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Geographic variation in animal colour polymorphisms and its role in speciation

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ABSTRACT

Polymorphic species, in which multiple variants coexist within a population, are often used as model systems in evolutionary biology. Recent research has been dominated by the hypothesis that polymorphism can be a precursor to speciation. To date, the majority of research regarding polymorphism and speciation has focused on whether polymorphism is maintained within a population or whether morphs within populations may diverge to form separate species (sympatric speciation); however, the geographical context of speciation in polymorphic systems is likely to be both diverse and complex. In this review, we draw attention to the geographic variation in morph composition and frequencies that characterises many, if not most polymorphic species. Recent theoretical and empirical developments suggest that such variation in the number, type and frequency of morphs present among populations can increase the probability of speciation. Thus, the geographical context of a polymorphism requires a greater research focus. Here, we review the prevalence, causes and evolutionary consequences of geographic variation in polymorphism in colour-polymorphic animal species. The prevalence and nature of geographic variation in polymorphism suggests that polymorphism may be a precursor to and facilitate speciation more commonly than appreciated previously. We argue that a better understanding of the processes generating geographic variation in polymorphism is vital to understanding how polymorphism can promote speciation.

Key words: clinal variation, co-adapted trait complexes, colour morph, correlational selection, diversity, gene flow, morph composition, population divergence.

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I. INTRODUCTION

Phenotypic variation, interacting with selection and drift, is generally a prerequisite for evolution. Polymorphism, the presence of multiple, discrete variants (or morphs) within a single population, the rarest of which is too common to be solely due to recurrent mutation (Ford, 1945; Gray & McKinnon, 2007), represents extreme, easily measurable intraspecific phenotypic variation. This is particularly true for species with morphs that differ in appearance, commonly colouration; for example, red, black and yellow head coloration in Gouldian finches, *Erythrura gouldiae* (Gilby, Pryke & Griffith, 2009) and multiple male colour variants in guppies, *Poecilia reticulata* (Olendorf *et al.*, 2006), in which colour can be used as a 'phenotypic marker'. Consequently, colour-polymorphic species are often used as model systems for the study of evolutionary processes, including natural selection in moths (Kettlewell, 1956), frequency-dependent selection in fish (Olendorf *et al.*, 2006), alternate reproductive strategies in lizards (Sinervo & Lively, 1996), and mate choice and genetic incompatibilities in birds (Pryke, 2010).

Recently, there has been a surge of interest in the role of polymorphism in speciation (Gray & McKinnon, 2007; Forsman *et al.*, 2008; McKinnon & Pierotti, 2010; Corl *et al.*, 2010*b*; Hugall & Stuart-Fox, 2012), with recent evidence linking polymorphism to rapid phenotypic evolution (Corl *et al.*, 2010*b*) and accelerated speciation rates (Hugall & Stuart-Fox, 2012). Speciation of polymorphic taxa has often been thought to necessitate sympatric speciation because polymorphism, by definition, entails the co-occurrence of phenotypically discrete morphs within a population. Due to the historical controversy surrounding sympatric speciation (Bolnick & Fitzpatrick, 2007; Mallet *et al.*, 2009), much research has focused on whether polymorphism can facilitate or be a precursor to sympatric speciation (reviewed in Gray & McKinnon, 2007). However, it is now generally accepted that substantial ecological and phenotypic divergence can occur despite gene flow, and that categorisation of speciation processes according to 'geographic mode' (e.g. sympatric, allopatric, parapatric) often does not adequately describe the complex spatial relationships between diverging populations (Marie Curie SPECIATION Network, 2012). Moreover, it is becoming increasingly apparent that polymorphic taxa often show population differences in the number, type and frequency of morphs present (Table 1). Recent phylogeographic studies indicate substantial population divergence and/or subspeciation in species showing such geographic variation in polymorphism (Spellman, Riddle & Klicka, 2007; Chapple *et al.*, 2008; Hull *et al.*, 2010; Iserbyt *et al.*, 2010; Corl *et al.*, 2010*b*). Thus, polymorphism may play an important role in much more common, geographically structured speciation processes and understanding the geographical context of a polymorphism is likely to be critical to understanding the role of polymorphism in speciation.

In this review, we specifically address the nature, causes and consequences of geographic variation in polymorphism to provide insight into the role of polymorphism in speciation. We begin by discussing the prevalence of geographic variation in polymorphism in colour-polymorphic animal species and argue that polymorphism predisposes species to showing geographic variation. We describe the primary processes affecting population morph frequencies: negative frequency-dependent selection, secondary contact and hybridisation, spatial variation in selection, stochastic processes and gene flow. We then discuss the potential evolutionary consequences of geographic variation in polymorphism with specific focus on circumstances and processes that can lead to speciation.

II. PREVALENCE OF GEOGRAPHIC VARIATION IN POLYMORPHISM

Geographic variation in polymorphism is likely to be common; however, despite its potentially important role in speciation, for most systems geographic variation has not been explicitly documented. The majority of well-studied polymorphic species exhibit population differences in the number, type and frequency of morphs present (Table 1). Examples include: the peppered moth, *Biston betularia* (Grant *et al.*, 1998) and the land snail, *Cepaea nemoralis* (Fig. 1; Ozgo, 2011) in which the frequency of morph types differ between populations, and the side-blotched lizard, *Uta stansburiana* (Corl *et al.*, 2010*b*), in which populations are either tri-, di- or monomorphic (see also Table 1). Furthermore, at least 20% of polymorphic bird species exhibit clinal variation in morph frequencies (Galeotti *et al.*, 2003), although this is likely to be an underestimate since most species have not been examined in any detail. Conversely, in some species, such as the Gouldian finch, *Erythrura gouldiae*, the frequency and composition of morphs is relatively consistent among populations (Gilby *et al.*, 2009). Understanding why some polymorphic species exhibit geographic variation while others do not could be important for identifying processes either maintaining the polymorphism or contributing to speciation.

Colour morphs can differ in traits other than appearance. Colouration is often the most obvious phenotypic expression of a suite of morphological, physiological and behavioural traits that differ between morphs, ranging from mating strategies to parasite resistance (reviewed in McKinnon & Pierotti, 2010). These trait complexes represent fitness optima and may allow multiple morphs to coexist in a population by balancing the polymorphism (Maynard-Smith, 1966; Sinervo & Lively, 1996). Consequently, polymorphic species are able to utilise a diverse range of habitats because different morphs are often adapted to different microhabitats. Theoretical models therefore predict that species with two or more morphs will occupy broader niches, have larger range sizes, have a greater probability of range expansion and colonisation and be less susceptible to environmental change and local extinction than monomorphic species (Forsman *et al.*, 2008). These

Table 1. Polymorphic species exhibiting geographic variation in polymorphism (GV). This list is non-exhaustive but highlights some systems in which the causes and/or consequences of geographic variation have been specifically studied

Study system	Polymorphism	Correlated traits	Geographic variation	Causes of GV	Consequences of GV	References
Invertebrates						
Land snail, *Cepaea nemoralis*	Brown, pink, yellow, banded, un-banded and combination shell	Thermo-regulatory traits	Populations differ in morph frequencies	Selection: climate and predation	—	Ozgo (2011)
Sedge-sprite damselfly, *Nehalennia irene*	Gynomorph and andromorph females	—	Andromorph frequencies vary between 0 and 90%	?Selection ?Genetic drift ?Founder effect	Genetic divergence	Iserbyt *et al.* (2010) and Van Gossum *et al.* (2007)
Blue-tailed damselfly, *Ischnura elegans*	Gynomorph, andromorph and infuscans-obsoleta females	Morphology	Trimorphic and dimorphic populations	?Selection: climate ?Genetic drift	—	Gosden *et al.* (2011) and Sanchez-Guillen *et al.* (2011)
Marsh blue-tail damselfly, *Ischnura senegalans*	Gynomorph and andromorph females	Larval development, body size	Clinal variation in morph frequencies	Selection: temperature and negative frequency-dependent	—	Takahashi *et al.* (2011)
Wingless grasshopper, *Phaulacridium vittatum*	Plain, striped and incomplete-striped	—	Populations differ in morph frequencies	?Selection: habitat type, proximity to forest	—	Dearn (1981, 1984)
Ladybird, *Adalia bipunctata*	Melanic and non-melanic (red) carapace	—	Clinal variation in morph frequencies	Selection: frequencies change clinally	—	Brakefield (1984)
Peppered moth, *Biston betularia*	Melanic and non-melanic	—	Populations differ in morph frequencies	Selection: morph frequencies related to air polution	—	Grant *et al.* (1998) and Saccheri *et al.* (2008)
Reptiles						
Side-blotched lizard, *Uta stansburiana*	Orange, yellow and blue throat colour	Reproductive strategy, immune response, territory size	Trimorphic, dimorphic and monomorphic populations.	?Selection: repeated loss of yellow morph	Populations differ in sexual size dimorphism	Corl *et al.* (2010*a*,*b*)
Skyros wall lizard, *Podarcis gaigeae*	Orange, yellow, white and combinations throat colour	—	Populations differ in morph number and frequency	Genetic drift ?Selection	—	Runemark *et al.* (2010)

Brown anole lizard, *Anolis sagrei*	Diamond, bar and diamond-bar dorsal pattern in females	Immune response	Populations differ in morph frequencies	Selection unlikely ?Genetic drift ?Founder effect	—	Calsbeek *et al.* (2009)
Slender anole lizard, *Anolis apletophallus*	Solid and basal dewlap colour	—	Monomorphic and dimorphic populations	?Selection: habitat	No genetic divergence	Stapley *et al.* (2011)
Tree lizard, *Urosaurus ornatus*	Orange, yellow, blue and combinations throat colour	Reproductive strategy	Monomorphic and polymorphic populations	Selection unlikely; not related to environmental factors	Populations differ in correlated behaviour of morphs	Carpenter (1995) and Hews *et al.* (1997)
White's skink, *Liopholis whitii*	Patterned, plain-back, patternless	Life history and reproductive traits (subtle)	Populations differ in morph number and frequencies	?Selection ?Genetic drift	—	Chapple *et al.* (2008)
Mesquite lizard, *Sceloporus grammicus*	Orange, yellow, blue, white and combination throat colour	Aggression levels	Populations differ in morph types and frequencies	?Selection: habitat, sensory drive	Populations differ in correlated behaviour of morphs	Bastiaans *et al.* (2013)
Birds						
Owl genera (*Otus*, *Megascops*, *Strix* and *Glaucidium*)	Pheomelanin- (red) & non- pheomelanin- (grey) based colouration	Immune response, parental investment (some species)	Populations differ in morph frequencies	Selection: frequencies change clinally with latitude	—	Roulin *et al.* (2011)
Bananaquit, *Coereba flaveola*	Yellow and black plumage	—	Clinal variation in morph frequencies	Selection: rainfall Gene flow	—	Wunderle (1981)
Eastern reef heron, *Egretta sacra*	White or dark plumage	—	Populations differ in morph frequencies	?Selection: climate, substrate type	—	Itoh (1991)
Mammals						
Rock pocket mouse, *Chaetodipus intermedius*	Light and melanic coat	—	Frequencies of both morphs vary between 0 and 100%	Selection: substrate type	—	Hoekstra *et al.* (2004)
Fish						
Brown dottyback, *Pseudochromis fuscus*	Yellow, brown, orange, pink and grey colouration	Dorsal fin ray number	Populations differ in morph type, number and frequencies	?Selection: habitat	Genetic divergence	Messmer *et al.* (2005)

? indicates a possible cause but a lack of evidence.

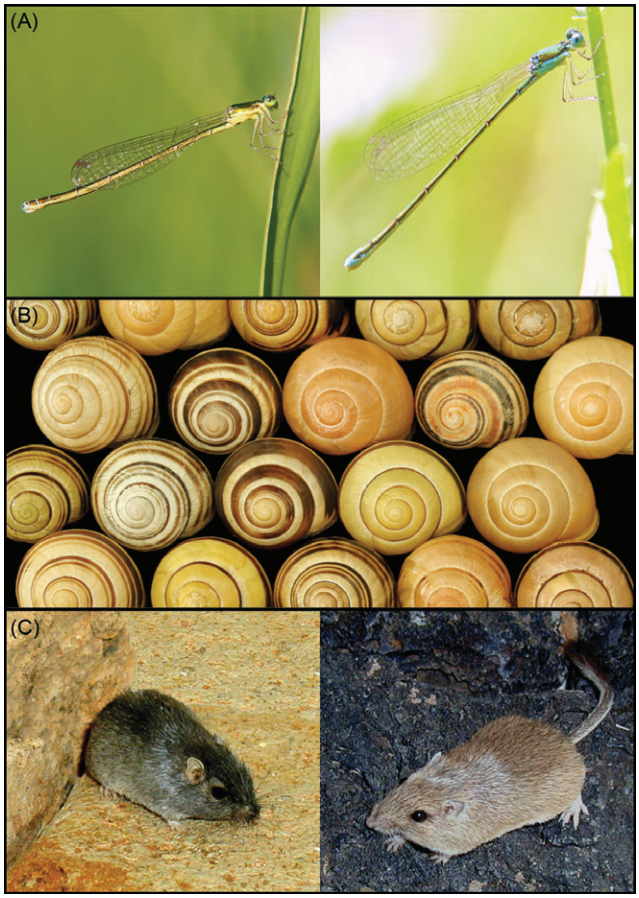

Fig. 1. Examples of polymorphisms exhibiting geographic variation. Gynomorph and andromorph female colouration in the damselfly, *Nehalennia irene* (A; photo credit: A. Iserbyt), shell pattern variation in the land snail, *Cepaea nemoralis* (B; photo credit: D. McIntyre, ©Custom Life Science Images), and light and dark coat colour in rock pocket mice, *Chaetodipus intermedius* (C; photo credit: H. Hoekstra).

predictions are supported by comparative studies of birds (Galeotti & Rubolini, 2004) and reptiles (Forsman & Aberg, 2008*a*,*b*), which show that polymorphic species have broad ecological niches and occupy many different habitats, although the latter studies confound polymorphism and geographic colour variation. As local selective pressures, and hence the fitness of different morphs, are likely to change across a landscape, polymorphism itself may predispose species to showing geographic variation. Consequently, it is not surprising that geographic variation in polymorphism appears to be common and taxonomically widespread in polymorphic species (Table 1; Fig. 1).

III. PROCESSES AFFECTING POPULATION MORPH FREQUENCIES

Processes affecting morph frequencies can contribute to the maintenance of polymorphism, or to geographic variation in polymorphism. For example, temporally variable selection at the local scale is likely to maintain polymorphism while broad-scale spatially variable selection is likely to facilitate population divergence. Temporal variation in morph frequencies is intrinsically linked to negative frequency-dependent selection, which we consider in more detail below. In this section, we discuss potential processes involved in the gain or loss of morphs or changes in morph frequencies among populations, including negative frequency-dependent selection, secondary contact and hybridisation, spatial variation in selection, stochastic processes and gene flow. Understanding these processes is essential to understanding how geographic variation in polymorphism can lead to diversification within and among species.

(1) Negative frequency-dependent selection

Both the initial spread and subsequent maintenance of new morphs is often due to negative frequency-dependent natural and sexual selection where rare individuals have a selective advantage (Gray & McKinnon, 2007). For example, negative frequency-dependent selection likely maintains remarkable colour variation in male guppies, *Poecilia reticulata* (Olendorf *et al.*, 2006). Female guppies show a preference for rare or novel morphs (Hughes *et al.*, 1999) and rare morphs have a higher survival rate, potentially due to search image formation (apostatic selection) by visual predators (Olendorf *et al.*, 2006). By forming a search image of common prey types, predators increase their foraging efficiency, particularly when searching for cryptic prey (Tinbergen, 1960). Frequency-dependent sexual conflict, due to increased male harassment of common morphs, also maintains female polymorphism in species of damselfly (Svensson, Abbott & Hardling, 2005; Takahashi *et al.*, 2010). Under negative frequency-dependent selection, morph frequencies are expected to fluctuate among populations and years as a function of their fitness. This pattern of morph frequency oscillations is observed in *Ischnura elegans* and *I. senegalensis* (Svensson *et al.*, 2005; Takahashi *et al.*, 2010), highlighting the importance of spatially and temporally replicated studies for identifying evolutionary processes influencing polymorphism (Svensson & Abbott, 2005; Svensson *et al.*, 2005).

Negative frequency-dependent selection can constrain population divergence (and subsequent speciation) by maintaining polymorphism across multiple populations and years and preventing fixation of a single morph type (Svensson *et al.*, 2005). However, frequency-dependent selection may interact with other evolutionary processes (Section V), to generate geographic variation in polymorphism. For example, cyclical changes in morph fitness maintains male colour polymorphism in the side-blotched lizard, *Uta stansburiana* (Sinervo & Lively, 1996), however, populations differ in the number and frequency of morph types (Corl *et al.*, 2010*b*). Corl *et al.* (2010*b*) propose that frequency-dependent selection provides the starting material for divergence by maintaining intraspecific diversity on which other processes can act. Negative frequency-dependent selection plays a role in geographic

variation in polymorphism in the marsh blue-tail damselfly, *I. senegalensis* (Takahashi *et al.*, 2011). In this species, local selective pressure, favouring one morph type, is balanced by negative frequency-dependent selection favouring the other, rarer morph type, producing smooth clinal variation in morph frequencies across the landscape (clinal variation discussed in Section III.2, 3; Takahashi *et al.*, 2011).

(2) Secondary contact and hybridisation

One way in which geographic variation in polymorphism can arise is when populations that have been evolving independently in allopatry, come into secondary contact (Roulin, 2004). Different site-specific selective pressures during separation result in the establishment of divergent phenotypes in the two populations. When these populations come into secondary contact, and assuming that genetic divergence is not too pronounced to prevent interbreeding, a clear polymorphism will exist at the contact zone while monomorphic populations will occur elsewhere (Fig. 2; Roulin, 2004, and references within). Coupled with gene flow, this can produce a geographic cline in morph frequencies; for example, the alpine weta, *Hemideina maori*, in the Rock and Pillar mountain range of New Zealand exhibits a colour morph cline ranging from primarily yellow in the north to black in the south (King *et al.*, 1996). Intermediate populations contain a combination of morph types, indicating that this area may represent a secondary contact zone between two differentiated populations (King *et al.*, 1996). If a polymorphism is formed by secondary contact and morph fitness is not equal over time, the polymorphism will be transient with one morph outcompeting the other (Ford, 1945; Huxley, 1955).

The potential influence of hybridisation in generating geographic variation in polymorphism may be more complex than a cline in morph frequencies due to secondary contact. Hybridisation may be a source of genetic diversity and contribute to variation in morph composition or frequencies, particularly if a few selectively advantageous alleles introgress into otherwise 'pure' parental genomes (Barton, 2001). For example, spatially variable interspecific hybridisation between the damselfly species *Ischnura elegans* and *I. graellsii* may partially explain the highly variable (non-clinal) androchrome frequencies (4–90%) among Spanish populations (Gosden, Stoks & Svensson, 2011). Gene–gene interactions generated by heterospecific introgression at population margins can also reduce population fitness and density, reducing the probability that locally advantageous alleles become fixed and maintaining diversity (Barton, 2001; Bridle & Vines, 2007). The way in which hybridisation may interact with other processes, such as frequency-dependent selection and gene flow, in polymorphic systems remains an open question.

(3) Spatial variation in selection

There is substantial evidence that spatial and temporal variation in selective regimes can influence morph frequencies (Hoekstra, Drumm & Nachman, 2004; Van Gossum *et al.*, 2007; Corl *et al.*, 2010*b*; Ozgo, 2011; Roulin, Burri & Antoniazza, 2011). While temporal variation in selection is likely to favour the maintenance of a polymorphism (Calsbeek, Bonvini & Cox, 2009), spatial variation in selection and local adaptations can lead to geographic variation in morph composition and frequencies (Arnqvist, 1992; Svensson & Sinervo, 2004). In a stable population, morph fitness will be equal; however, when site-specific conditions favour certain trait combinations (and therefore morphs) over others, a polymorphism can be destabilised. As a result, morphs at a selective advantage may increase in frequency while disadvantaged morphs may be lost from the population.

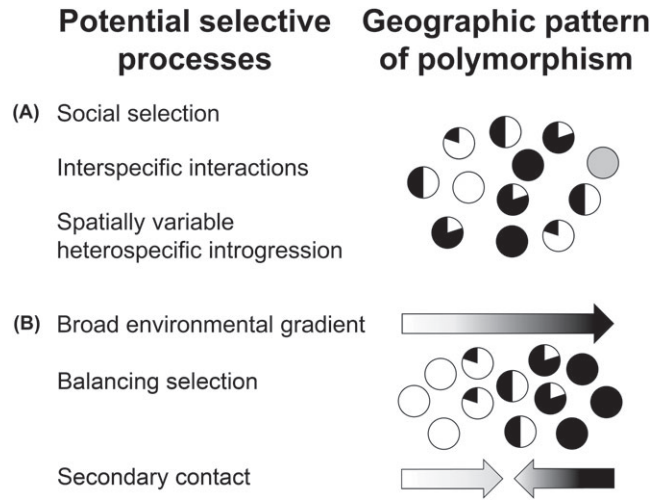

Fig. 2. Potential selective processes generating mosaic (A) and clinal (B) patterns of variation in morph composition and frequency. Under some circumstances, selective processes (combined with limited gene flow, particularly at range margins) can lead to the evolution of novel morphs (grey circle in A), in addition to monomorphic core populations (white and black circles). Arrows in (B) represent morph frequency clines. Clinal variation may result from a gradual change in selective pressure over a species distribution, a balance between local selection favouring an alternate morph at either end of the cline and negative frequency-dependent selection or secondary contact between divergent populations coupled with gene flow. Note that environmental gradients and secondary contact produce the same geographic pattern.

Spatial variation in selection can be in the form of a cline, where selection changes smoothly over a species distribution (Fig. 2). Morph frequencies are likely to change in a clinal fashion if a trait is under selection associated with some environmental gradient, such as temperature. For example, melanin-based colouration in owl species is associated with adaptations to warm climates and therefore increases in frequency, in a clinal fashion, towards the equator (Roulin *et al.*, 2011). As morphs often vary in colour, shape and size, all of which affect an organism's thermal properties, temperature will differentially affect morphs, particularly in ectotherms. For instance, temperature has been shown to

affect morph performance differentially in species of insects (Van Dyck & Matthysen, 1998; Forsman, 1999; Bots *et al.*, 2009), so that morph frequencies may vary as a function of temperature. Climatic factors such as temperature could also affect morph frequencies indirectly through their effect on morph-specific social interactions. For example, Gosden *et al.* (2011) hypothesise that colder temperatures may affect levels of male mating harassment in the blue-tailed damselfly, *Ischnura elegans*, which differentially affects female morphs (Gosden & Svensson, 2007, 2009). Correlations between morph frequencies and environmental clines may provide evidence that selection is generating geographic variation in morph composition (Hoekstra *et al.*, 2004; Ozgo, 2011; Roulin *et al.*, 2011). Other, indirect evidence for the influence of abiotic factors on morph frequencies comes from data showing consistent, long-term changes in morph frequencies over time as well as space. For example, although negative frequency-dependent selection contributes to variation in morph frequencies and polymorphism maintenance in *I. elegans*, a study of 12 Swedish populations over four generations showed a consistent decline in the frequency of andromorph females over time (Svensson & Abbott, 2005). This long-term parallel decline in morph frequencies suggests an abiotic driver such as temperature (Svensson & Abbott, 2005). However, as environmental factors are likely to be correlated (e.g. rainfall will influence vegetation type), it may be difficult to determine definitively the source of selection.

Conversely, social selection, defined as competition between conspecifics for resources, including sexual selection in which the resource is a mate (West-Eberhard, 1983), is likely to form a more unpredictable selection mosaic pattern (Fig. 2; Gosden & Svensson, 2008). While other forms of selection change smoothly over a species range in association with some environmental gradient, social selection is highly dependent on population density (Arnqvist, 1992) and frequencies of morph types within a population (Pryke & Griffith, 2009*b*). Thus, changes in morph frequencies due to social selection are likely to be abrupt and non-clinal. Social selection can alter gene frequencies if possessing a particular trait allows a morph to outcompete others. This advantage could be due, for example, to female preference for a particular colour morph in a given visual environment (Fuller, Houle & Travis, 2005) or male adaptations to compete with other males (Stuart-Fox *et al.*, 2006). Another example of social selection is sexual conflict over mating frequency. Frequency-dependent sexual conflict occurs in the blue-tailed damselfly, *Ischnura elegans*, a species in which male mating harassment reduces female fitness (Svensson & Abbott, 2005). Common female morphs suffer increased mating harassment because males learn to target locally abundant morphs, similar to apostatic selection by predators (Svensson *et al.*, 2005; Verzijden *et al.*, 2012). This ability to switch preference between morph types may be facilitated by plastic mate preference in males (Finke, 2004; Verzijden *et al.*, 2012). The result of this frequency-dependent sexual conflict and harassment is fine-grained spatial variation in selective regimes in the form of a selection mosaic (Gosden & Svensson, 2008), which may produce a highly variable geographic pattern of morph frequencies.

Interspecific interactions, such as predation or parasitism, may also produce a non-clinal selective pattern (Fig. 2; Brodie, Ridenhour & Brodie, 2002). Some morph types may be more susceptible than others in a given environment due, for example, to differences in behaviour, conspicuousness (Forsman & Appelqvist, 1998; Van Gossum *et al.*, 2004) or immunocompetence (Roulin *et al.*, 2000; Svensson, Sinervo & Comendant, 2001; Pryke *et al.*, 2007; Calsbeek, Bonneaud & Smith, 2008). Furthermore, predators may alter their strategies depending on habitat, prey density and frequency of prey types (Bond & Kamil, 2006). Consequently, predation risk may be dependent on the frequency as well as the conspicuousness of morph types. Similarly, susceptibility to parasites may depend on population structure. In the Gouldian finch, *Erythrura gouldiae*, the immune response of red-headed finches decreases when the frequency of red-headed individuals in the population is high, due to changes in hormone levels associated with an aggressive social environment (Pryke *et al.*, 2007). However, although selection may be frequency dependent and expected to maintain polymorphism, populations are likely to differ in the number and/or type of predators, parasites or prey present, imposing different selective pressures on morphs in different populations (Merilaita, 2006). Therefore, intra- and interspecific interactions may not produce a predictable pattern of selection, as selective regimes will depend on localised ecological factors (Gosden & Svensson, 2008). Consequently, any antagonistic or mutualistic interactions within and between species can produce a mosaic pattern of selection (Thompson, 1994, 1997). By investigating the pattern of geographic variation in polymorphism (cline, mosaic), researchers may gain insight into the types of selection generating geographic variation and population divergence, which may also be important processes in speciation.

(4) Stochastic processes

Non-adaptive forces such as gene flow and genetic drift and historical events such as founder effects can also contribute to geographic variation in polymorphic species (Reillo & Wise, 1988). In most cases, spatial variation in polymorphism cannot be explained by selection alone (Van Gossum *et al.*, 2007; Calsbeek *et al.*, 2009) and it is therefore likely that stochastic processes and gene flow also play a role in determining morph frequencies. The relative importance of selection and drift in evolution remains a topic of debate (Lenormand, Roze & Rousset, 2009; Marie Curie SPECIATION Network, 2012). The potential contribution of genetic drift will be dependent on population size, location and connectedness, with small, isolated populations and populations on the edge of a species range being more susceptible to drift (Wright, 1931; Brakefield, 1990; Vucetich & Waite, 2003). However, stochastic processes can occur at the gene, individual and population levels, so may have

an important influence even in very large populations (Lenormand *et al.*, 2009).

A commonly employed method for determining the roles of genetic drift *versus* selection in morph frequencies is to investigate whether the population distribution of morphs differs from the neutral expectation derived from neutral genetic markers (e.g. microsatellites; Hoffman *et al.*, 2006; Abbott *et al.*, 2008; Runemark *et al.*, 2010). Specifically, if genetic drift is the predominant force acting on morph frequencies then morph frequency divergence should not differ from neutral genetic divergence, with the converse if selection is the more important force (with consideration of gene flow implicit in this comparison). Runemark *et al.* (2010) found that population divergence for throat colour morph frequencies in the Skyros wall lizard, *Podarcis gaigeae*, fell within the estimated neutral distribution and therefore could not exclude genetic drift as an explanation for the observed interpopulational variation in morph frequencies. These findings, coupled with small effective population size, suggest that genetic drift is a relatively strong force in this system (Runemark *et al.*, 2010). However, even in systems where drift is important, morphs often differ in a suite of traits and it is unlikely that these will not be subject to selection, thus making the neutral expectation model difficult to test (Marie Curie SPECIATION Network, 2012). Geographically variable polymorphic species may provide good models for studying the interaction between drift, selection and gene flow during speciation because they may show multiple instances of incipient speciation in different environments across their geographic range.

(5) Gene flow

Adaptive divergence represents a balance between the opposing forces of local selection and gene flow (reviewed in Slatkin, 1987). Selection promotes adaptation to local environments and divergence between populations, while gene flow constrains adaptation by introducing alleles from populations with different selective pressures, and preventing populations from reaching adaptive peaks (Garcia-Ramos & Kirkpatrick, 1997). Reduced gene flow may be a cause or consequence of population differentiation. Low levels of gene flow can facilitate divergence by allowing populations to adapt to local selective environments. Alternatively, decreased gene flow may be the result, rather than the cause, of reproductive isolation caused by adaptive divergence (Nosil & Crespi, 2004). That is, if selection is strong enough then divergence will occur despite gene flow, with gene flow being subsequently reduced due to assortative mating or divergent habitat preferences (Rosenblum, 2006; de Leon *et al.*, 2010). In either scenario, low levels of gene flow between populations are associated with population divergence. Consequently, there are many examples of inverse relationships between trait divergence and level of gene flow (e.g. Riechert, 1993; King & Lawson, 1995; Hendry, Taylor & McPhail, 2002).

In the case of polymorphisms, reduced gene flow is likely to result in populations that differ in morph composition (e.g. Sandoval, 1994). When local selection favours certain morphs over others, these morphs increase in frequency and maladapted alleles may be lost from the population. Furthermore, isolated populations are more susceptible to stochastic processes and are more likely to lose morphs by chance (Brakefield, 1990; Eckert & Barrett, 1992). However, in the presence of high levels of gene flow, maladapted alleles will be continually supplied from adjacent populations thus preventing fixation of a single morph type and maintaining the polymorphism. Gene flow is also likely to be asymmetric with greater gene flow from the range centre towards the range margins, counteracting processes that facilitate divergence at the edges of species ranges, such as more variable selective environments and hybridisation (Haldane, 1956; Lenormand, 2001). Conversely, population divergence in the presence of high levels of gene flow is indicative of strong selective pressures in those populations (Rice & Hostert, 1993). In the isopod, *Idotea baltica*, colour morphs are cryptic in different habitats. Predation risk is highly dependent on crypsis; however, although morph frequencies differ among populations, they are not correlated with habitat. High levels of gene flow between populations appear to be interfering with local selective pressures in this species (Merilaita, 2001).

Studies that have investigated geographic patterns of variation in polymorphism in detail indicate that multiple processes generating geographic variation are likely to be at play. One of the most studied examples is the blue-tailed damselfly, *Ischnura elegans*. In this species, the relative frequency of andromorphs varies in a broadly clinal fashion from high in the north to low in the south, which may be related to large-scale climatic factors such as temperature and rainfall and/or differential dispersal tendencies or colonisation abilities of the three different morphs at the range margins (Hammers & Van Gossum, 2008; Gosden *et al.*, 2011). However, there are also several examples in this species of marked local variation in morph frequencies (Gosden *et al.*, 2011). For instance, some of the southern Spanish populations have unusually high andromorph frequencies, which Gosden *et al.* (2011) attribute to the interaction between numerous processes, particularly at range margins. These processes include hybridisation, asymmetric gene flow from the centre of the species range, and increased genetic drift operating in combination with frequency-dependent selection and non-equilibrium genetic dynamics at the range margins. Other notable exceptions to the broad clinal pattern of morph frequencies at the northern part of the range (Sweden) may be due to locally different microclimates, potentially interacting with local population density, affecting rates of male harassment (Gosden *et al.*, 2011). Gosden *et al.* (2011) p. 784 conclude that 'the interactions between colonization, dispersal, differential temperature tolerance and temperature preference, frequency-dependent selection, and interspecific interactions are likely to jointly influence the large-scale biogeographic patterns in morph frequencies in *I. elegans* and other polymorphic species.' The processes generating

geographic variation in morph composition and frequency, and their relative contributions, are likely to differ among systems and populations. It is therefore important to use a research framework that considers and investigates the role of multiple processes (hybridisation, selection, drift, gene flow), and their interactions, in population divergence (see Section V).

IV. EVOLUTIONARY CONSEQUENCES OF GEOGRAPHIC VARIATION IN POLYMORPHISM

When coupled with high levels of gene flow, geographic variation can maintain polymorphism (e.g. Merilaita, 2001). Specifically, gene flow between populations can prevent rare morphs from being lost due to selection and stochastic processes. Conversely, when the homogenising effect of gene flow is low or absent, speciation can occur between populations that differ in morph composition or along a morph-frequency cline. For example, clinal variation is often the result of local selection favouring an alternate morph at either end of a selective cline. The cline may be maintained by either a balance between local selection and frequency-dependent selection (Takahashi *et al.*, 2011), or by gene flow along the cline allowing less fit morphs to persist in areas where they would otherwise be outcompeted. In the absence of gene flow and frequency-dependent selection, one morph will outcompete the other, resulting in the formation of monomorphic populations that, with subsequent evolution and divergence, can evolve into separate monomorphic species. Below, we discuss consequences of geographic variation in morph composition and frequency, other than the interaction with gene flow, with a focus on processes that can lead to speciation.

(1) Reinforcement

When geographic variation in a polymorphism (including clinal variation) is formed through secondary contact, speciation may occur *via* reinforcement due to reduced fitness of hybrids. Hybrids produced by mixed morph crosses may have lower fitness because they exhibit an intermediate phenotype that is maladapted to the environment (e.g. Nosil, Crespi & Sandoval, 2003) or due to genetic incompatibilities between morphs creating inviable or sterile offspring (discussed in Section IV.3). Alternatively, mating with an alternate morph may impose direct costs on individuals through incompatible morphology or behaviour during mating. For example, *Timema* spp. walking sticks are wingless insects that feed on one of two host-plant species. Colour morphs of *T. cristinae* are cryptic on their own host plant but conspicuous on the host plant of the alternate morph. Consequently, individuals that mate with the alternate morph are more conspicuous and therefore at greater risk of predation during mating (Nosil *et al.*, 2003). When there are costs associated with hybridization, selection will favour the development of traits that prevent mixed breeding between morphs (assortative mating), a process known as reinforcement (Dobzhansky, 1937). Reinforcement will result in a polymorphism that is transient and the speciation process, which began in allopatry, will culminate in the formation of monomorphic daughter species.

Despite ongoing debate surrounding reinforcement (Servedio & Noor, 2003), several studies provide convincing evidence that reinforcement can play a role in speciation (reviewed in Ortiz-Barrientos, Grealy & Nosil, 2009). The most compelling evidence for reinforcement driving reproductive isolation within a polymorphic species is within the *Timema* spp. walking sticks. In *T. cristinae*, host-specific selection against immigrants and hybrids results in divergent mate and host preferences and consequently, genetically based pre-mating isolation between populations on different hosts (Nosil, 2007). Although the potential for reinforcement may be more common than previously thought (Servedio & Noor, 2003), a lack of empirical data seems to indicate that speciation *via* reinforcement is rare, with specific conditions needing to be met in order for it to occur (Rice & Hostert, 1993; Sætre & Sæther, 2010; Bank, Hermisson & Kirkpatrick, 2012). Consequently, reinforcement is probably not the most important mechanism for speciation in polymorphic species.

(2) Evolution of new traits and assortative mating

(*a*) *Changes in intra- and interspecific interactions*

Changes in morph composition and/or frequencies within a population can change the nature of correlational and frequency-dependent selection acting on the remaining morphs, facilitating the breakdown of co-adapted trait complexes and the formation of new ones (Sinervo & Svensson, 2002; McKinnon & Pierotti, 2010). This can occur in a number of ways. Firstly, the loss or gain of a morph can alter social selection dynamics, because selection favours the evolution of alleles that enhance a morph's ability to compete with other morphs. When a morph is lost from a population, traits that were formerly advantageous for competition with conspecifics may become deleterious with selection favouring the evolution of new traits. For example, male side-blotched lizards, *Uta stansburiana*, from dimorphic populations are larger than males from trimorphic populations (Corl *et al.*, 2010*b*). This may be because, with the loss of a morph, the competitive environment has changed and the remaining male morphs have evolved larger size to assist in male contests (Fig. 3; Corl *et al.*, 2010*b*). Similarly, changes in morph composition or frequencies can affect interspecific interactions. Predation on morph types is often frequency dependent with more common morphs experiencing higher predation rates (e.g. Olendorf *et al.*, 2006). Changes in morph frequencies or the loss of a morph can cause a shift in predator strategy resulting in an increase in predation rate on remaining morphs (reviewed in Bond, 2007). This will impose new selective pressure on morphs that formerly experienced low levels of predation, possibly resulting in the evolution of new traits to avoid predation. Therefore,

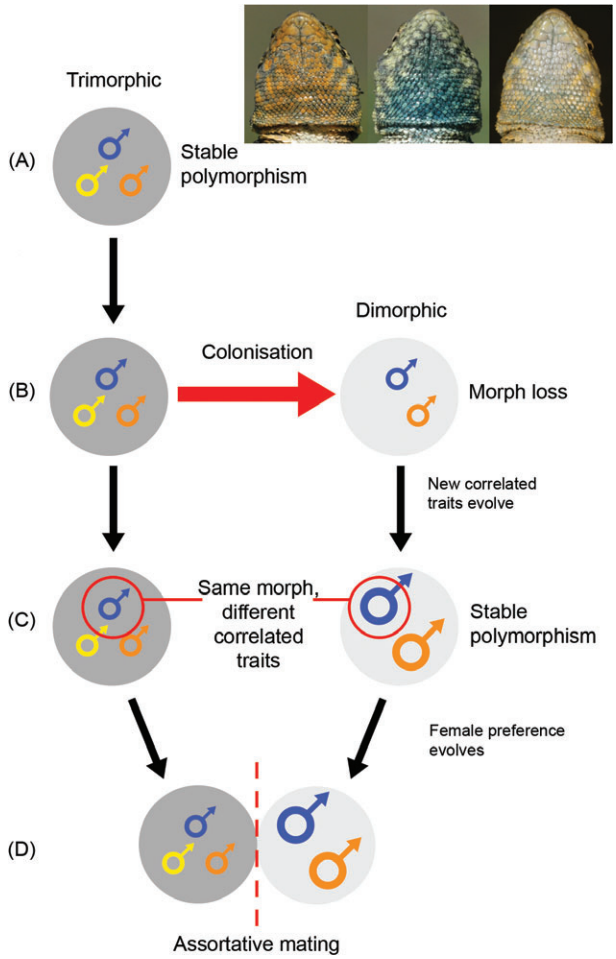

Fig. 3. Diagram describing how geographic variation in polymorphism may facilitate population divergence in the side-blotched lizard, *Uta stansburiana*. (A) Three male throat colour morphs (pictured; photo credits: A. Corl and M. Mulks) utilise alternate reproductive strategies whereby each morph can beat and is beaten by one other. (B) During colonisation of a new population, a morph may be lost due, for example, to selection, chance or founder events. The loss of a morph destabilises the competitive interaction between the remaining morphs and intrasexual selection favours the evolution of larger size to assist in male contests. (C) The same morph has different correlated traits in different populations. If larger size is advantageous, females from the dimorphic population may develop a preference for larger males. (D) Females from the dimorphic population may then mate assortatively with large males from their own population over smaller males from neighbouring trimorphic populations (Corl *et al.*, 2010*b*). Reproductive isolation and speciation may follow.

changes in morph composition and frequencies are likely to alter both intra- and interspecific interactions.

(*b*) *'Character release'*

The production of multiple phenotypes imposes evolutionary constraints on the genomes of polymorphic species (West-Eberhard, 1986). New alleles will only be able to spread if they benefit all morphs or if the fitness cost in one morph is less than the fitness benefit in the other morph/s. The loss of a morph from a population can free the genome from these constraints, allowing new alleles to spread in the population and leading to rapid phenotypic specialisation in the remaining morphs, a process known as 'character release' (West-Eberhard, 1986). In *Uta stansburiana* there are two female morph types which differ in life history strategies; *r*-strategy females which produce large quantities of smaller offspring and *k*-strategy females which invest more in fewer offspring (Sinervo, Svensson & Comendant, 2000). Corl *et al.* (2010*a*) found that populations that had become fixed for male morph type had also become fixed for *r*-strategy females and females in these populations were larger. This may be because alleles for specialisation on fecundity (e.g. larger size) that were disadvantageous when both life-history strategies were present in the population, were able to spread with the fixation of the *r*-strategy morph (Corl *et al.*, 2010*a*).

Changes in intra- and interspecific interactions and 'character release' can lead to the evolution of new co-adapted trait complexes. Consequently, a morph (or morphs) common to multiple populations may have different correlated traits in different localities. Correlational selection acting on the morph will therefore differ among populations, facilitating divergence between populations and potentially leading to assortative mating with, for example, females choosing to mate with males from their own population over males from other populations. In *U. stansburiana*, if larger size is advantageous for males, females from dimorphic populations may develop a preference for new trait optima in size, and mate assortatively with large males from their own populations over smaller males from trimorphic populations (Corl *et al.*, 2010*a*) potentially leading to reproductive isolation between populations (Fig. 3). However, there is also evidence that females from trimorphic populations prefer larger males (Calsbeek & Sinervo, 2002), consequently an alternative result may be that gene flow between populations is restricted and unidirectional.

(3) Genetic incompatibilities

In addition to prezygotic reproductive isolation (assortative mating), geographic variation in polymorphism can generate postzygotic reproductive isolation (genetic incompatibilities). Genetic incompatibilities exist between morph types of the Gouldian finch, *Erythrura gouldiae*. In this species, mixed crosses between red- and black-headed individuals result in decreased hatching success and greater mortality of offspring than pure crosses (Pryke & Griffith, 2009*a*). Although this is an example of incompatibilities between morphs within a population, genetic incompatibilities could also arise between populations that differ in morph composition. In fact, one possible explanation for the genetic incompatibility between *E. gouldiae* morphs is that populations may have been isolated in the past, giving rise to red and black colour morphs in allopatry before coming into secondary contact and forming a colour polymorphism (discussed in Section III.2; Pryke & Griffith, 2009*a*).

In some systems, genetic incompatibilities between populations that differ in morph composition may be caused by polyploidy or gene transposition (Orr, Masly & Phadnis, 2007). Alternatively, and probably more frequently, genetic incompatibilities can arise due to the evolution of new co-adapted trait complexes in different populations. This may be particularly likely among polymorphic populations that differ in morph composition because of the prevalence of correlational selection on morphs. More generally, new traits, and their underlying alleles, are likely to evolve under selection to increase morph fitness in a given selective environment, or by chance if alleles are neutral and do not affect fitness (Shuker *et al.*, 2005). However, alleles that have evolved in separate populations may not be functional when brought together by interbreeding between populations. Consequently, mixed matings can result in hybrid sterility or inviability. These genetic incompatibilities, known as Dobzhansky-Muller incompatibilities (Dobzhansky, 1937; Muller, 1942), are expected to increase in number the longer two populations have been separated (Orr & Turelli, 2001) and can generate postzygotic reproductive isolation. Consequently, phenotypic and associated genetic incompatibilities can arise between populations that differ in morph composition and speciation may follow.

V. FUTURE DIRECTIONS

Macroevolutionary and phylogenetic studies can provide an indication of whether polymorphism promotes speciation in a particular group and whether geographically structured selection plays a role. If colour polymorphism promotes speciation we may predict that: (*i*) speciation rates (estimated from phylogenies) are higher for polymorphic than monomorphic lineages; (*ii*) divergence between extant colour polymorphic species and their sister lineages should be more recent than between pairs of monomorphic lineages; and (*iii*) within closely related groups, polymorphic species should be ancestral and monomorphic lineages derived. These predictions have been upheld in isolated groups but the generality of the patterns remains unclear. Hugall & Stuart-Fox (2012) showed that speciation rates were significantly higher for polymorphic than monomorphic lineages in three of the five families of non-passerine birds they examined. Furthermore, polymorphic species had shorter terminal branches (i.e. divergence was relatively more recent) in four of the families, as well as in the Passeriformes. Corl *et al.* (2010*b*) showed that between populations and sub-species of the side-blotched lizard, *Uta stansburiana*, trimorphic lineages were ancestral, while dimorphic and monomorphic lineages were derived. Similarly, in two genera of North American damselflies, species with female-limited polymorphism are ancestral whereas monomorphic species are derived in most cases (Van Gossum & Mattern, 2008). In these groups, available evidence points to geographic variation in polymorphism facilitating population divergence. In the bird families in which speciation rates are higher for polymorphic species, colour polymorphism is associated with occupation of more spatially and temporally variable environments and larger range size (Galeotti & Rubolini, 2004), suggesting that ecologically based, geographically structured divergent selection is likely to be important for speciation associated with colour polymorphism in these groups. In *U. stansburiana*, a number of the dimorphic and monomorphic lineages are isolated and/or at the range margin and one of these is recognised as a separate species (*U. squamata*); again suggesting that geographic variation in the polymorphism is associated with processes of population divergence (Corl *et al.*, 2010*b*).

Phylogeographic studies are essential to determine how phenotypic divergence (in morph composition and frequencies) relates to genetic divergence. As a starting point, genetic studies are necessary to test whether divergence in morph composition or frequency differs significantly from neutral genetic divergence and whether morph frequencies are associated with levels of gene flow. However, as morphs possess phenotypic traits that will be subject to a range of selective pressures, drift or gene flow alone is unlikely to explain observed variation in morph frequencies. Phylogeographic and population genetic studies are also necessary to identify cases of incipient speciation and the potential role of current or past hybridisation in generating and maintaining geographic variation in polymorphism. For example, examination of the areas between divergent lineages may lead to the identification of geographic barriers to gene flow or zones of secondary contact. Detailed examination of contact zones can elucidate patterns of introgression. Evidence of some degree of reproductive isolation between intermixing lineages would be indicative of incipient speciation.

Stochastic processes are also likely to play an important role in facilitating population divergence in polymorphic systems due to the potential for the loss of rare morphs, particularly during founder or colonisation events. For example, among the 120 populations of the blue-tailed damselfly, *Ischnura elegans*, studied by Gosden *et al.* (2011), the infuscans-obsoleta female morph has been lost in 17 of the populations, potentially from stochastic process such as drift or founder events. In *I. elegans*, where one morph is a male mimic, morph loss can result in sexually dimorphic or monomorphic populations, and could facilitate population divergence (Gosden *et al.*, 2011). However, genetic differentiation among *I. elegans* populations across Europe is quite weak (Sanchez-Guillen *et al.*, 2011; Wellenreuther *et al.*, 2011), suggesting that the combination of gene flow and negative frequency-dependent selection maintaining the polymorphism may be strong enough to counteract population divergence associated with local morph loss (Andres, Sanchez-Guillen & Rivera, 2000; Abbott *et al.*, 2008). Other processes apart from stochastic processes are clearly necessary to complete speciation. In most instances, stochastic processes such as successful colonisation and founder events, or loss of rare morphs, will interact with other processes, such as local selection pressures, frequency-dependent selection, changes in inter- and intraspecific

interactions and 'character release' to give rise to population divergence. For example, in the side-blotched lizard, *Uta stansburiana*, the same yellow-throated 'sneaker' morph is consistently lost, suggesting a role for selection in the observed variation in morph composition among populations. Consequently, future research needs to consider multiple processes that may generate geographic variation in polymorphism, by integrating studies of correlational selection and the adaptive function of morphs, frequency-dependent selection, environmental correlates of morph frequencies, population demographics and genetic structure.

Spatially and temporally replicated studies are essential not only to detect geographic variation in polymorphism, but also to distinguish stochastic variation in morph frequencies from deterministic processes. Studies providing a single snapshot of morph frequencies in space or time are unable to identify the evolutionary processes driving morph frequency dynamics. As highlighted in this review, different processes will produce different spatial and temporal patterns. For example, negative frequency-dependent selection is expected to produce temporal oscillations in morph frequencies, a pattern evident in systems in which negative frequency-dependent selection has been shown to maintain polymorphism (Sinervo & Lively, 1996; Sinervo *et al.*, 2000; Svensson *et al.*, 2005; Takahashi *et al.*, 2010). Conversely, broad-scale environmental factors will consistently affect morph frequencies across multiple populations or over multiple generations, as highlighted by the synchronous temporal changes in morph frequencies across 12 Swedish populations of the blue-tailed damselfly, *Ischnura elegans*, potentially due to increasing summer temperatures (Svensson & Abbott, 2005).

Spatially replicated studies of correlational selection on morphs are also ultimately necessary to understand how correlational selection varies in relation to morph frequency or composition, and how this, in turn, influences population divergence. Few studies have assessed the relationship between colour and correlated traits in more than one population but two that have done so show clear differences in the relationship between colour morph and behaviour (Carpenter, 1995; Bastiaans *et al.*, 2013). In both the tree lizard, *Urosaurus ornatus*, and the mesquite lizard, *Sceloporus grammicus*, the aggression of males with orange throats, relative to other morphs, varies depending on which morphs are present in the population (Carpenter, 1995; Bastiaans *et al.*, 2013). Divergence in life-history or reproductive strategies associated with colour morphs may increase the probability of pre-mating isolation between populations. Therefore, it would be particularly informative to assess changes in correlational selection, and how this influences mating or competitive interactions, in populations that have independently lost or gained the same morph.

VI. CONCLUSIONS

(1) Geographic variation in polymorphism is likely to be common, thus polymorphic species may harbour greater biodiversity than previously appreciated. Population divergence in morph composition and frequency has the potential to promote speciation; however, the geographical context of polymorphism, with specific focus on the causes and consequences of geographic variation, has been investigated in relatively few systems.

(2) Broad-scale studies of polymorphic species are essential to document geographic patterns of variation in morph composition and frequencies, and are crucial for understanding the role of polymorphism in speciation. Once the geographical and genetic context of a polymorphism has been documented, the causes and consequences of geographic variation can be investigated. As a starting point, the geographic pattern of variation in polymorphism (cline, mosaic) can provide insight into potential processes at work.

(3) Geographic variation in polymorphism is likely to be shaped by multiple evolutionary processes. Therefore, species with geographically variable, heritable polymorphisms may be good models to study complex evolutionary processes, such as the interaction between frequency-dependent selection, local adaptation, gene flow and stochastic processes.

(4) Finally, detailed knowledge of a polymorphism, including information on the mode of inheritance and correlated traits, is critical to understand the causes and consequences of geographic variation in polymorphism. Explicitly considering both spatial and temporal variation in polymorphism, and the underlying environmental and genetic mechanisms, will enable researchers to understand the processes linking polymorphism and speciation.

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