	43.5	17	338	33.5
Xantusia	1	300	37	2	16	28.5
Cnemidophorus	4	1392	41.5	17	221	34
Eumeces	3	425	37	9	1151	43
Elgaria	1	566	63	6	94	33.2
Anniella	1	47	37.5	1	3	28.5
Snakes						
Nerodia	4	1412	39	5	439	37
Thamnophis	5	2692	50	12	568	40
Chionactis	1	280	38	1	47	32.5
Heterodon	1	3211	46	2	1404	43
Masticophis	1	1664	41	4	634	39
Elaphe	2	2213	43	2	344	39
Lampropeltis	3	2058	40	3	814	42
Crotalus	5	1498	41	9	514	34

Note: Values for range size are means computed across *N* species within each genus. Values for number of habitat types used are means computed across (*N*) species within each genus. Genera consisting of only variable or only non-variable species are not included.

non-variable coloration, 35.6°N (95%CI = 32.9–38.4°N). The more northern geographic range limit of species with variable compared with non-variable colour patterns is highly significant (repeated-measures MANOVA, effect of colour pattern: $F_{1,15} = 12.84$, $P = 0.0027$; Fig. 1) and equally pronounced in lizards and in snakes (as evidenced by the non-significant colour × order interaction effect: $F_{1,15} = 2.04$, $P = 0.17$). There also was no difference in northern geographic range limit between lizards and snakes ($F_{1,15} = 1.79$, $P = 0.20$). Our findings are robust to choice of statistical test, in that we also arrive at the conclusion that variable coloration is associated with more northern distribution limits if we analyse our data using the non-parametric Wilcoxon matched-paired signed ranks test (Siegel and Castellan, 1988). Range distributions extended further north in species with variable coloration in eight of nine lizard genera ($P < 0.01$) and in seven of eight snake genera ($P < 0.05$; Table 1).

Variable coloration is associated with larger range sizes

Species with variable coloration have an average range size of 1.4×10^6 km^2 (least squares means as obtained from a two-factor ANOVA with colour and order as independent class

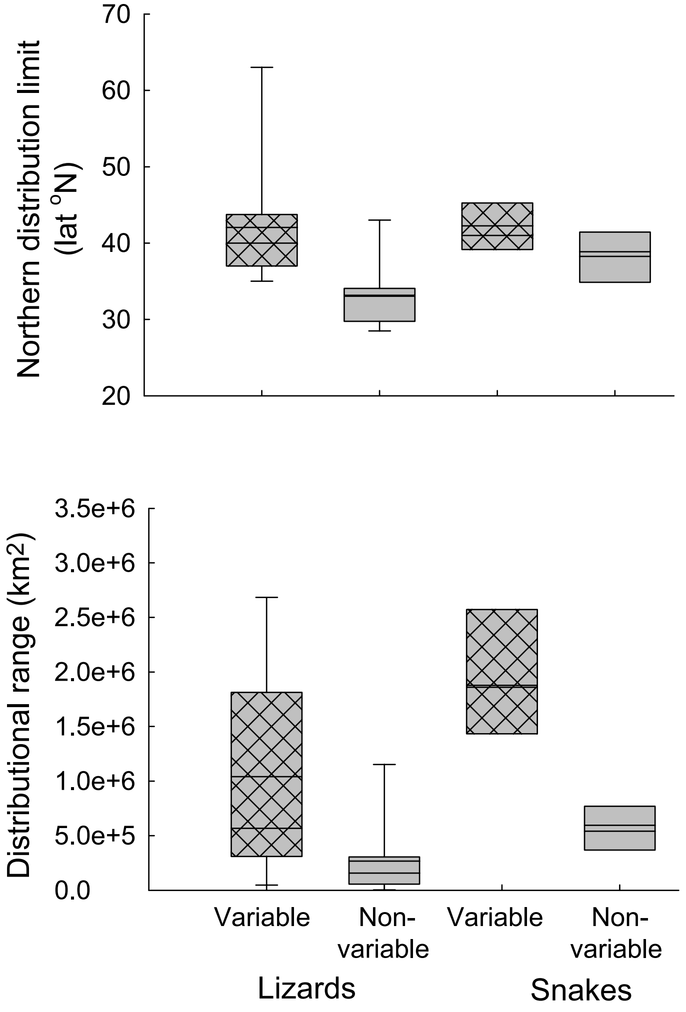

Fig. 1. Comparison of northern distribution limits (top panel) and sizes of distributional range (bottom panel) for North American species of lizards and snakes with variable and non-variable coloration. Figure is based on generic means using data provided in Table 1. The solid and dotted lines within the box indicate the median and mean, the boundaries of the box indicate the 25th and 75th percentiles, whiskers below and above indicate the 10th and 90th percentiles.

variables), which is three times larger than the corresponding value for species with non-variable coloration, 4.3×10^5 km^2. The difference in range size between species with variable versus non-variable colour patterns is highly significant (repeated-measures MANOVA, effect of colour pattern: $F_{1,15} = 25.53$, $P = 0.0001$; Fig. 1). The association of variable coloration with larger range size does not differ between lizards and snakes (as evidenced by the non-significant colour × order interaction effect: $F_{1,15} = 1.57$, $P = 0.23$). Among the species included in our data set, snakes had larger geographic range sizes on average than lizards ($F_{1,15} = 4.79$, $P = 0.045$). We also arrive at the conclusion that range size is associated with variable versus non-variable coloration if we analyse our data using non-parametric analysis. Range size was largest in the species with variable coloration in eight of nine lizard genera and in all eight snake genera (Wilcoxon matched-paired signed ranks test, both $P < 0.05$; Table 1).

Range size increased with increasing latitude in both lizards ($F_{1,16} = 13.42$, $P < 0.01$) and snakes ($F_{1,14} = 27.64$, $P < 0.0001$), consistent with Rapoport's rule (Rapoport, 1982).

DISCUSSION

Our comparative analyses of North American lizards and snakes show that the geographic distribution ranges of species with variable colour patterns extend further north and cover much larger areas, compared with those of congeneric species with non-variable colour patterns (Fig. 1). The observed associations of coloration with geographic distribution boundaries were strong. Species with variable coloration had geographic range distributions that extended 6 degrees of latitude further north, on average, compared with species with non-variable coloration. This difference exceeds the north to south latitudinal span of nearly all the states of the USA, the exceptions being Alaska, Texas, California, and Nevada. The effect size for range size was equally strong. Species with variable colour patterns had an average range size almost three times larger than that of their congeneric counterparts with non-variable coloration. Our approach of estimating range sizes and northern distribution limits from distribution maps in field guides is admittedly somewhat imprecise. We see no reason, however, why such imprecision in our data should show any systematic bias with regard to species classified as having variable versus non-variable colour patterns. Any inaccuracies also would be trivial relative to the magnitude of the effect sizes seen in our results, and so are not likely to have affected our results and conclusions.

We are not aware of any previous studies that have explored the relationship between variable coloration and northern distribution limits. Our finding that species with variable coloration have larger range sizes, however, concurs with the results of earlier comparative studies in birds (Fowlie and Krüger, 2003; Roulin and Wink, 2004) and *Drosophila* (Brisson *et al.*, 2006). An association of variable coloration with larger range size is evident also in the lizards and snakes of Australia (Forsman and Åberg, 2008). That the association is repeated across several different taxonomic groups suggests that the pattern is real but does not unravel the underlying mechanism.

Our previous comparative analyses of Australian reptiles offer some insights as to why species with variable coloration have larger ranges, because species of lizards and snakes with variable colour patterns were found to use a greater diversity of habitat types than species with non-variable coloration (Forsman and Åberg, 2008). This finding was not an epiphenomenon caused by species with variable coloration having larger ranges; the utilization of a larger number of habitat types by species with variable coloration was evident also when differences in range size were controlled for. This supports one of the underlying mechanisms [i.e. the use of more diverse resources – broader niches – by polymorphic species (Dobzhansky, 1951; Mayr, 1963; Selander, 1966; Schoener and Schoener, 1976)] envisaged by Forsman *et al.* (2008) to positively influence the dynamics and persistence of polymorphic populations, and their ability to conquer novel environments. We do not have the information necessary to test for an association of coloration with habitat types among the species in our present data set, but we can see no reason as to why the pattern of broader niches in species with variable coloration seen among Australian reptiles should not be found among the reptiles of North America.

Our present finding of more northerly geographic distribution limits and larger range sizes in North American reptile species with variable coloration is consistent with the hypothesis that the co-existence within a population of alternative colour variants may facilitate colonization and establishment of populations in novel environments and result in a faster rate of post-glacial range expansion. There are, however, alternative explanations to our findings. An increased incidence of polymorphism with declining species diversity (i.e. at higher latitudes) is expected also under the hypothesis that polymorphism evolves more easily in species-poor communities as a consequence of character release (Robinson and Schluter, 2000). We also cannot determine, based on the available evidence, whether colour polymorphism has promoted range expansions, or if variable colour patterns have evolved more readily in species that inhabit larger or more northern areas (Cain and Sheppard, 1954; Forsman *et al.*, 2008). Increments in the size and northern limit of distribution ranges may result in novel selection regimes on coloration that favour the evolution of variation. Novel mutations, and hence evolution of polymorphism, also is more likely in large populations of wider range with many individuals for pure statistical reasons. To determine whether it is more likely that polymorphism has promoted range expansions or if variable colour patterns have evolved more readily in species that inhabit larger areas may be possible for groups of organisms (unlike North American reptiles) for which a molecular phylogeny with information on branch lengths is available (Pagel and Meade, 2006). Finally, the pattern of variability correlating with range size may in part be a consequence of taxonomic practices and incomplete knowledge of phylogenetic affinities. Nominal species with large ranges are more likely to be variable across the range. If such variable species represent imperfectly resolved groups that have subsequently been re-described as distinct, more range-limited, and less variable taxa, then this taxonomic splitting may have contributed to the association of monomorphism with smaller ranges. Unfortunately, it is not possible to discriminate among these alternative hypotheses and explanations to the patterns observed in this study based on available evidence.

In summary, we show that the geographic distribution ranges of North American reptile species with variable colour patterns extend further north and cover larger areas than those of congeneric species with non-variable colour patterns. The observed associations are strong and consistent with the hypothesis that the co-existence of two or more colour morphs has positively influenced population processes and enhanced the rate of post-glacial range expansions. Because our study is based on correlational data, however, we cannot discard alternative explanations to our findings and our conclusions must therefore be treated as tentative. Future comparative approaches should address the challenge of examining the influence of colour variability on recent range shifts directly, rather than establishing associations with current states. Conclusive evidence that polymorphism promotes colonization, establishment, and persistence of populations in novel environments, however, can only be obtained by experimentally introducing propagules that differ in diversity, and monitoring their establishment. It would also be interesting to examine if variable coloration and polymorphism may help identify potential invasive species before they become invasive. Our present findings suggest that such endeavours are likely to be worthwhile.

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REFERENCES

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Arnold, S.J., Pfrender, M.E. and Jones, A.G. 2001. The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica*, **112/113**: 9–32.

Brisson, J.A., Wilder, J. and Hollocher, H. 2006. A phylogenetic analysis of the *cardini* group of *Drosophila* with respect to changes in pigmentation. *Evolution*, **60**: 1228–1241.

Brodie, E.D. 1989. Genetic correlation between morphology and antipredator behaviour in natural populations of the garter snake *Thamnophis ordinoides*. *Nature*, **342**: 542–543.

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

Cain, A.J. and Sheppard, P.M. 1954. The theory of adaptive polymorphism. *Am. Nat.*, **88**: 321–326.

Conant, R. and Collins, T. 1998. *A Field Guide to Reptiles and Amphibians of Eastern/Central North America*. New York: Houghton Mifflin.

Crozier, L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology*, **85**: 231–241.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection*. London: Murray.

Dobzhansky, T. 1951. *Genetics and the Origin of Species*. New York: Columbia University Press.

Endler, J.A. 1995. Multiple-trait coevolution and environmental gradients in guppies. *Trends Ecol. Evol.*, **10**: 22–29.

Ernst, C.H. and Ernst, E.M. 2003. *Snakes of the United States and Canada*. Washington, DC: Smithsonian Books.

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

Ferrière, R., Dieckmann, U. and Couvet, D., eds. 2004. *Evolutionary Conservation Biology*. Cambridge: Cambridge University Press.

Fisher, R.A. 1958. Polymorphism and natural selection. *Bulletin de l'Institute International de Statistique*, **36**: 284–289 (also in *Journal of Ecology*, **246**: 289–293).

Forsman, A. 1995. Opposing fitness consequences of color pattern in male and female snakes. *J. Evol. Biol.*, **8**: 53–70.

Forsman, A. and Åberg, V. 2008. Associations of variable coloration with niche breadth and conservation status among Australian reptiles. *Ecology*, **89**: 1201–1207.

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

Forsman, A. and Shine, R. 1995. The adaptive significance of color pattern polymorphism in the Australian scincid lizard *Lampropholis delicata*. *Biol. J. Linn. Soc.*, **55**: 273–291.

Forsman, A., Ringblom, K., Civantos, E. and Ahnesjö, J. 2002. Coevolution of color pattern and thermoregulatory behavior in polymorphic pygmy grasshoppers *Tetrix undulata*. *Evolution*, **56**: 349–360.

Forsman, A., Ahnesjö, J., Caesar, S. and Karlsson, M. 2008. A model of ecological and evolutionary consequences of color polymorphism. *Ecology*, **89**: 34–40.

Fowlie, M.K. and Krüger, O. 2003. The evolution of plumage polymorphism in birds of prey and owls: the apostatic selection hypothesis revisited. *J. Evol. Biol.*, **16**: 577–583.

Garcia-Ramos, G. and Rodrigues, D. 2002. Evolutionary speed of species invasions. *Evolution*, **56**: 661–668.

Gilman, S.E. 2006. Life at the edge: an experimental study of a poleward range boundary. *Oecologia*, **148**: 270–279.

Greene, H.W. 1997. *Snakes: The Evolution of Mystery in Nature*. Berkeley, CA: University of California Press.

Greer, A.E. 1989. *The Biology and Evolution of Australian Lizards*. Chipping Norton, UK: Beatty & Sons.

Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.*, **8**: 993–1009.

Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A. *et al.* 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecol. Lett.*, **8**: 91–101.

Hedrick, P.W. 2006. Genetic polymorphism in heterogeneous environments: the age of genomics. *Annu. Rev. Ecol. Syst.*, **37**: 67–93.

Hoffman, A.A. and Blows, M.W. 1994. Species borders: ecological and evolutionary perspectives. *Trends Ecol. Evol.*, **9**: 223–227.

Jackson, J.F., Ingram, W., III and Campbell, H.W. 1976. The dorsal pigmentation pattern of snakes as an antipredator strategy: a multivariate approach. *Am. Nat.*, **110**: 1029–1053.

King, R.B. 1987. Colour pattern polymorphism in the Lake Erie water snake, *Nerodia sipedon insularum*. *Evolution*, **41**: 241–255.

Kolbe, J.J., Glor, R.E., Schettino, L.R.G., Lara, A.C., Larson, A. and Losos, J.B. 2004. Genetic variation increases during biological invasion by a Cuban lizard. *Nature*, **431**: 177–181.

Lockwood, J.L., Cassey, P. and Blackburn, T. 2005. The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.*, **20**: 223–228.

Maddison, W.P. 2000. Testing character correlation using pairwise comparisons on a phylogeny. *J. Theor. Ecol.*, **202**: 195–204.

Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, MA: Harvard University Press.

Møller, A.P. and Birkhead, T.R. 1992. A pairwise comparative method as illustrated by copulation frequency in birds. *Am. Nat.*, **139**: 644–656.

Pagel, M. and Meade, A. 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am. Nat.*, **167**: 808–825.

Peterson, C.R., Gibson, A.R. and Dorcas, M.E. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. In *Snakes – Ecology and Behavior* (R.A. Seigel and J.T. Collins, eds.), pp. 241–314. New York: McGraw-Hill.

Pielou, E.C. 1992. *After the Ice Age: The Return of Life to Glaciated North America*. Chicago, IL: University of Chicago Press.

Porter, W.P. 1967. Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. *Ecol. Monogr.*, **37**: 273–296.

Poulton, E.B. 1890. *The Colour of Animals: Their Meaning and Use*. London: Kegan Paul, Trench, Trubner.

Rapoport, E.H. 1982. *Areography: Geographical Strategies of Species*. Oxford: Pergamon Press.

Robinson, B.W. and Schluter, D. 2000. Natural selection and the evolution of adaptive genetic variation in northern freshwater fishes. In *Adaptive Genetic Variation in the Wild* (T.A. Mousseau, B. Sinervo and J.A. Endler, eds.), pp. 65–94. Oxford: Oxford University Press.

Roulin, A. and Wink, M. 2004. Predator–prey relationships and the evolution of colour polymorphism: a comparative analysis in diurnal raptors. *Biol. J. Linn. Soc.*, **81**: 565–578.

Ruxton, G.D., Sherratt, T.N. and Speed, M. 2004. *Avoiding Attack the Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford: Oxford University Press.

Sanford, E., Holzman, S.B., Haney, R.A., Rand, D.M. and Bertness, M.D. 2006. Larval tolerance, gene flow, and the northern geographic range limit of fiddler crabs. *Ecology*, **87**: 2882–2894.

SAS Institute Inc. 2004. *SAS/STAT 9 1 User's Guide*. Cary, NC: SAS Institute Inc.

Schoener, T.W. and Schoener, A. 1976. The ecological context of female pattern polymorphism in the lizard *Anolis sagrei*. *Evolution*, **30**: 650–658.

Selander, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor*, **68**: 113–151.

Shine, R., Ambariyanto, Harlow, P.S. and Mumpuni. 1998. Ecological divergence among sympatric colour morphs in blood pythons, *Python brongersmai*. *Oecologia*, **116**: 113–119.

Siegel, S. and Castellan, N.J.J. 1988. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.

Sinervo, B., Svensson, E. and Comendant, T. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. *Nature*, **406**: 985–988.

Stebbins, R.C. 2003. *A Field Guide to Western Reptiles and Amphibians*. New York: Houghton Mifflin.

Stevenson, R.D. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am. Nat.*, **126**: 362–386.

Wade, M.J. and Kalisz, S. 1990. The causes of natural selection. *Evolution*, **44**: 1947–1955.

Wolf, M. and Werner, Y.L. 1994. The striped colour pattern and striped/non-striped polymorphism in snakes (Reptilia: Ophidia). *Biol. Rev.*, **69**: 599–610.