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Convergence and divergence in lizard colour polymorphisms

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ABSTRACT

Colour polymorphic species are model systems for examining the evolutionary processes that generate and maintain discrete phenotypic variation in natural populations. Lizards have repeatedly evolved strikingly similar polymorphic sexual signals in distantly related lineages, providing an opportunity to examine convergence and divergence in colour polymorphism, correlated traits and associated evolutionary processes. Herein, we synthesise the extensive literature on lizard colour polymorphisms in both sexes, including recent advances in understanding of the underlying biochemical, cellular and genetic mechanisms, and correlated behavioural, physiological and life-history traits. Male throat, head or ventral colour morphs generally consist of red/orange, yellow and white/blue morphs, and sometimes mixed morphs with combinations of two colours. Despite these convergent phenotypes, there is marked divergence in correlated behavioural, physiological and life-history traits. We discuss the need for coherence in morph classification, particularly in relation to 'mixed' morphs. We highlight future research directions such as the genetic basis of convergent phenotypes and the role of environmental variation in the maintenance of polymorphism. Research in this very active field promises to continue to provide novel insights with broad significance to evolutionary biologists.

Key words: correlational selection, convergence, genetic architecture, mating strategies, sexual signal, Squamata

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I. INTRODUCTION

Colour polymorphic species are frequent model systems in evolutionary biology because discrete colour variants are an easily scored phenotypic marker that can be used to track changes in allele frequencies in the wild. For this reason, colour polymorphic species have provided significant insights into evolutionary processes, long before the modern evolutionary synthesis or the widespread availability of genomic data, and they continue to do so (Svensson, 2017). Colour polymorphism is defined as the presence of multiple, discrete colour 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). Colour polymorphism has evolved repeatedly and independently in all major taxonomic groups. In several of these groups, such as birds, lizards, fish and insects, an increasing number of colour polymorphic species have been characterised in recent years (Gubili *et al.*, 2016; McLean *et al.*, 2017; Saenko *et al.*, 2019; Ahi *et al.*, 2020), providing the opportunity to examine similarities and differences in the processes generating and maintaining discrete phenotypic variation. Such comparisons can be especially powerful when polymorphism has evolved on multiple independent occasions within taxonomic groups, which share similarities in their basic biology (Roulin, 2004; Jamie & Meier, 2020).

Lizards are one group in which colour polymorphism has evolved independently multiple times and has been well characterised in numerous species, both within and among different families, from across the world. In most cases, the polymorphism involves coloration on the throat, head or ventral body regions, and one or both sexes may be polymorphic. There appears to be remarkable convergence in throat/head/ventral colour polymorphism with either males or both sexes exhibiting a red/orange morph, a yellow morph, and a white/blue morph. For example, the suborder Iguania, consisting of Old World agamids and chameleons (subclade Acrodonta) and New World iguanids (Pleurodonta; Blankers *et al.*, 2013), separated by ~120 million years of evolution, contain multiple species exhibiting notably similar male morph combinations (Fig. 1). Despite apparent convergence in the colour polymorphism, there are important differences in the nature of the colour variation, underlying genetic, biochemical and cellular mechanisms, and the behavioural, physiological and life-history traits associated with colour morphs. Unlike most other taxonomic groups, a number of geographically and phylogenetically distant colour polymorphic lizard systems have been extensively studied, providing a valuable opportunity to examine convergence and divergence in colour polymorphism, the underlying mechanisms and correlated traits.

Here, we synthesise the literature on colour polymorphism in lizards, focusing on throat/head/ventral colour polymorphism, which is prominently displayed during social interactions and likely functions as an intraspecific signal. Although some lizards exhibit polymorphism in dorsal or lateral coloration (e.g. polymorphism in the white lateral stripe in some skinks; Chapple, 2005; Chapple *et al.*, 2008), these polymorphisms could have multiple functions (e.g. protection against predators *via* cryptic or disruptive coloration, signalling, thermoregulation) which remain poorly understood. We refer to polymorphism in throat/head/ventral intraspecific colour signals as 'polymorphism' henceforth for brevity. We begin by describing variation in polymorphism, including its taxonomic distribution, and variation in polymorphism within and between the sexes. We then summarise current knowledge of the biochemical, cellular and genetic mechanisms underlying the polymorphisms, before turning our attention to function and evolution. Specifically, we discuss how colour morphs within each sex differ in associated behavioural, physiological and life-history traits and how strategies associated with the polymorphism may be influenced by environmental variation. We discuss implications for the evolution and maintenance of polymorphism in lizards, including frequency-dependent selection, spatiotemporal variation in environmental conditions and geographic variation in morph composition. Lastly, we identify key research gaps and evaluate how insights drawn from colour polymorphism in lizards have shaped our understanding of evolutionary processes relating to the generation and maintenance of phenotypic variation.

II. VARIATION IN LIZARD COLOUR POLYMORPHISMS

Polymorphism has been reported in at least seven different families of lizards (Table 1). Most of these are Iguanians, including both acrodonts in the family Agamidae, and pleurodonts in the families Dactyloidae, Liolaemidae, Phrynosomatidae and Tropiduridae (Table 1). Polymorphism is also relatively common among wall lizards (family Lacertidae), including at least eight species in the genus *Podarcis*, and has been recorded in two species of gecko (family Sphaerodactylidae; Table 1). Most polymorphic species within these highly divergent groups have evolved remarkably similar colour combinations, with a red or orange, and a yellow morph, and an additional blue, white or grey morph in some populations (Fig. 1). An exception is the striped lava lizard (*Tropidurus semitaeniatus*), in which males are either black or yellow (Bruinjé, Leivas, & Costa, 2018; Bruinjé *et al.*, 2019*b*). The Roze's gecko (*Gonatodes rozei*) also has strikingly different male morphs, with throats that are orange-yellow, dull yellow, grey-brown with pale yellow markings, or grey-brown with black suffusions between yellow markings (Rivero-Blanco & Schargel, 2012). Additionally, the extendable throat dewlaps of *Anolis apletophallus* are either entirely orange ('solid') or have an orange centre surrounded by a white margin ('basal'; Stapley *et al.*, 2011). Besides these exceptions, blue morphs appear least common among polymorphic species, yet have evolved in agamids (*Ctenophorus pictus*) and iguanids (*Sceloporus grammicus*, *Urosaurus ornatus*, and *Uta stansburiana*). Interestingly, even in species that have both white/grey and blue

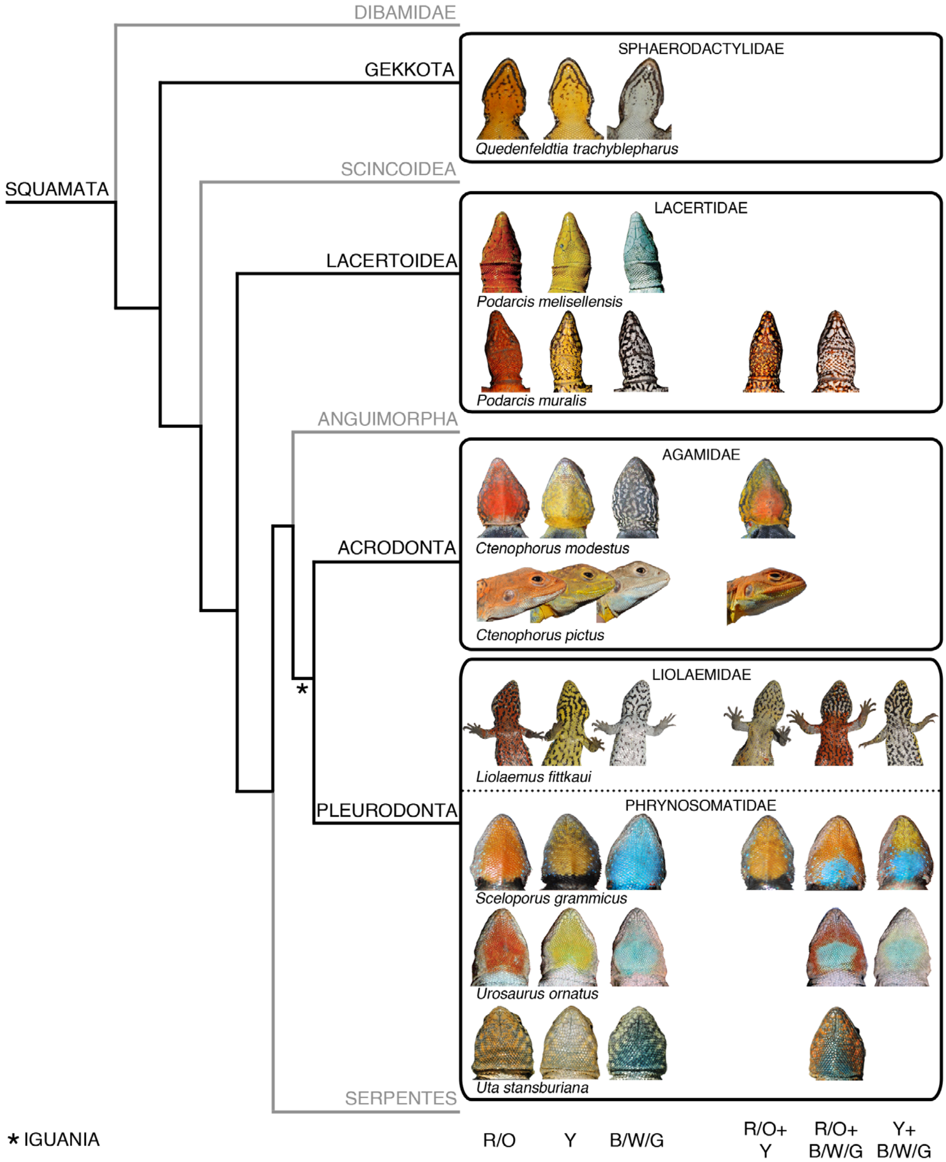


Fig 1. Pure and mixed male colour morphs in well-studied polymorphic species across the order Squamata (lizards and snakes). Black branches contain species with known throat/head/ventral colour polymorphism while grey branches do not. Phylogenetic tree adapted from Pyron, Burbrink, & Wiens (2013). Images used with permission: *Quedenfeldtia trachyblepharus* (from Blouin-Demers *et al.*, 2013); *Podarcis melisellensis* (from Huyghe *et al.*, 2007); *Podarcis muralis* (from Andrade *et al.*, 2019); *Ctenophorus modestus* (from McLean *et al.*, 2013); *Ctenophorus pictus* (from Friesen *et al.*, 2017*b*); *Liolaemus fittkaui* (from Jiménez-Robles *et al.*, 2016); *Sceloporus grammicus* (from Bastiaans *et al.*, 2014); *Urosaurus ornatus* (from Meyers *et al.*, 2006); *Uta stansburiana* (from Corl *et al.*, 2010). B/W/G, blue/white/grey; R/O, red/orange; Y, yellow.

morphs, these two morphs do not seem to co-exist within a single population (Bastiaans *et al.*, 2014).

While polymorphism has been reported more commonly in male lizards, polymorphism is also exhibited by some female agamids (Tobler *et al.*, 2011), iguanids (Svensson *et al.*, 2001a; Lattanzio *et al.*, 2014), lacertids (Sacchi *et al.*, 2007*b*; Vercken *et al.*, 2007*b*; Runemark & Svensson, 2012), and the Atlas day gecko (*Quedenfeldtia trachyblepharus*; Blouin-Demers *et al.*, 2013). In these species, males and females either have the same colour morphs (*Podarcis muralis*, *Podarcis gaigeae*, *Sceloporus undulates erythrocheilus*, *Quedenfeldtia trachyblepharus*), or females lack a white (*Zootoca vivipara*; formerly *Lacerta vivipara*) or blue morph (*Urosaurus ornatus* and *Uta stansburiana*; see Table 1). Males and females can also differ in number and type of polymorphic traits; in the painted dragon (*Ctenophorus pictus*), females are only polymorphic in the presence or absence of a yellow 'bib', whereas males are also polymorphic for head colour (Tobler *et al.*, 2011). To date, there have been no reports of species where females are polymorphic but males are not. However,

Table 1. Evidence for associations between colour morph and behavioural, physiological and life-history traits in lizards. For species with more than two morphs, not all studies compared traits among all morphs, which can explain some (but not all) discrepancies in results. 'Mixed' evidence for correlation refers to where a study found evidence for an association in some contexts, but not in others. * indicates that there was only evidence for differences among morphs in interaction with the environment (including social environment), other traits, or in specific contexts

Family	Species	Sex	Morph colours	Trait	Evidence for correlation	References
Agamidae	Swift rock dragon (*Ctenophorus modestus)*	Male	Orange, yellow, grey, orange-yellow	Aggression	Yes	Yewers, Pryke, & Stuart-Fox (2016)
				Bite force	No	Yewers, Jessop, & Stuart-Fox (2017)
				Body temperature	Yes	Yewers *et al.* (2017)
				Boldness	Yes	Yewers *et al.* (2016)
				Immunity (ectoparasite load)	Yes	Hacking *et al.* (2018)
				Stress response (corticosterone)	No	Yewers *et al.* (2017)
				Testosterone/other androgens	Yes*	Yewers *et al.* (2017)
	Painted dragon (*Ctenophorus pictus*)	Female	Yellow bib, no bib	Body mass	No	Tobler, Healey, & Olsson (2011)
				Body size	No	Tobler *et al.* (2011)
				Morphology (digit ratio)	Yes	Tobler *et al.* (2011)
		Male	Yellow bib, no bib	Antipredator behaviour	Yes	Tobler, Healey, & Olsson (2012)
				Body condition	Yes*	Healey & Olsson (2009)
					No	McDiarmid *et al.* (2017)
				Body mass	No	Tobler *et al.* (2011)
				Body size	No	Tobler *et al.* (2011)
				Copulation duration	Yes	Friesen *et al.* (2020)
				Dominance	Yes (bib quality)	McDiarmid *et al.* (2017)
				Endurance/stamina	Yes	Tobler *et al.* (2012)
				Mate choice (by female)	Yes	McDiarmid *et al.* (2017)
				Resting metabolic rate	Yes	Friesen, Johansson, & Olsson (2017a)
				Morphology (digit ratio)	Yes	Tobler *et al.* (2011)
				Sperm number	Yes	Friesen *et al.* (2020)
				Sperm performance	Yes	Friesen *et al.* (2020)
					No	McDiarmid *et al.* (2017)
				Sperm telomere length	Yes	Friesen *et al.* (2020)
				Superoxide levels	Yes	Olsson *et al.* (2012)
					No	Friesen *et al.* (2020)
			Orange, red, yellow, blue (head colour)	Body condition	Yes*	Olsson *et al.* (2007*b*); Friesen *et al.* (2017*b*)
				Body mass	No	Olsson *et al.* (2007*b*); Tobler *et al.* (2011)
				Body size	No	Olsson *et al.* (2007*b*), Tobler *et al.* (2011)
				Copulation duration	No	Friesen *et al.* (2020)
				Dominance	Yes	Healey, Uller, & Olsson (2007)
				Endurance/stamina	No	Tobler *et al.* (2012)
				Mate choice (by female)	No	Healey, Uller, & Olsson (2008)
				Reproductive strategy	Yes	Olsson *et al.* (2009*b*)
				Sperm number	No	Friesen *et al.* (2020)
				Sperm performance	No	Friesen *et al.* (2020)

(Continues)

Table 1. *(Cont.)*

Family	Species	Sex	Morph colours	Trait	Evidence for correlation	References
				Sperm telomere length	Yes	Friesen *et al.* (2020)
				Stress response (corticosterone)	Non-significant trend	Olsson, Healey, & Astheimer (2007a)
				Superoxide levels	Yes	Olsson *et al.* (2012)
					No	Friesen *et al.* (2020)
				Territory acquisition	No	Healey & Olsson (2008)
				Territory quality	Yes	Olsson *et al.* (2007*b*)
				Territory size	No	Olsson *et al.* (2007*b*, 2008)
				Testosterone	Yes	Olsson *et al.* (2007*a*)
Dactyloidae	*Anolis apletophallus*	Male	Orange, orange-white	—	—	Stapley, Wordley, & Slate (2011)
	Bark anole (*Anolis distichus favillarum*)	Male	Orange, yellow	—	—	MacGuigan, Geneva, & Glor (2017); Ng, Ossip-Klein, & Glor (2016)
Lacertidae	European common or viviparous lizard (*Zootoca vivipara*; previously *Lacerta vivipara*)	Female	Orange, yellow, orange-yellow	Body mass	No	Vercken *et al.* (2007*b*)
				Dominance	Yes	Vercken & Clobert (2008*b*)
				Offspring behaviour	Yes	Vercken, Sinervo, & Clobert (2012)
				Reproductive strategy	Yes*	Vercken, Clobert, & Sinervo (2010); Vercken *et al.* (2007b)
				Social behaviour	Yes*	Vercken & Clobert (2008*a*)
				Stress response (behaviour)	Yes	Vercken & Clobert (2008*b*)
		Male	Orange, yellow, white, orange-yellow, orange-white, yellow-white	Body mass	Yes	Sinervo *et al.* (2007)
				Endurance/stamina	Yes	Sinervo *et al.* (2007)
				Survival	Yes	Sinervo *et al.* (2007)
	Podarcis bocagei	Unknown	Orange, yellow, white	—	—	Andrade *et al.* (2019)
	Skyros wall lizard (*Podarcis gaigeae*)	Female	Orange, yellow, white, orange-yellow, orange-white, yellow-white	Mate choice (by male)	No	Runemark & Svensson (2012)
		Male	Orange, yellow, white, orange-yellow, orange-white, yellow-white	Mate choice (by female)	Yes	Runemark & Svensson (2012)
	Podarcis liolepis	Unknown	Orange, yellow, white	—	—	Andrade *et al.* (2019)

Table 1. *(Cont.)*

Family	Species	Sex	Morph colours	Trait	Evidence for correlation	References
*****	Dalmation wall lizard (*Podarcis melisellensis*)	Male	Orange, yellow, white	Activity patterns	No	Huyghe *et al.* (2007)
				Bite force	Yes	Huyghe *et al.* (2007, 2009)
				Body size	Yes	Huyghe *et al.* (2007)
				Body temperature	No	Huyghe *et al.* (2007)
				Endurance/stamina	No	Huyghe *et al.* (2007)
				Immunity (ectoparasite prevalence and load)	No	Huyghe *et al.* (2010)
				Immunity (endoparasite load)	Yes	Huyghe *et al.* (2010)
				Immunity (endoparasite prevalence)	Yes*	Huyghe *et al.* (2010)
				Immunity (phytohaemagluttinin response)	No Yes*	Huyghe *et al.* (2009) Huyghe *et al.* (2010)
				Morphology (head size)	Yes	Huyghe *et al.* (2007)
				Morphology (limb length)	No	Huyghe *et al.* (2007)
				Sprint speed	No	Huyghe *et al.* (2007)
				Stress response (corticosterone)	Yes	Huyghe *et al.* (2009)
				Testosterone	No	Huyghe *et al.* (2009)
	Common wall lizard (*Podarcis muralis*)	Female	Orange/red, yellow, white, orange-yellow, orange-white	Body size	Yes	Sacchi *et al.* (2007*b*); Calsbeek, Hasselquist, & Clobert (2010)
				Diet	Yes	Scali *et al.* (2016)
				Habitat use	Yes	Pérezi de Lanuza & Carretero (2018)
				Homing ability	Yes	Scali *et al.* (2013)
				Immunity (endoparasite prevalence and load)	Yes	Calsbeek *et al.* (2010)
				Immunity (humoral immune response)	No	Calsbeek *et al.* (2010)
				Immunity (phytohaemagluttinin response)	Yes	Sacchi *et al.* (2017*a*)
				Mate choice (assortative mating)	Yes	Pérezi de Lanuza, Font, & Carazo (2013); Sacchi *et al.* (2018)
					No	Sacchi *et al.* (2015)
				Morphology (head height)	Yes	Sacchi *et al.* (2007*b*)
				Reproductive strategy	Yes	Galeotti *et al.* (2013)
				Sprint speed	No	Zajitschek *et al.* (2012)
				Stress response (endoparasite load)	No	Galeotti *et al.* (2010)
				Stress response (white blood cell ratio)	Yes*	Galeotti *et al.* (2010)

(Continues)

Table 1. *(Cont.)*

Family	Species	Sex	Morph colours	Trait	Evidence for correlation	References
		Male	Orange/red, yellow, white, orange-yellow, orange-white	Aggression	No	Sacchi *et al.* (2009); Abalos *et al.* (2016)
				Antipredator behaviour	Yes	Pellitteri-Rosa *et al.* (2017)
				Body condition	No	Abalos *et al.* (2016)
				Body size	Yes (marginal)	Calsbeek *et al.* (2010)
					No	Sacchi *et al.* (2007a, 2007b); Abalos *et al.* (2016)
				Diet	Yes	Scali *et al.* (2016)
				Dominance	No	Sacchi *et al.* (2009)
					Yes	Abalos *et al.* (2016)
				Femoral gland secretions (chemical profile)	Yes	Pellitteri-Rosa *et al.* (2014)
				Habitat use	Yes	Pérezi de Lanuza & Carretero (2018)
				Homing ability	Yes	Scali *et al.* (2013)
				Immunity (endoparasite prevalence and load)	Yes	Calsbeek *et al.* (2010)
				Immunity (humoral immune response)	No	Calsbeek *et al.* (2010)
				Immunity (phytohaemagluttinin response)	Yes	Sacchi *et al.* (2007*a*) Sacchi *et al.* (2017*a*)
				Mate choice (assortative mating)	Yes	Pérezi de Lanuza et al. (2013); Pérezi de Lanuza, Font, & Carretero (2016))
				Morphology (head height)	No	Sacchi *et al.* (2007*b*)
				Sprint speed	No	Zajitschek *et al.* (2012)
				Stress response (endoparasite load)	No	Galeotti *et al.* (2010)
				Stress response (white blood cell ratio)	Yes*	Galeotti *et al.* (2010)
				Testosterone	Yes*	Sacchi *et al.* (2017*b*)
	P. sicula	Unknown	Orange, white, orange-white	—	—	Andrade *et al.* (2019)
	P. vaucheri	Unknown	Orange, yellow, white	—	—	Andrade *et al.* (2019)
	P. wagleriana	Unknown	Orange-white, orange-yellow	—	—	Andrade *et al.* (2019)

Table 1. *(Cont.)*

Family	Species	Sex	Morph colours	Trait	Evidence for correlation	References
Liolaemidae	*Liolaemus fittkaui*	Male	Red, yellow, white, red-yellow, yellow-white, red-white	—	—	Jiménez-Robles *et al.* (2016)
	Liolaemus sarmientoi	Male	Red, yellow, red-yellow	Aggression	Yes	Fernandez *et al.* (2018)
				Body size	No	Fernandez *et al.* (2018)
				Body temperature	Yes	Fernandez *et al.* (2018)
				Endurance/stamina	No	Fernandez *et al.* (2018)
				Morphology (head height)	Yes	Fernandez *et al.* (2018)
				Morphology (head length)	No	Fernandez *et al.* (2018)
				Morphology (head width)	No	Fernandez *et al.* (2018)
Phrynosomatidae	Mesquite lizard (*Sceloporus grammicus*)	Male	Orange, yellow, blue or white, orange-yellow, orange-blue, yellow-blue	Mate choice (by female)	Yes	Bastiaans *et al.* (2014)
	Eastern fence lizard (*Sceloporus undulates erythrocheilus*)	Female	Orange, yellow, white	—	—	Rand (1992)
		Male	Orange, yellow, white	—	—	Rand (1992)
	Long-tailed brush lizard (*Urosaurus graciosus*)	Male	Orange, yellow	Dominance	Yes*	Brown & Lattanzio (2018)
	Tree lizard (*Urosaurus ornatus*)	Female	Orange, yellow	Mate choice (by female)	Yes	Lattanzio, Metro, & Miles (2014)
				Mate choice (by male)	Yes	Krohmaly, Martin, & Lattanzio (2018)
		Male	Orange, yellow/green, blue, green, yellow/green with blue/green patch, orange with blue/green patch	Aggression	Yes	Thompson & Moore (1991*b*, 1992)
				Antipredator behaviour	Yes	Thaker, Lima, & Hews (2009)
				Bite force	No	Meyers *et al.* (2006)
				Body condition	No	Taylor & Lattanzio (2016)
				Body mass after food limitation	No	Jaworski & Lattanzio (2017)
				Body size	Yes	Hover (1985)
					No	Thompson & Moore (1992); Meyers *et al.* (2006); Taylor & Lattanzio (2016)
				Body temperature	No	Paterson & Blouin-Demers (2018)
				Boldness	Yes	Taylor & Lattanzio (2016)
				Diet	Yes*	Lattanzio & Miles (2016)
				Display behaviour	Yes	McElroy *et al.* (2007); Hover (1985); Thompson & Moore (1992)
				Display duration	No	McElroy *et al.* (2007)
				Dominance	Yes (but results not entirely consistent)	Hover (1985); Carpenter (1995*a*); Thompson & Moore (1991*b*); Taylor & Lattanzio (2016)

(Continues)

Table 1. *(Cont.)*

Family	Species	Sex	Morph colours	Trait	Evidence for correlation	References
				Endurance/stamina	Yes	Jaworski & Lattanzio (2017)
				Endurance/stamina after food limitation	No	Jaworski & Lattanzio (2017)
				Growth rate	Yes	Thompson, Moore, & Moore (1993); Thompson & Moore (1991*b*)
				Mate choice (by female)	Yes	Lattanzio *et al.* (2014)
				Mate choice (by male)	Yes	Krohmaly *et al.* (2018)
				Morphology (body height, head length)	No	Meyers *et al.* (2006)
				Morphology (head shape, jaw length)	Yes*	Lattanzio & Miles (2016)
				Mating behaviour	Yes	Krohmaly *et al.* (2018); Thompson & Moore (1991*b*)
				Sprint speed	No	Meyers *et al.* (2006)
				Stress response (corticosterone)	No	Thompson & Moore (1992); Knapp *et al.* (2003)
				Survival	No	Paterson & Blouin-Demers (2018)
				Territory quality	Yes	Paterson & Blouin-Demers (2018)
				Territory size	Yes	Paterson & Blouin-Demers (2018)
				Testosterone	Yes* No	Knapp *et al.* (2003) Thompson & Moore (1992)
	Side-blotched lizard (*Uta stansburiana*)	Female	Orange, yellow	Immunity (humoral immune response)	Yes*	Svensson, Sinervo, & Comendant (2001a); Svensson, Sinervo, & Comendant (2001b)
				Mate choice (by female)	Yes	Bleay & Sinervo (2007)
				Offspring fitness	Yes*	Sinervo, Bleay, & Adamopoulou (2001)
				Reproductive costs	Yes	Svensson *et al.* (2001*a*); Svensson, Sinervo, & Comendant (2002); Bleay & Sinervo (2007)
				Reproductive strategy	Yes*	Lancaster, McAdam, & Sinervo (2010); Sinervo, Svensson, & Comendant (2000b)
				Social behaviour	Yes	Svensson *et al.* (2002); Comendant *et al.* (2003)
				Stress response (corticosterone)	Yes*	Comendant *et al.* (2003)
		Male	Orange, yellow, blue, orange-blue	Anti-predator behaviour	Yes	Thaker *et al.* (2009)
				Endurance/stamina	Yes	Mills *et al.* (2008)
				Immunity (humoral immune response)	No	Mills *et al.* (2008)
				Mate choice (by female)	Yes	Bleay & Sinervo (2007)
				Reproductive strategy	Yes	Sinervo & Lively (1996)
				Social behaviour	Yes	Bleay, Comendant, & Sinervo (2007)
				Sprint speed	No	Mills *et al.* (2008)

Table 1. *(Cont.)*

Family	Species	Sex	Morph colours	Trait	Evidence for correlation	References
				Stress response (corticosterone)	No	Mills *et al.* (2008)
				Testosterone	Yes	Sinervo *et al.* (2000*a*); Mills *et al.* (2008)
Sphaerodactylidae	Atlas day gecko (*Quedenfeldtia trachyblepharus*)	Female	Orange, yellow, white	Body condition	No	Blouin-Demers *et al.* (2013)
				Body size	No	Blouin-Demers *et al.* (2013)
				Immunity (ectoparasite prevalence)	No	Blouin-Demers *et al.* (2013)
				Morphology (relative jaw size)	No	Blouin-Demers *et al.* (2013)
		Male	Orange, yellow, white	Body condition	No	Blouin-Demers *et al.* (2013)
				Body size	No	Blouin-Demers *et al.* (2013)
				Immunity (ectoparasite prevalence)	No	Blouin-Demers *et al.* (2013)
				Morphology (relative jaw length)	Yes	Blouin-Demers *et al.* (2013)
	Roze's gecko (*Gonatodes rozei*)	Male	Orange/yellow, dull yellow, grey-brown with pale yellow markings, grey-brown with black suffusions between yellow markings	—	—	Rivero-Blanco & Schargel (2012)
Tropiduridae	Striped lava lizard (*Tropidurus semitaeniatus*)	Male	Yellow, black	Aggression	Yes	Bruinjé *et al.* (2019*a*)
				Body size	Yes	Bruinjé *et al.* (2019*b*)
				Dominance	Yes	Bruinjé *et al.* (2019*a*)
				Sprint speed	No	Bruinjé *et al.* (2019*a*)

there are many more species for which female polymorphism has never been studied, including some species for which male polymorphism has received extensive attention. Additionally, for autosomally inherited colour polymorphisms, females may carry the underlying genotype without expressing the colour polymorphism (Olsson *et al.*, 2007*b*, 2012; Rankin & Stuart-Fox, 2015; Rankin *et al.*, 2016). The evolution and maintenance of polymorphism in females is therefore an emerging area of research.

Polymorphic lizards can have anywhere from two to six different morphs, typically including up to three 'pure' colour morphs (with the exception of the painted dragon, *Ctenophorus pictus*, which has four: red, orange, yellow and blue) and up to three 'mixed' morphs (Table 1). These mixed morphs can have either a central coloured patch with different surrounding colour (some iguanids and agamids), throat stripes (some iguanids), or a mosaic of differently coloured ventral scales (lacertids). However, defining the number of mixed morphs can be challenging, and definitions are not always consistent across studies. One challenging aspect is that the amount of colour can vary continuously within morphs (Thompson & Moore, 1991*a*; Teasdale, Stevens, & Stuart-Fox, 2013). For example, four morphs, including only one mixed morph (an orange centre surrounded by yellow), are recognised in *Ctenophorus modestus* (Teasdale *et al.*, 2013) [formerly northern lineage tawny dragon, *C. decresii* (Dong *et al.*, in press]. Mixed orange-grey and yellow-grey morphs are not recognised because the relative extent of these colours varies continuously, making it impossible visually to distinguish a mixed-morph individual (orange-grey or yellow-grey) from a pure-morph individual (orange or yellow). Importantly, categories were defined in this species objectively, based on clustering of quantified colour variation (Teasdale *et al.*, 2013); however, mixed-morph categories in other species have generally been defined subjectively, which can contribute to inconsistencies in the number of morphs described (Pérezi de Lanuza *et al.*, 2013; Pérez i de Lanuza *et al.*, 2019).

Distinguishing colour morphs is further complicated by the fact that not all researchers describe coloration in the same way. For example, in tree lizards (*Urosaurus ornatus*), researchers have described the same male morph as either yellow (e.g. Thompson & Moore, 1991*a*) or green (Paterson & Blouin-Demers, 2017). Additionally, orange- or yellow/green-throated males with a central blue/green throat patch have been referred to as green (Hover, 1985) or blue-green (Zucker, 1994). To add further to the confusion, studies have also described a solid blue morph (e.g. Thompson & Moore, 1991*a*), a mottled blue morph (Thaker *et al.*, 2009), or an additional solid green morph, distinct from the other yellow/green morph (Carpenter, 1995a, 1995b). Consequently, a green-throated male tree lizard could, depending on the study, potentially refer to several different morphs. Even establishing the existence of discrete colour morphs can be controversial. For example, while some studies report discrete colour morphs in female European common lizards (*Zootoca vivipara*; Vercken & Clobert, 2008*b*; Vercken *et al.*, 2007a, 2007b; Vercken, Sinervo, & Clobert, 2008) others have argued that the ventral colour variation in this species is continuous (Cote *et al.*, 2008; discussed in detail in Olsson, Stuart-Fox, & Ballen, 2013). Changing and researcher-specific definitions of coloration can therefore present challenges when attempting to compare and replicate studies, which highlights the importance of assessing which categories are recognised by the intended receivers (i.e. conspecific lizards; for example Pérezi de Lanuza *et al.*, 2018).

III. BIOCHEMICAL AND CELLULAR BASIS

In lizards, colour is produced by the combination of chromatophore cells and structural components of the dermis

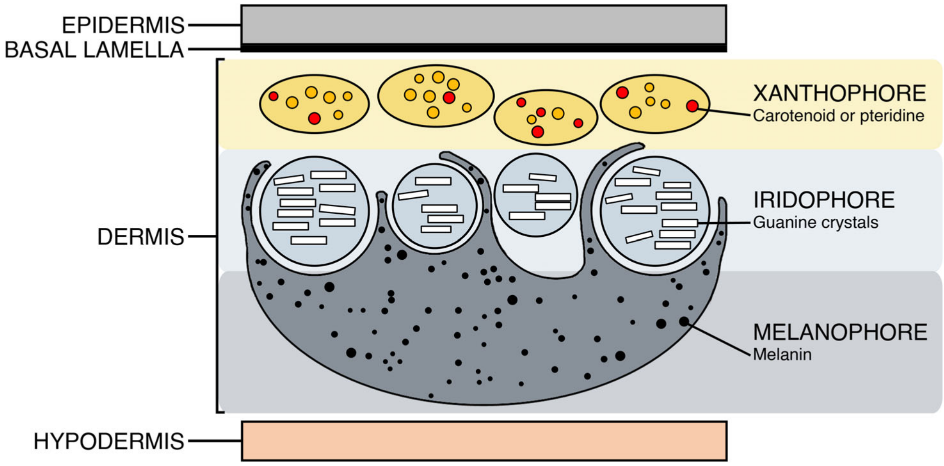


Fig 2. Schematic representation of the cellular structure of lizard skin including the three chromatophore types: brown-black melanophores containing melanin pigments, colourless iridophores containing light-reflecting guanine crystals, and yellow-red xanthophores containing carotenoid and/or pteridine pigments. Note that the melanophore dendritic processes can extend around and above the overlying iridophores.

(e.g. collagen and connective tissue; Fig. 2). There are three chromatophore cell types, conserved across poikilothermic vertebrates: melanophores containing brown to black melanin pigments, iridophores containing light-scattering guanine crystals, and xanthophores containing red to yellow carotenoid and/or pteridine pigments (reviewed in Bagnara & Matsumoto, 2006; Grether, Kolluru, & Nersissian, 2004; Ligon & McCartney, 2016; Olsson *et al.*, 2013). These three pigment cell types form a layered system with xanthophores in the uppermost layer, melanophores in the deepest layer and iridophores in between (Bagnara, Fernandez, & Fujii, 2007). Different colour morphs can be attributed to both the relative number and arrangement of chromatophore types as well as the type and concentration of pigments within them (or density and arrangement of guanine crystals in the case of iridophores; Lewis *et al.*, 2017). For example, blue-coloured skin usually has a low density of xanthophores, a high density of iridophores containing regularly spaced guanine crystals producing thin-film interference, and varying density of underlying melanophores that absorb light and influence the intensity of ultra-violet and blue (Morrison, Rand, & Frost-Mason,- 1995; Macedonia *et al.*, 2000).

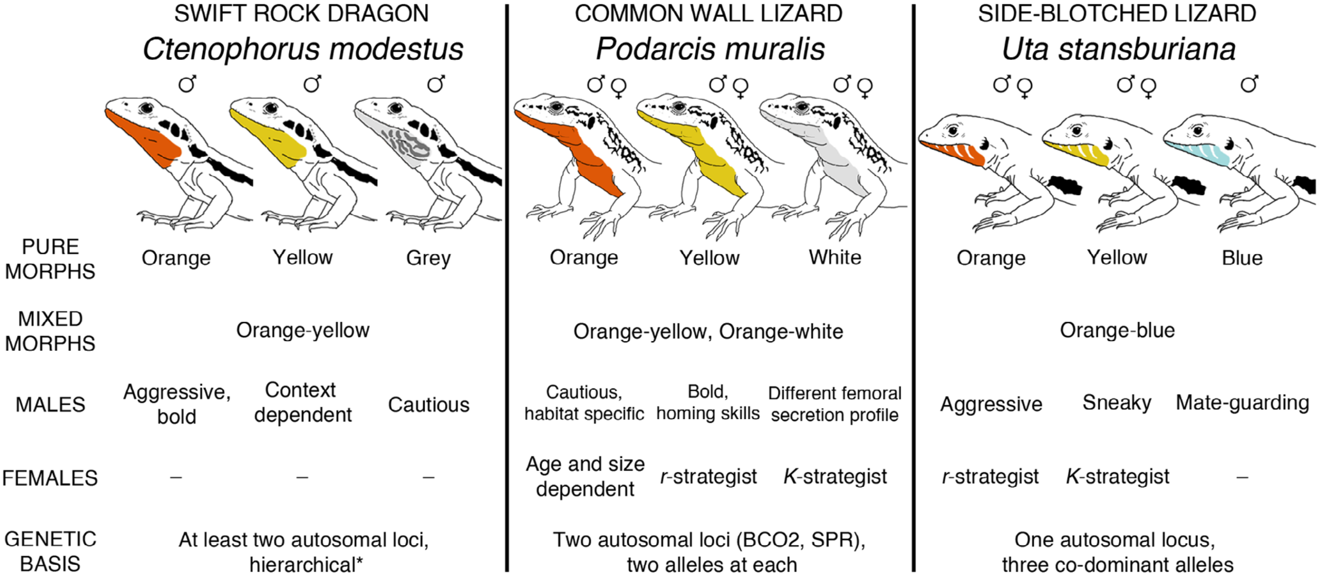
The biochemical and cellular basis of lizard colour polymorphisms has been characterised in detail for several species, including *Zootoca vivipara* (Fitze *et al.*, 2009), *Podarcis muralis* (Andrade *et al.*, 2019), *Sceloporus undulatus erythrocheilus* (Morrison *et al.*, 1995), *Uta stansburiana* (Haisten *et al.*, 2015) and *Ctenophorus modestus* (McLean *et al.*, 2017). All these species have orange and yellow morphs, but they differ in their biochemical basis. Red to yellow colours are produced by two different classes of pigment in the xanthophores; carotenoids and pteridines (Cooper & Greenberg, 1992; Bagnara & Matsumoto, 2006; Olsson *et al.*, 2013). Carotenoids must be obtained directly through the diet or metabolically converted from dietary carotenoids (in the case of red ketocarotenoids; Hill & McGraw, 2006), while pteridines are synthesised within chromatophores from purine molecules (Ziegler, 2003; Braasch, Schartl, & Volff, 2007). In *Zootoca vivipara*, red to yellow colours are produced exclusively by carotenoids, with the orange morph having a higher concentration of carotenoids than the yellow morph (Fitze *et al.*, 2009). By contrast, orange and yellow in *Sceloporus undulatus erythrocheilus* appear to be produced exclusively by pteridines, with the orange morph having a higher concentration of the red pteridine, drosopterin (Morrison *et al.*, 1995). In *Uta stansburiana*, *Podarcis muralis* and *Ctenophorus modestus*, orange and yellow morphs both have a combination of pteridines and carotenoids but differ in their relative proportions (Haisten *et al.*, 2015; McLean *et al.*, 2017; Andrade *et al.*, 2019). The yellow morph has a relatively higher concentration of dietary yellow carotenoids while the orange morph has a relatively higher concentration of red/orange pteridines (riboflavin and/or drosopterin) in all three species.

Differences in the biochemical basis of polymorphism has implications for the cost and information content of colour signals. Specifically, costs associated with synthesis of coloured pteridines, acquisition and metabolism of carotenoids, and trade-offs in allocation to colour signals *versus* other physiological functions, all clearly differ for different types of pigments (McLean *et al.*, 2019). Consequently, the extent to which colour signals individual condition may differ for different morphs within species, or for similar morphs among species.

IV. GENETIC BASIS

Although the biochemical and cellular basis of colour polymorphism in lizards is relatively well understood, the genetic basis is unknown for most species. Given that colour is just one of a suite of traits which differ among morphs, the genetic basis of polymorphism is expected to involve pleiotropic regulation of, or tight physical linkage between, genes associated with both colour production and coadapted traits. Andrade *et al.* (2019) recently showed that the orange, yellow and white colour morphs of the common wall lizard (*Podarcis muralis*) are associated with two small regulatory regions near genes associated with pteridine [sepiapterin reductase (SPR)] and carotenoid [beta-carotene oxygenase 2 (BCO2)] metabolism. The presence of orange coloration is determined by a recessive allele at the SPR locus (oo), whereas the presence of yellow coloration is determined by a recessive allele at the BCO2 locus (yy), both of which are autosomal (Andrade *et al.*, 2019). Alleles at these loci were shared with six other *Podarcis* species exhibiting similar colour polymorphisms, with haplotype divergence among species indicating that variation at these loci likely evolved from a combination of ancestral genetic diversity and introgression by hybridisation (Andrade *et al.*, 2019). Whether this simple genetic architecture controls the multiple behavioural and physiological traits that differ among morphs, or whether these loci are also involved in similar colour polymorphisms in lizards from other families, remain open questions.

As in *Podarcis muralis*, autosomal loci underpin colour polymorphism in the three other species in which inheritance has been examined: *Uta stansburiana* (Sinervo, 2001; Sinervo *et al.*, 2001), *Ctenophorus modestus* (Rankin *et al.*, 2016) and *Ctenophorus pictus* (Olsson *et al.*, 2007*b*). Polymorphism in the side-blotched lizard (*Uta stansburiana*) appears to be controlled by a single locus with three, co-dominant alleles (o, b and y), with both alleles expressed in heterozygotes (Sinervo & Zamudio, 2001). Homozygous males have solid throat colours [orange (oo), blue (bb), or yellow (yy)], whereas heterozygotes have throats striped with two colours corresponding to the two alleles (i.e. ob, oy or by). Although alleles at the OBY locus have co-dominant effects on colour expression, they have dominant effects on male strategy. Specifically, the o allele conferring the aggressive O phenotypic strategy is dominant to the y allele conferring the sneaky Y strategy, which is dominant to the b allele conferring the cooperative mate-guarding B



	SWIFT ROCK DRAGON *Ctenophorus modestus*			COMMON WALL LIZARD *Podarcis muralis*			SIDE-BLOTCHED LIZARD *Uta stansburiana*		
	♂	♂	♂	♂♀	♂♀	♂♀	♂♀	♂♀	♂
PURE MORPHS	Orange	Yellow	Grey	Orange	Yellow	White	Orange	Yellow	Blue
MIXED MORPHS	Orange-yellow			Orange-yellow, Orange-white			Orange-blue		
MALES	Aggressive, bold	Context dependent	Cautious	Cautious, habitat specific	Bold, homing skills	Different femoral secretion profile	Aggressive	Sneaky	Mate-guarding
FEMALES	–	–	–	Age and size dependent	*r*-strategist	*K*-strategist	*r*-strategist	*K*-strategist	–
GENETIC BASIS	At least two autosomal loci, hierarchical*			Two autosomal loci (BCO2, SPR), two alleles at each			One autosomal locus, three co-dominant alleles		

Fig 3. Colour polymorphism in three well-studied lizard species: the Australian swift rock dragon, *Ctenophorus modestus* (formerly northern lineage *C. decresii*), the European common wall lizard, *Podarcis muralis*, and the North American side-blotched lizard, *Uta stansburiana*. Each species has three pure morphs, which are present in males or both sexes, and at least one mixed morph. Male and/or female morphs differ in behavioural, physiological and/or life-history traits (details in Table 1). In all three species, the polymorphisms appear to be underpinned by a few autosomal loci of major effect. *In *C. modestus*, the most likely model of inheritance is one where a bi-allelic locus determines whether or not orange and/or yellow is expressed, and one or more loci subsequently determine the expression of orange or yellow. BCO2, beta-carotene oxygenase 2; SPR, sepiapterin reductase.

strategy (Sinervo, 2001; Sinervo & Clobert, 2003). Sinervo *et al.* (2007) assumed a similar genetic basis (one autosomal locus, three co-dominant alleles) for polymorphism in the European common lizard (*Zootoca vivipara*) although did not test or consider alternative models of inheritance. In the painted dragon (*Ctenophorus pictus*), the precise mechanism of inheritance could not be determined due to limited data; however, a single-locus three-allele model could not be rejected (Olsson *et al.*, 2007*b*). Notably, none of these studies formally considered models of inheritance with more than one locus. By contrast, in *Ctenophorus modestus*, the best supported model was one with two bi-allelic loci (an 'orange' and a 'yellow' locus) showing complete dominance (i.e. with the allele coding for orange or yellow expression respectively being dominant; Rankin *et al.*, 2016). However, these studies of inheritance are all constrained by the models considered and statistical power (i.e. the number of offspring in the pedigree).

For *Ctenophorus modestus* we considered an alternative model of inheritance (using data in Rankin *et al.*, 2016), where one autosomal, bi-allelic locus ('colour locus') determines whether or not individuals express orange and/or yellow (gg = grey throat; Gg, gG or GG = orange and/or yellow) and one or more loci subsequently determine the expression of orange and yellow in Gg, gG or GG individuals. Assuming that orange, orange-yellow or yellow individuals have an equal probability of possessing a Gg, gG or GG genotype at the colour locus, observed frequencies of grey offspring *versus* those with orange or yellow (12 *versus* 46 respectively) precisely match those expected (12.21, 45.70; likelihood ratio test: $G_1 = 0.008$; $P = 0.93$; model cannot be rejected). We next considered whether the expression of orange and yellow is consistent with the presence of a second locus with co-dominant alleles (i.e. orange = OO, orange-yellow = OY and yellow = YY), but this hypothesis can be confidently rejected (likelihood ratio test: $G_3 = 18.38$; $P = 0.0004$). Full details of the breeding design and analysis are given in Rankin *et al.* (2016).

Rankin *et al.* (2016) showed that although inheritance of the discrete colour morphs is consistent with a few loci of major effect, there is continuous and highly heritable variation in the extent of orange or yellow coloration within *Ctenophorus modestus* morphs (i.e. the extent of colour expression within morphs behaves as a quantitative trait). Such continuous variation within morphs is a common, although under-appreciated feature of many polymorphic systems. The model proposed above for *Ctenophorus modestus* is consistent with the suggestion of hierarchical genetic control of colour expression, whereby at least two independently segregating loci determine the discrete morphs (i.e. presence or absence of orange, yellow or both), and multiple genes influence the extent of colour expression within morphs. For orange, yellow and orange-yellow morphs, quantitative colour expression is likely produced through a physiological cascade involving multiple genes in combination with environmental effects. Rankin *et* *al.* (2016) also found evidence of potential genetic covariation between yellow and orange expression, suggesting that the loci influencing quantitative colour expression affect both yellow and orange. In a subsequent study, Lewis *et al.* (2017) found experimentally elevated stress levels impact luminance and patterning, but have little effect on the intensity or proportion of orange or yellow coloration.

Together, emerging evidence on the genetic basis of colour polymorphism in lizards confirms that discrete morphs are governed by a few loci of major effect as expected (Fig. 3), but inheritance of colour variation is unlikely to be determined by a single locus. For example, geographic variation in the polymorphism in *Uta stansburiana* indicates that the genetic basis is more complex than a single OBY locus with three co-dominant alleles. Some populations are fixed for blue throats surrounded by orange (Corl *et al.*, 2010). If the OBY locus determines colour expression in these populations, all individuals would be heterozygous (although OB individuals in the trimorphic populations have orange and blue striped throats rather than blue surrounded by orange). This would require exceptionally strong heterozygote advantage (i.e. very strong selection against OO and BB individuals), in addition to loss of the Y allele. Thus, additional genetic mechanisms are likely to influence genetic variation in *Uta stansburiana*. This may also be true of *Zootoca vivipara*, in which Sinervo *et al.* (2007) proposed a genetic mechanism analogous to the OBY locus, given the complex colour variation in this species (see above). Ultimately, genomic studies such as that of Andrade *et al.* (2019), are essential to resolve the genetic basis of colour polymorphism and correlated strategies.

Comparison of the genetic basis of colour morphs among species may further reveal whether polymorphism is associated with shared ancestry (homology), the repeated use of the same genes or pathways (parallelism), or multiple independent genetic solutions resulting in the same outcome. Lizard colour polymorphisms may be a good system for studying the link between phenotypic and genetic convergence for a number of reasons. Firstly, colour morphs have independently evolved multiple times in highly divergent lineages, allowing for comparisons of the underlying molecular mechanisms between both closely and distantly related species (Fig. 1). Importantly, lineages contain both polymorphic and non-polymorphic species, which is vital for confirming associations with candidate genes. Secondly, as described above, colour morphs are highly heritable in species where inheritance has been tested, confirming that the trait has a genetic basis which is likely to involve a few loci of major effect (Fig. 3). Colour morphs have also been shown to be underpinned by genes associated with pigment production and/or metabolism, which can be targeted in molecular studies. For these reasons, lizard colour polymorphisms provide a promising opportunity to assess the genetic basis of convergent phenotypes.

V. CORRELATED BEHAVIOURAL, PHYSIOLOGICAL AND LIFE-HISTORY TRAITS

The presence of multiple throat colour morphs is often, if not always, associated with a suite of other behavioural, physiological and life-history traits (McKinnon & Pierotti, 2010; Table 1). Morphs can be considered to display alternative strategies when they differ in multiple traits that affect fitness in combination. These strategies may represent different adaptive peaks on the fitness landscape, generated by correlational selection (Sinervo & Svensson, 2002; McKinnon & Pierotti, 2010; Roff & Fairbairn, 2012). Correlational selection is expected to generate genetic correlations between the traits under selection (Roff & Fairbairn, 2012). Genetic correlations between colour, immunity, egg mass, clutch size and laying date have been demonstrated in side-blotched lizards (*Uta stansburiana*) (Svensson *et al.*, 2001*a*, 2009*a*; Sinervo & Svensson, 2002; Calsbeek & Sinervo, 2007; Svensson, McAdam, & Sinervo, 2009b). However, formal selection analyses and estimates of genetic correlations have been conducted in relatively few polymorphic lizard species, so in most cases, non-adaptive pleiotropy cannot be ruled out as an explanation for correlated traits. Nevertheless, correlational selection is implicated by the large number of studies showing that morphs differ in diverse traits that affect fitness (Table 1).

(1) Male reproductive tactics

Many polymorphic agamids and iguanids have dominance hierarchies among male morphs, where one morph is more likely to win against another in male–male contests (see Table 1). Interestingly, although the most dominant morph colour varies, yellow morphs tend to be least dominant across species (e.g. Bruinjé *et al.*, 2019*a*; Healey *et al.*, 2007; Sinervo & Lively, 1996; Taylor & Lattanzio, 2016; but see Abalos *et al.*, 2016; Yewers *et al.*, 2016). Where these hierarchies are present, less-dominant morphs can gain reproductive success through pre- or post-copulatory reproductive tactics that do not depend upon contest success.

The rock–paper–scissors system of male side-blotched lizards (*Uta stansburiana*) is a particularly well-characterised example of alternative strategies (Fig. 3; Sinervo *et al.*, 2006; Sinervo & Lively, 1996; Sinervo *et al.*, 2000*a*; Zamudio & Sinervo, 2000). Each strategy – orange/aggressive, yellow/sneaky and blue/mate-guarding – is more successful against one other strategy, but loses against the third, as in a game of 'rock–paper–scissors' (Sinervo & Lively, 1996). Each strategy entails correlated physiological traits; for example, orange males have higher levels of testosterone, which is linked with endurance and territoriality (Sinervo *et al.*, 2000*a*). Different morphs also show different tactics for escaping predators, which are more successful (as indicated by survival rates) when combined with specific dorsal patterns (Lancaster, Hipsley, & Sinervo, 2009; Lancaster *et al.*, 2010). Accordingly, females show preferences for males that exhibit beneficial combinations of traits (Lancaster *et al.*, 2009). *Uta stansburiana* is arguably one of the best-known examples of pre-copulatory reproductive strategies corresponding to male colour morphs – in lizards or any other taxon; however, it is certainly not the only example.

Male tree lizard (*Urosaurus ornatus*) morphs exhibit similarly distinct pre-copulatory reproductive strategies. Blue males are dominant and aggressive, and defend large territories; orange males are non-territorial, occupy smaller home ranges, and can become nomadic when environmental conditions are stressful; and yellow males sneak copulations with females around the territories of blue males (Moore, Hews, & Knapp, 1998; Lattanzio & Miles, 2016; Paterson & Blouin-Demers, 2018). The level of specialisation and flexibility required for each strategy appears to give rise to other differences between morphs. Blue males are dietary specialists, whereas yellow males show plasticity in dietary preferences and orange males are generalists (Lattanzio & Miles, 2016). Blue males prefer yellow females, which tend to have larger clutch sizes (Zucker & Boecklen, 1990), whereas yellow males show no preference and interact with more females overall (Krohmaly *et al.*, 2018). In captivity, blue males also compete more successfully for higher quality perches (Taylor & Lattanzio, 2016); however, in the wild, yellow males are most likely to occupy higher quality, densely populated habitat near creek beds (Paterson & Blouin-Demers, 2018). This latter finding may be because blue males defend territories more successfully in less densely populated areas, whereas the sneaking strategy of yellow males benefits from dense populations of females (Paterson & Blouin-Demers, 2018).

Less-dominant male morphs may also succeed through alternative post-copulatory tactics. Yellow-headed painted dragon (*Ctenophorus pictus*) males tend to be less aggressive, lose contests, and reside on lower quality territories, compared with red-headed males (Healey *et al.*, 2007; Olsson *et al.*, 2007*b*). On the other hand, yellow-headed males have larger testes (relative to their body size and condition), copulate for less time, and sire three times as many offspring per copulation (Olsson *et al.*, 2009*b*). These two distinct strategies appear to be equally successful, as there is no evidence for a difference in reproductive success between morphs (Olsson *et al.*, 2007*b*) or female preferences for different head colour morphs (Healey *et al.*, 2008). However, females prefer males with a yellow bib (McDiarmid *et al.*, 2017) and the cost of having a bib, which is condition dependent (Olsson *et al.*, 2009*a*), appears to differ depending on head colour, linking these two polymorphic traits (Healey & Olsson, 2009).

(2) Non-reproductive correlated traits

Other trade-offs and selective pressures, unrelated to dominance, might also favour alternative fitness optima among male morphs. In common wall lizards (*Podarcis muralis*), orange morphs (both male and female) are more conspicuous to conspecifics and predators than yellow or white morphs, respectively (Pérezi de Lanuza & Font, 2015; Fig. 3). Greater risk of predation might therefore explain why orange morphs, after successive predatory threats, take progressively longer to emerge from a refuge compared with other morphs (Pellitteri-Rosa *et al.*, 2017). Likewise, orange morphs tend to be more restricted to vegetated habitat close to water (Pérezi de Lanuza & Carretero, 2018). Yellow males also differ from other morphs in a number of traits, the adaptive value of which are perhaps less clear. For example, yellow males have a lower immune response than white and orange males (Sacchi *et al.*, 2007a; Sacchi *et al.*, 2017*a*), different seasonal patterns of testosterone (Sacchi *et al.*, 2017*b*), better homing abilities (Scali *et al.*, 2013), different diets (particularly when compared with the orange males (Scali *et al.*, 2016); and show more rapid desensitisation to predatory threats (Pellitteri-Rosa *et al.*, 2017). Otherwise, these morphs are similar in body size (Sacchi *et al.*, 2007a, 2007b; but see Calsbeek *et al.*, 2010), body condition (Abalos *et al.*, 2016), and aggression (Sacchi *et al.*, 2009). Even though differences among morphs have been reported (Table 1), for many polymorphic lizard species, including *P. muralis*, it is unclear whether or how these traits relate to alternative fitness optima or strategies.

(3) Correlated traits in females

In species with polymorphic females, different female morphs can exhibit alternative life-history strategies. Specifically, one female morph may produce many, small offspring (*r*-strategy) while another produces fewer, large offspring (*K*-strategy). For example, in *Uta stansburiana*, orange females are *r*-strategists and yellow females are *K*-strategists (Sinervo *et al.*, 2000b). In *Podarcis muralis*, yellow and white females may be *r*-and *K*-strategists respectively, whereas orange females may change their strategy depending on their size and age (Galeotti *et al.*, 2013). *Urosaurus ornatus* shows more continuous variation in clutch size, with females with yellower throats having larger clutches (Zucker & Boecklen, 1990). *Zootoca vivipara* shows the opposite trend, with yellow females tending to lay smaller clutches than orange or mixed females, which have higher hatching success (Vercken *et al.*, 2007*b*).

As in males, female morphs have correlated behavioural and physiological traits that likely relate to their life-history strategies. For example, in *Uta stansburiana*, orange and yellow morphs differ in the relationship between clutch size, local social environment (number of orange or yellow neighbours), immunocompetence, condition and survival (Svensson *et al.*, 2002). However, not all findings are consistent across studies (Svensson *et al.*, 2002; Comendant *et al.*, 2003) and there is also evidence in some species that females may modulate their strategy depending on mate morph (Galeotti *et al.*, 2013).

(4) Environmental effects on correlated traits

In both male and female lizards, environment, including social environment, can have an important influence on the strategies of different morphs. For example, having a bib is more costly for male *Ctenophorus pictus*, particularly yellow-headed males, when exposed to more red-headed, aggressive neighbours (Healey & Olsson, 2009). Consequently, although bibbed males are preferred by females, their relative success likely varies depending on their social context. Dominance hierarchies are also not necessarily fixed across space and time. In a study of long-tailed brush lizards (*Urosaurus graciosus*), orange males were dominant over yellow males in an initial experiment, but yellow males became increasingly aggressive over successive experiments until this hierarchy was no longer apparent (Brown & Lattanzio, 2018). In female lizards, the success of alternative reproductive strategies is likely highly dependent on environment, with *K*-strategies favoured when populations exceeded carrying capacity and *r*-strategies favoured at lower densities (Sinervo *et al*., 2000*b*). However, if clutch size is unrelated to the rate of hatching success or offspring development, the opposite trend may be true. In *Zootoca vivipara*, orange females produce fewer offspring when female density is high, and also when yellow females are more frequent in the population (Vercken *et al*., 2007*b*). This adjustment in reproductive output may represent strategic allocation of resources, as orange females appear to be weaker competitors (Vercken & Clobert, 2008*b*); therefore, it may be more beneficial for orange females to allocate more resources to reproduction when their offspring have greater likelihood of survival. Such variation in morph-specific responses to environmental conditions, as well as the fitness consequences, may play a critical role in the maintenance of the colour polymorphism.

VI. MAINTENANCE OF POLYMORPHISM WITHIN POPULATIONS

Like all heritable polymorphisms, the maintenance of colour polymorphism over time requires balancing selection, that is, selection to maintain the different alleles that underlie the polymorphism. The most common mechanism generating balancing selection in polymorphic systems is negative frequency-dependent selection, whereby the fitness of each morph is higher at relatively lower frequencies. One of the best-known examples is the 'rock–paper–scissors' system of male reproductive strategies in the side-blotched lizard (*Uta stansburiana*) (see Section V.1). The fitness of each strategy depends on its relative frequency within the population; for example, the yellow sneaker strategy has higher fitness when it is rare relative to the frequency of the aggressive orange strategy from which it sneaks mating opportunities. Similarly, the blue mate-guarding strategy has higher fitness when it is rare relative to the yellow sneaker strategy. Consequently, the frequency of each strategy varies cyclically and the polymorphism is maintained (Sinervo & Lively, 1996).

Frequency-dependent selection is not the only mechanism generating balancing selection. Balancing selection may be generated by heterozygote advantage (Gray & McKinnon, 2007), although we are not aware of any examples of heterozygote advantage maintaining colour polymorphism in lizards. Balancing selection can also be generated by spatiotemporal variation in environmental conditions affecting morph fitness (Svensson, 2017). Environmental characteristics could affect relative morph fitness directly (e.g. through costs of acquiring dietary carotenoids) or indirectly by altering inter- and intra-specific interactions (e.g. the competitive advantage of morphs could differ depending on resources and population density). Evidence for environmental effects on relative morph fitness can be found in *Ctenophorus modestus*, where populations in more arid environments have a higher proportion of orange males, and fewer yellow males (McLean, Stuart-Fox, & Moussalli, 2015). Similarly, in *Uta stansburiana*, the fitness of female morphs depends on population density, which is a function of environmental conditions (Sinervo *et al*., 2001). Because environmental variation is generally cyclical over short timescales (even though it may be directional over long timescales), temporal variation in selection likely contributes to the maintenance of polymorphism in many species.

Sexual selection is also an important mechanism influencing the maintenance of polymorphism because it affects the evolution of alternative reproductive strategies and assortative mating. For example, in the common wall lizard (*Podarcis muralis*), there are more male colour morphs in populations with male-biased sex ratios, suggesting a relationship between the intensity of male intrasexual selection and male morph diversity (Pérezi de Lanuza, Carretero, & Font, 2017). Additionally, unless counteracted by some form of balancing selection, the tendency to mate assortatively might drive further divergence between morphs, and if heteromorphic pairs are sufficiently rare, could even eventually lead to speciation. Assortative mating may be favoured by correlational selection to maintain optimal trait combinations and prevent their breakdown by recombination (Lancaster *et al*., 2014; Jamie & Meier, 2020). By contrast, disassortative mating can prevent the loss of rare morphs and maintain polymorphism (Gray & McKinnon, 2007; Lancaster *et al*., 2014; Wellenreuther, Svensson, & Hansson, 2014). Disassortative mating can be promoted by negative frequency-dependent selection because females should mate with rare male morphs to produce the fittest offspring (Lancaster *et al*., 2014). Conversely, negative frequency-dependent selection can promote disassortative mating because rarer morphs have more mating opportunities and thus higher fitness (Jamie & Meier, 2020). A combination of assortative and disassortative mating strategies could contribute to maintenance of colour polymorphism in *Podarcis muralis* (Sacchi *et al*., 2018). Females of different morphs appear to show both assortative and disassortative association preferences in captivity (Sacchi *et al*., 2015; Sacchi *et al*., 2018), although it is unclear the extent to which these preferences determine pairings in the wild. Same-morph (homomorphic) pairs are more commonly found than heteromorphic pairs in wild populations (Pérezi de Lanuza *et al*., 2013; Pérezi de Lanuza *et al*., 2016), and yellow homomorphic pairs achieve higher breeding success than any other morph-pair combination (Galeotti *et al*., 2013) although it is not known whether this pattern varies over time. Ultimately, the maintenance of polymorphism will depend on the complex interaction between correlational selection, balancing selection and mating patterns, all of which may vary depending on environmental conditions that affect population density and relative morph fitness.

Processes maintaining polymorphism are best determined using direct measures of selection on colour morphs in the wild. This has been attempted in several lizard species that reach sexual maturity within a year: side-blotched lizards (*Uta stansburiana*), common lizards (*Lacerta vivipara*) and painted dragons (*Ctenophorus pictus*). Measurement of selection in the wild is challenging for lizard species with longer lifespans, overlapping generations, and that take longer than a year to reach sexual maturity. Therefore, in many polymorphic lizards, processes that might maintain the polymorphism are inferred indirectly from hypothesised fitness advantages of the life-history, reproductive or behavioural strategies corresponding to the morphs.

VII. GEOGRAPHIC VARIATION IN POLYMORPHISM

Geographic variation in the number, type and/or frequency of colour morphs is common in polymorphic species. Given that McLean & Stuart-Fox (2014) have extensively reviewed this topic previously, we discuss it only briefly here. Most widespread polymorphic lizard species exhibit geographic variation in morphs. For example, some populations and subspecies of *Uta stansburiana* are trimorphic, while others are dimorphic or monomorphic, and phylogenetic reconstruction suggests that the polymorphism has been independently lost eight times (Corl *et al.*, 2010). Similarly, polymorphism is likely to have been lost from *Ctenophorus decresii* (sister species to *C. modestus*, previously recognised as divergent lineages of the same species), resulting in the evolution of a unique blue-throated morph (McLean, Stuart-Fox, & Moussalli, 2014). Morph frequencies also vary substantially among polymorphic populations in both of these species (Corl *et al.*, 2010; McLean *et al.*, 2015), as well as *Podarcis muralis* (Sacchi *et al.*, 2007*b*; Pérezi de Lanuza & Carretero, 2018), *Podarcis gaigeae* (Runemark *et al.*, 2010), *Anolis distichus favillarum* (Ng *et al.*, 2017), *Urosaurus ornatus* (Thompson & Moore, 1991*a*; Hews *et al.*, 1997), and *Sceloporus grammicus* (Bastiaans *et al.*, 2014). Such geographic variation reflects the balance between local selective pressures, gene flow and stochastic processes (Svensson, 2017), and may play an important role in speciation if populations with different morph compositions become reproductively isolated (McLean & Stuart-Fox, 2014).

VIII. CONCLUSIONS AND FUTURE DIRECTIONS

(1) Lizards show remarkable convergence in polymorphism of throat/head/ventral colour signals, with red/orange, yellow, white/blue/grey and mixed-colour morphs. Despite similarities in the polymorphisms, the number of recognised morphs, particularly mixed-morph categories, differ among species. This may be partially attributed to the way in which colour variation has been measured and categorised by researchers, or may reflect biological differences in the mechanisms generating and maintaining the polymorphism.

(2) We suggest that colour variation should be quantified using objective measures, ideally based on receiver (i.e. lizard) colour vision (e.g. Teasdale *et al.*, 2013; Pérezi de Lanuza & Carretero, 2018; Pérez i de Lanuza *et al.*, 2019). Such measures can now be obtained relatively easily from both spectral data and digital images using free software (Maia *et al.*, 2019; van den Berg *et al.*, 2020). Morph categories should ideally be determined based on clear statistical clustering (i.e. discontinuities in the variation). Even when categories can be statistically defined, however, it does not mean that they are biologically relevant. This is particularly the case for mixed morphs, which may be objectively categorised but exhibit behavioural or life-history strategies similar to the pure morph of one of the constituent colours.

(3) An outstanding question is whether seemingly convergent colour morphs in distantly related species arise from similar or different genetic mechanisms. Recent studies in lizards suggest that the genetic basis of colour polymorphism is likely to be more complex than a single locus, with at least two loci generating the polymorphism. Sequencing skin transcriptomes across developmental stages may help to pinpoint genes associated with colour production and polymorphism. Studies of the genetic basis of lizard polymorphisms have sampled adult lizards, but it would be informative to investigate gene expression at the onset of ventral coloration, or in developing scale buds. Genomic studies of lizard colour polymorphisms, especially in relation to the genetic basis of convergent phenotypes, are an exciting area of future research.

(4) Despite apparent convergence in lizard colour polymorphisms, there is substantial divergence in correlated traits or strategies. While in some species, morphs differ in life-history or reproductive strategies (and associated behavioural and physiological traits), in others the differences appear to be more subtle.

(5) Most discussion of the maintenance of polymorphism has focussed on the role of frequency-dependent selection. We suggest that temporal variation in environmental conditions may play an equally important role and warrants further research. Environmental variation may affect morph fitness both directly and indirectly (e.g. by affecting population density) and may interact with frequency-dependent selection *via* its effects on morph frequencies.

(6) There is a growing appreciation of geographic variation in polymorphism within species or closely related groups of species. Polymorphism may predispose populations to diverge in colour traits, ultimately leading to speciation (McLean & Stuart-Fox, 2014). Geographic variation in colour polymorphism and its role in speciation has been reviewed in detail elsewhere (McLean & Stuart-Fox, 2014) but lizards are a promising group in which to examine these processes.

(7) The study of colour polymorphism in lizards has contributed substantially to our understanding of the evolutionary processes generating and maintaining discrete phenotypic variation in natural populations. Research in this very active field promises to continue to provide novel insights with broad significance to evolutionary biologists.

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X. REFERENCES

Abalos, J., Pérezi de Lanuza, G., Carazo, P. & Font, E. (2016). The role of male coloration in the outcome of staged contests in the European common wall lizard (*Podarcis muralis*). *Behaviour* **153**, 607–631.

Ahi, E. P., Lecaudey, L. A., Ziegelbecker, A., Steiner, O., Glabonjat, R., Goessler, W., Hois, V., Wagner, C., Lass, A. & Sefc, K. M. (2020). Comparative transcriptomics reveals candidate carotenoid color genes in an East African cichlid fish. *BMC Genomics* **21**, 1–15.

Andrade, P., Pinho, C., Pérezi de Lanuza, G., Afonso, S., Brejcha, J., Rubin, C.-J., Wallerman, O., Pereira, P., Sabatino, S. J., Bellati, A., Pellitteri-Rosa, D., Bosakova, Z., Bunikis, I., Carretero, M. A., Feiner, N., et al. (2019). Regulatory changes in pterin and carotenoid genes underlie balanced color polymorphisms in the wall lizard. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 5633–5642.

Bagnara, J. T., Fernandez, P. J. & Fujii, R. (2007). On the blue coloration of vertebrates. *Pigment Cell Research* **20**, 14–26.

Bagnara, J. T. & Matsumoto, J. (2006). Comparative anatomy and physiology of pigment cells in nonmammalian tissues. In *The pigmentary system: physiology and pathophysiology*, 2nd Edition (eds J. J. Nordlund, R. E. Boissy, V. J. Hearing, R. A. King, W. S. Oetting and J.-P. Ortonne), pp. 11–59. Blackwell Publishing Ltd, Oxford.

Bastiaans, E., Bastiaans, M., Morinaga, G., Castaneda Gaytan, J. G., Marshall, J. C., Bane, B., Mendez de la Cruz, F. & Sinervo, B. (2014). Female preference for sympatric vs. allopatric male throat color morphs in the Mesquite lizard (*Sceloporus grammicus*) species complex. *PLoS One* **9**, e93197.

Blankers, T., Townsend, T. M., Pepe, K., Reeder, T. W. & Wiens, J. J. (2013). Contrasting global-scale evolutionary radiations: phylogeny, diversification, and morphological evolution in the major clades of iguanian lizards. *Biological Journal of the Linnean Society* **108**, 127–143.

Bleay, C., Comendant, T. & Sinervo, B. (2007). An experimental test of frequency-dependent selection on male mating strategy in the field. *Proceedings of the Royal Society B-Biological Sciences* **274**, 2019–2025.

Bleay, C. & Sinervo, B. (2007). Discrete genetic variation in mate choice and a condition-dependent preference function in the side-blotched lizard: implications for the formation and maintenance of coadapted gene complexes. *Behavioral Ecology* **18**, 304–310.

Blouin-Demers, G., Lourdais, O., Bouazza, A., Verreault, C., El Mouden, H. & Slimani, T. (2013). Patterns of throat colour variation in *Quedenfeldtia trachyblepharus*, a high-altitude gecko endemic to the High Atlas Mountains of Morocco. *Amphibia-Reptilia* **34**, 567–572.

Braasch, I., Schartl, M. & Volff, J.-N. (2007). Evolution of pigment synthesis pathways by gene and genome duplication in fish. *BMC Evolutionary Biology* **7**, 74.

Brown, D. M. & Lattanzio, M. S. (2018). Resource variability and the collapse of a dominance hierarchy in a colour polymorphic species. *Behaviour* **155**, 443–463.

Bruinjé, A. C., Coelho, F. E. A., Paiva, T. M. A. & Costa, G. C. (2019a). Aggression, color signaling, and performance of the male color morphs of a Brazilian lizard (*Tropidurus semitaeniatus*). *Behavioral Ecology and Sociobiology* **73**, 72.

Bruinjé, A. C., Leivas, P. T. & Costa, G. C. (2018). Characterization of sexual dimorphism and male colour morphs of *Tropidurus semitaeniatus* (Spix, 1825) in three populations from northeast of Brazil. *Herpetology Notes* **11**, 755–760.

Bruinjé, A. C., Moura, M. O., Maggi, B. S., Sao-Pedro, V. A., Pessoa, D. M. A. & Costa, G. C. (2019b). Conspecifics of the Striped Lava Lizard are able to distinguish sex and male colour morphs in apparently homogeneous dull dorsal colouration. *Amphibia-Reptilia* **40**, 149–162.

Calsbeek, B., Hasselquist, D. & Clobert, J. (2010). Multivariate phenotypes and the potential for alternative phenotypic optima in wall lizard (*Podarcis muralis*) ventral colour morphs. *Journal of Evolutionary Biology* **23**, 1138–1147.

Calsbeek, R. & Sinervo, B. (2007). Correlational selection on lay date and life-history traits: Experimental manipulations of territory and nest site quality. *Evolution* **61**, 1071–1083.

Carpenter, G. C. (1995a). Modeling dominance: The influence of size, coloration and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetological Monographs* **9**, 88–101.

Carpenter, G. C. (1995b). The ontogeny of a variable social badge - throat color development in tree lizards (*Urosaurus ornatus*). *Journal of Herpetology* **29**, 7–13.

Chapple, D. G. (2005). Life history and reproductive ecology of White's skink, *Egernia whitii*. *Australian Journal of Zoology* **53**, 353–360.

Chapple, D. G., Hutchinson, M. N., Maryan, B., Plivelich, M., Moore, J. A. & Keogh, J. S. (2008). Evolution and maintenance of colour pattern polymorphism in Liopholis (Squamata: Scincidae). *Australian Journal of Zoology* **56**, 103–115.

Comendant, T., Sinervo, B., Svensson, E. I. & Wingfield, J. (2003). Social competition, corticosterone and survival in female lizard morphs. *Journal of Evolutionary Biology* **16**, 948–955.

Cooper, W. & Greenberg, N. (1992). Reptilian coloration and behavior. *Biology of the Reptilia* **18**, 298–422.

Corl, A., Davis, A. R., Kuchta, S. R. & Sinervo, B. (2010). Selective loss of polymorphic mating types is associated with rapid phenotypic evolution during morphic speciation. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 4254–4259.

Cote, J., Le Galliard, J. F., Rossi, J. M. & Fitze, P. S. (2008). Environmentally induced changes in carotenoid-based coloration of female lizards: a comment on Vercken et al. *Journal of Evolutionary Biology* **21**, 1165–1172.

Dong, C. M., Johnston, G. R., Stuart-Fox, D., Moussalli, A., Rankin, K. J. & McLean, C. A. (in press). Elevation of divergent color polymorphic and monomorphic lizard lineages (Squamata: Agamidae) to species level. *Copeia*.

Fernandez, J. B., Bastiaans, E., Medina, M., Mendez De la Cruz, F. R., Sinervo, B. R. & Ibarguengoytia, N. R. (2018). Behavioral and physiological polymorphism in males of the austral lizard *Liolaemus sarmientoi*. *Journal of Comparative Physiology A-Neuroethology Sensory Neural and Behavioral Physiology* **204**, 219–230.

Fitze, P. S., Cote, J., San-Jose, L. M., Meylan, S., Isaksson, C., Andersson, S., Rossi, J.-M. & Clobert, J. (2009). Carotenoid-based colours reflect the stress response in the common lizard. *PLoS One* **4**, e5111.

Ford, E. B. (1945). Polymorphism. *Biological Reviews* **20**, 73–88.

Friesen, C. R., Johansson, R. & Olsson, M. (2017a). Morph-specific metabolic rate and the timing of reproductive senescence in a color polymorphic dragon. *Journal of Experimental Zoology Part A - Ecological and Integrative Physiology* **327**, 433–443.

Friesen, C. R., Rollings, N., Wilson, M., Whittington, C. M., Shine, R. & Olsson, M. (2020). Covariation in superoxide, sperm telomere length and sperm velocity in a polymorphic reptile. *Behavioral Ecology and Sociobiology* **74**, 74.

Friesen, C. R., Wilson, M. R., Rollings, N., Sudyka, J., Whittington, C. M., Giraudeau, M. & Olsson, M. (2017b). Conditional handicaps in exuberant lizards: Bright color in aggressive males is correlated with high levels of free radicals. *Frontiers in Ecology and Evolution* **5**, 1.

Galeotti, P., Pellitteri-Rosa, D., Sacchi, R., Gentilli, A., Pupin, F., Rubolini, D. & Fasola, M. (2010). Sex-, morph- and size-specific susceptibility to stress measured by haematological variables in captive common wall lizard *Podarcis muralis*. *Comparative Biochemistry and Physiology Part A* **157**, 354–363.

Galeotti, P., Sacchi, R., Pellitteri-Rosa, D., Bellati, A., Cocca, W., Gentilli, A., Scali, S. & Fasola, M. (2013). Colour polymorphism and alternative breeding strategies: Effects of parent's colour morph on fitness traits in the common wall lizard. *Evolutionary Biology* **40**, 385–394.

Gray, S. M. & McKinnon, J. S. (2007). Linking color polymorphism maintenance and speciation. *Trends in Ecology & Evolution* **22**, 71–79.

Grether, G. F., Kolluru, G. R. & Nersissian, K. (2004). Individual colour patches as multicomponent signals. *Biological Reviews* **79**, 583–610.

Gubili, C., Ritter, C. D., Motta, J., Farias, I. P., Bates, J., Canton, R., Capurucho, J. M., Cornelius, C., Feldheim, K. A. & Ribas, C. C. (2016). Isolation and characterization of polymorphic microsatellite DNA Markers from an Amazonian white-sand vegetation specialist bird, *Xenopipo atronitens* (Aves: Pipridae). *The Wilson Journal of Ornithology* **128**, 668–672.

Hacking, J. D., Stuart-Fox, D., Godfrey, S. S. & Gardner, M. G. (2018). Specific MHC class I supertype associated with parasite infection and color morph in a wild lizard population. *Ecology and Evolution* **8**, 9920–9933.

Haisten, D. C., Paranjpe, D., Loveridge, S. & Sinervo, B. (2015). The cellular basis of polymorphic coloration in common side-blotched lizards, *Uta stansburiana*. *Herpetologica* **71**, 125–135.

Healey, M. & Olsson, M. (2008). Territory acquisition in a polymorphic lizard: An experimental approach. *Austral Ecology* **33**, 1015–1021.

Healey, M. & Olsson, M. (2009). Too big for his boots: Are social costs keeping condition-dependent status signalling honest in an Australian lizard? *Austral Ecology* **34**, 636–640.

Healey, M., Uller, T. & Olsson, M. (2007). Seeing red: morph-specific contest success and survival rates in a colour-polymorphic agamid lizard. *Animal Behaviour* **74**, 337–341.

Healey, M., Uller, T. & Olsson, M. (2008). Variety is the spice of life: female lizards choose to associate with colour-polymorphic male dyads. *Ethology* **114**, 231–237.

Hews, D. K., Thompson, C. W., Moore, I. T. & Moore, M. C. (1997). Population frequencies of alternative male phenotypes in tree lizards: geographic variation and common-garden rearing studies. *Behavioral Ecology and Sociobiology* **41**, 371–380.

Hill, G. E. & McGraw, K. J. (2006). *Bird coloration: Mechanisms and measurements*. Harvard University Press, Cambridge.

Hover, E. L. (1985). Differences in aggressive-behavior between two throat color morphs in a lizard, *Urosaurus ornatus*. *Copeia* **1985**, 933–940.

Huyghe, K., Husak, J. F., Herrel, A., Tadic, Z., Moore, I. T., Van Damme, R. & Vanhooydonck, B. (2009). Relationships between hormones, physiological performance and immunocompetence in a color-polymorphic lizard species, *Podarcis melisellensis*. *Hormones and Behavior* **55**, 488–494.

Huyghe, K., Van Oystaeyen, A., Pasmans, F., Tadic, Z., Vanhooydonck, B. & Van Damme, R. (2010). Seasonal changes in parasite load and a cellular immune response in a colour polymorphic lizard. *Oecologia* **163**, 867–874.

Huyghe, K., Vanhooydonck, B., Herrel, A., Tadic, Z. & Van Damme, R. (2007). Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis*. *Integrative and Comparative Biology* **47**, 211–220.

Jamie, G. A. & Meier, J. I. (2020). The persistence of polymorphisms across species radiations. *Trends in Ecology & Evolution* **35**, 795–808.

Jaworski, K. E. & Lattanzio, M. S. (2017). Physiological consequences of food limitation for a color polymorphic lizard: Are coping responses morph-specific? *Copeia* **105**, 689–695.

Jiménez-Robles, O., Butron-Galvez, P., Carpio, R. & De la Rival, I. (2016). Revised distribution, phenotypic variation, and conservation status of *Liolaemus fittkaui* (Squamata: Liolaemidae), a lizard endemic to the Andes of Central Bolivia. *Phyllomedusa* **15**, 7–20.

Knapp, R., Hews, D. K., Thompson, C. W., Ray, L. E. & Moore, M. C. (2003). Environmental and endocrine correlates of tactic switching by nonterritorial male tree lizards (*Urosaurus ornatus*). *Hormones and Behavior* **43**, 83–92.

Krohmaly, K. I., Martin, Z. W. & Lattanzio, M. S. (2018). Male mate choice and the potential for complex mating dynamics in the tree lizard (*Urosaurus ornatus*). *Ethology* **124**, 236–244.

Lancaster, L. T., Hipsley, C. A. & Sinervo, B. (2009). Female choice for optimal combinations of multiple male display traits increases offspring survival. *Behavioral Ecology* **20**, 993–999.

Lancaster, L. T., McAdam, A. G., Hipsley, C. A. & Sinervo, B. R. (2014). Frequency-dependent and correlational selection pressures have conflicting consequences for assortative mating in a color-polymorphic lizard, *Uta stansburiana*. *American Naturalist* **184**, 188–197.

Lancaster, L. T., McAdam, A. G. & Sinervo, B. (2010). Maternal adjustment of egg size organizes alternative escape behaviors, promoting adaptive phenotypic integration. *Evolution* **64**, 1607–1621.

Lattanzio, M. S., Metro, K. J. & Miles, D. B. (2014). Preference for male traits differ in two female morphs of the tree lizard, *Urosaurus ornatus*. *PLoS One* **9**, e101515.

Lattanzio, M. S. & Miles, D. B. (2016). Trophic niche divergence among colour morphs that exhibit alternative mating tactics. *Royal Society Open Science* **3**, 150531.

Lewis, A. C., Rankin, K. J., Pask, A. J. & Stuart-Fox, D. (2017). Stress-induced changes in color expression mediated by iridophores in a polymorphic lizard. *Ecology and Evolution* **7**, 8262–8272.

Ligon, R. A. & McCartney, K. L. (2016). Biochemical regulation of pigment motility in vertebrate chromatophores: a review of physiological color change mechanisms. *Current Zoology* **62**, 237–252.

Macedonia, J. M., James, S., Wittle, L. W. & Clark, D. L. (2000). Skin pigments and coloration in the Jamaican radiation of Anolis lizards. *Journal of Herpetology* **34**, 99–109.

MacGuigan, D. J., Geneva, A. J. & Glor, R. E. (2017). A genomic assessment of species boundaries and hybridization in a group of highly polymorphic anoles (distichus species complex). *Ecology and Evolution* **7**, 3657–3671.

Maia, R., Gruson, H., Endler, J. A. & White, T. E. (2019). pavo 2: new tools for the spectral and spatial analysis of colour in R. *Methods in Ecology and Evolution* **10**, 1097–1107.

McDiarmid, C. S., Friesen, C. R., Ballen, C. & Olsson, M. (2017). Sexual coloration and sperm performance in the Australian painted dragon lizard, *Ctenophorus pictus*. *Journal of Evolutionary Biology* **30**, 1303–1312.

McElroy, E. J., Marien, C., Meyers, J. J. & Irschick, D. J. (2007). Do displays send information about ornament structure and male quality in the ornate tree lizard, *Urosaurus ornatus*? *Ethology* **113**, 1113–1122.

McKinnon, J. S. & Pierotti, M. E. R. (2010). Colour polymorphism and correlated characters: genetic mechanisms and evolution. *Molecular Ecology* **19**, 5101–5125.

McLean, C. A., Lutz, A., Rankin, K. J., Elliott, A., Moussalli, A. & Stuart-Fox, D. (2019). Red carotenoids and associated gene expression explain colour variation in frillneck lizards. *Proceedings of the Royal Society B* **286**, 20191172.

McLean, C. A., Lutz, A., Rankin, K. J., Stuart-Fox, D. & Moussalli, M. (2017). Revealing the biochemical and genetic basis of color variation in a polymorphic lizard. *Molecular Biology and Evolution* **34**, 1924–1935.

McLean, C. A., Moussalli, A., Sass, S. & Stuart-Fox, D. (2013). Taxonomic assessment of the *Ctenophorus decresii* complex (Reptilia: Agamidae) reveals a new species of dragon lizard from Western New South Wales. *Records of the Australian Museum* **65**, 51–63.

McLean, C. A. & Stuart-Fox, D. (2014). Geographic variation in animal colour polymorphisms and its role in speciation. *Biological Reviews* **89**, 860–873.

McLean, C. A., Stuart-Fox, D. & Moussalli, A. (2014). Phylogeographic structure, demographic history and morph composition in a colour polymorphic lizard. *Journal of Evolutionary Biology* **27**, 2123–2137.

McLean, C. A., Stuart-Fox, D. & Moussalli, A. (2015). Environment, but not genetic divergence, influences geographic variation in colour morph frequencies in a lizard. *BMC Evol Biology* **15**, 156–165. https://doi.org/10.1186/s12862-015-0442-x

Meyers, J. J., Irschick, D. J., Vanhooydonck, B. & Herrel, A. (2006). Divergent roles for multiple sexual signals in a polygynous lizard. *Functional Ecology* **20**, 709–716.

Mills, S. C., Hazard, L., Lancaster, L., Mappes, T., Miles, D., Oksanen, T. A. & Sinervo, B. (2008). Gonadotropin hormone modulation of testosterone, immune function, performance, and Behavioral trade-offs among male morphs of the lizard *Uta stansburiana*. *American Naturalist* **171**, 339–357.

Moore, M. C., Hews, D. K. & Knapp, R. (1998). Hormonal control and evolution of alternative male phenotypes: Generalizations of models for sexual differentiation. *American Zoologist* **38**, 133–151.

Morrison, R. L., Rand, M. S. & Frost-Mason, S. K. (1995). Cellular basis of color differences in three morphs of the lizard *Sceloporus undulatus erythrocheilus*. *Copeia* **1995**, 397–408.

Ng, J., Geneva, A. J., Noll, S. & Glor, R. E. (2017). Signals and speciation: Anolis dewlap color as a reproductive barrier. *Journal of Herpetology* **51**, 437–447.

Ng, J., Ossip-Klein, A. G. & Glor, R. E. (2016). Adaptive signal coloration maintained in the face of gene flow in a Hispaniolan anolis lizard. *BMC Evolutionary Biology* **16**, 193.

Olsson, M., Healey, M. & Astheimer, L. (2007a). Afternoon T: testosterone level is higher in red than yellow male polychromatic lizards. *Physiology & Behavior* **91**, 531–534.

Olsson, M., Healey, M., Wapstra, E., Schwartz, T., Lebas, N. & Uller, T. (2007b). Mating system variation and morph fluctuations in a polymorphic lizard. *Molecular Ecology* **16**, 5307–5315.

Olsson, M., Healey, M., Wapstra, E. & Uller, T. (2009a). Testing the quality of a carrier: a field experiment on lizard signalers. *Evolution* **63**, 695–701.

Olsson, M., Healey, M., Wilson, M. & Tobler, M. (2012). Polymorphic male color morphs visualized with steroids in monomorphic females: a tool for designing analysis of sex-limited trait inheritance. *Journal of Experimental Biology* **215**, 575–577.

Olsson, M., Schwartz, T., Uller, T. & Healey, M. (2009b). Effects of sperm storage and male colour on probability of paternity in a polychromatic lizard. *Animal Behaviour* **77**, 419–424.

Olsson, M., Stuart-Fox, D. & Ballen, C. (2013). Genetics and evolution of colour patterns in reptiles. *Seminars in Cell & Developmental Biology* **24**, 529–541.

Olsson, M., Wapstra, E., Healey, M., Schwartz, T. & Uller, T. (2008). Selection on space use in a polymorphic lizard. *Evolutionary Ecology Research* **10**, 621–627.

Paterson, J. E. & Blouin-Demers, G. (2017). Distinguishing discrete polymorphism from continuous variation in throat colour of tree lizards, *Urosaurus ornatus*. *Biological Journal of the Linnean Society* **121**, 72–81.

Paterson, J. E. & Blouin-Demers, G. (2018). Male throat colour polymorphism is related to differences in space use and in habitat selection in tree lizards. *Journal of Zoology* **306**, 101–109.

Pellitteri-Rosa, D., Bellati, A., Cocca, W., Gazzola, A., Martin, J. & Fasola, M. (2017). Urbanization affects refuge use and habituation to predators in a polymorphic lizard. *Animal Behaviour* **123**, 359–367.

Pellitteri-Rosa, D., Martin, J., Lopez, P., Bellati, A., Sacchi, R., Fasola, M. & Galeotti, P. (2014). Chemical polymorphism in male femoral gland secretions matches polymorphic coloration in common wall lizards (*Podarcis muralis*). *Chemoecology* **24**, 67–78.

Pérezi de Lanuza, G., Abalos, J., Bartolome, A. & Font, E. (2018). Through the eye of a lizard: hue discrimination in a lizard with ventral polymorphic coloration. *Journal of Experimental Biology* **221**, jeb169565.

Pérez i de Lanuza, G., Bellati, A., Pellitteri-Rosa, D., Font, E. & Carretero, M. A. (2019). Colour variation between different lineages of a colour polymorphic lizard. *Journal of Zoology* **308**, 175–187.

Pérezi de Lanuza, G. & Carretero, M. A. (2018). Partial divergence in microhabitat use suggests environmental-dependent selection on a colour polymorphic lizard. *Behavioral Ecology and Sociobiology* **72**, 138.

Pérezi de Lanuza, G., Carretero, M. A. & Font, E. (2017). Intensity of male-male competition predicts morph diversity in a color polymorphic lizard. *Evolution* **71**, 1832–1840.

Pérezi de Lanuza, G. & Font, E. (2015). Differences in conspicuousness between alternative color morphs in a polychromatic lizard. *Behavioral Ecology* **26**, 1432–1446.

Pérezi de Lanuza, G., Font, E. & Carazo, P. (2013). Color-assortative mating in a color-polymorphic lacertid lizard. *Behavioral Ecology* **24**, 273–279.

Pérezi de Lanuza, G., Font, E. & Carretero, M. A. (2016). Colour assortative pairing in a colour polymorphic lizard is independent of population morph diversity. *Science of Nature* **103**, 82.

Pyron, R. A., Burbrink, F. T. & Wiens, J. J. (2013). A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* **13**, 1–54.

Rand, M. S. (1992). Hormonal control of polymorphic and sexually dimorphic coloration in the lizard *Sceloporus undulatus erythrocheilus*. *General and Comparative Endocrinology* **88**, 461–468.

Rankin, K. & Stuart-Fox, D. (2015). Testosterone-induced expression of male colour morphs in females of the polymorphic tawny dragon lizard, *Ctenophorus decresii*. *PLoS One* **10**, e0140458.

Rankin, K. J., McLean, C. A., Kemp, D. J. & Stuart-Fox, D. (2016). The genetic basis of discrete and quantitative colour variation in the polymorphic lizard, Ctenophorus decresii. *BMC Evolutionary Biology* **16**, 1–14.

Rivero-Blanco, C. & Schargel, W. E. (2012). A strikingly polychromatic new species of *Gonatodes* (Squamata: Sphaerodactylidae) from northern Venezuela. *Zootaxa* **3518**, 66–78.

Roff, D. A. & Fairbairn, D. J. (2012). A test of the hypothesis that correlational selection generates genetic correlations. *Evolution* **66**, 2953–2960.

Roulin, A. (2004). The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews* **79**, 815–848.

Runemark, A., Hansson, B., Pafilis, P., Valakos, E. D. & Svensson, E. I. (2010). Island biology and morphological divergence of the Skyros wall lizard *Podarcis gaigeae*: a combined role for local selection and genetic drift on color morph frequency divergence? *BMC Evolutionary Biology* **10**, 269.

Runemark, A. & Svensson, E. I. (2012). Sexual selection as a promoter of population divergence in male phenotypic characters: a study on mainland and islet lizard populations. *Biological Journal of the Linnean Society* **106**, 374–389.

Sacchi, R., Coladonato, A. J., Ghitti, M., Mangiacotti, M., Scali, S., Bovo, M. & Zuffi, M. (2018). Morph-specific assortative mating in common wall lizard females. *Current Zoology* **64**, 449–453.

Sacchi, R., Ghitti, M., Scali, S., Mangiacotti, M., Zuffi, M. A. L., Sannolo, M., Coladonato, A. J., Pasquesi, G., Bovo, M. & Pellitteri-Rosa, D. (2015). Common wall lizard females (*Podarcis muralis*) do not actively choose males based on their colour morph. *Ethology* **121**, 1145–1153.

Sacchi, R., Mangiacotti, M., Scali, S., Ghitti, M. & Zuffi, M. A. L. (2017a). Effects of colour morph and temperature on immunity in males and females of the common wall lizard. *Evolutionary Biology* **44**, 496–504.

Sacchi, R., Pupin, F., Gentilli, A., Rubolini, D., Scali, S., Fasola, M. & Galeotti, P. (2009). Male-male combats in a polymorphic lizard: Residency and size, but not color, affect fighting rules and contest outcome. *Aggressive Behavior* **35**, 274–283.

Sacchi, R., Rubolini, D., Gentilli, A., Pupin, F., Razzetti, E., Scali, S., Galeotti, P. & Fasola, M. (2007a). Morph-specific immunity in male *Podarcis muralis*. *Amphibia-Reptilia* **28**, 408–412.

Sacchi, R., Scali, S., Mangiacotti, M., Sannolo, M., Zuffi, M. A. L., Pupin, F., Gentilli, A. & Bonnet, X. (2017b). Seasonal variations of plasma testosterone among colour-morph common wall lizards (*Podarcis muralis*). *General and Comparative Endocrinology* **240**, 114–120.

Sacchi, R., Scali, S., Pupin, F., Gentilli, A., Galeotti, P. & Fasola, M. (2007b). Microgeographic variation of colour morph frequency and biometry of common wall lizards. *Journal of Zoology* **273**, 389–396.

Saenko, S. V., Chouteau, M., Piron-Prunier, F., Blugeon, C., Joron, M. & Llaurens, V. (2019). Unravelling the genes forming the wing pattern supergene in the polymorphic butterfly Heliconius numata. *EvoDevo* **10**, 16.

Scali, S., Sacchi, R., Azzusi, M., Daverio, S., Oppedisano, T. & Mangiacotti, M. (2013). Homeward bound: factors affecting homing ability in a polymorphic lizard. *Journal of Zoology* **289**, 196–203.

Scali, S., Sacchi, R., Mangiacotti, M., Pupin, F., Gentilli, A., Zucchi, C., Sannolo, M., Pavesi, M. & Zuffi, M. A. L. (2016). Does a polymorphic species have a "polymorphic" diet? A case study from a lacertid lizard. *Biological Journal of the Linnean Society* **117**, 492–502.

Sinervo, B. (2001). Runaway social games, genetic cycles driven by alternative male and female strategies, and the origin of morphs. *Genetica* **112**, 417–434.

Sinervo, B., Bleay, C. & Adamopoulou, C. (2001). Social causes of correlational selection and the resolution of a heritable throat color polymorphism in a lizard. *Evolution* **55**, 2040–2052.

Sinervo, B., Chaine, A., Clobert, J., Calsbeek, R., Hazard, L., Lancaster, L., McAdam, A. G., Alonzo, S., Corrigan, G. & Hochberg, M. E. (2006). Self-recognition, color signals, and cycles of greenbeard mutualism and altruism. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 7372–7377.

Sinervo, B. & Clobert, J. (2003). Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science* **300**, 1949–1951.

Sinervo, B., Heulin, B., Surget-Groba, Y., Clobert, J., Miles, D. B., Corl, A., Chaine, A. & Davis, A. (2007). Models of density-dependent genic selection and a new rock-paper-scissors social system. *American Naturalist* **170**, 663–680.

Sinervo, B. & Lively, C. M. (1996). The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* **380**, 240–243.

Sinervo, B., Miles, D. B., Frankino, W. A., Klukowski, M. & DeNardo, D. F. (2000a). Testosterone, endurance, and Darwinian fitness: Natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior* **38**, 222–233.

Sinervo, B. & Svensson, E. (2002). Correlational selection and the evolution of genomic architecture. *Heredity* **89**, 329–338.

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

Sinervo, B. & Zamudio, K. R. (2001). The evolution of alternative reproductive strategies: Fitness differential, heritability, and genetic correlation between the sexes. *Journal of Heredity* **92**, 198–205.

Stapley, J., Wordley, C. & Slate, J. (2011). No evidence of genetic differentiation between anoles with different dewlap color patterns. *Journal of Heredity* **102**, 118–124.

Svensson, E., Sinervo, B. & Comendant, T. (2001a). Condition, genotype-by-environment interaction, and correlational selection in lizard life-history morphs. *Evolution* **55**, 2053–2069.

Svensson, E., Sinervo, B. & Comendant, T. (2001b). Density-dependent competition and selection on immune function in genetic lizard morphs. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 12561–12565.

Svensson, E. I. (2017). Back to basics: using colour polymorphisms to study evolutionary processes. *Molecular Ecology* **26**, 2204–2211.

Svensson, E. I., Abbott, J. K., Gosden, T. P. & Coreau, A. (2009a). Female polymorphisms, sexual conflict and limits to speciation processes in animals. *Evolutionary Ecology* **23**, 93–108.

Svensson, E. I., McAdam, A. G. & Sinervo, B. (2009b). Intralocus sexual conflict over immune defense, gender load, and sex-specific signaling in a natural lizard population. *Evolution* **63**, 3124–3135.

Svensson, E. I., Sinervo, B. & Comendant, T. (2002). Mechanistic and experimental analysis of condition and reproduction in a polymorphic lizard. *Journal of Evolutionary Biology* **15**, 1034–1047.

Taylor, J. N. & Lattanzio, M. S. (2016). Boldness, dominance, and territoriality in the color polymorphic tree lizard, *Urosaurus ornatus*. *Ethology* **122**, 892–901.

Teasdale, L., Stevens, M. & Stuart-Fox, D. (2013). Discrete colour polymorphism in the tawny dragon lizard (*Ctenophorus decresii*) and differences in signal conspicuousness among morphs. *Journal of Evolutionary Biology* **26**, 1035–1046.

Thaker, M., Lima, S. L. & Hews, D. K. (2009). Acute corticosterone elevation enhances antipredator behaviors in male tree lizard morphs. *Hormones and Behavior* **56**, 51–57.

Thompson, C. W., Moore, I. T. & Moore, M. C. (1993). Social, environmental and genetic-factors in the ontogeny of phenotypic differentiation in a lizard with alternative male reproductive strategies. *Behavioral Ecology and Sociobiology* **33**, 137–146.

Thompson, C. W. & Moore, M. C. (1991a). Syntopic occurrence of multiple dewlap color morphs in male tree lizards, *Urosaurus ornatus*. *Copeia* **1991**, 493–503.

Thompson, C. W. & Moore, M. C. (1991b). Throat colour reliably signals status in male tree lizards *Urosaurus ornatus*. *Animal Behaviour* **42**, 745–754.

Thompson, C. W. & Moore, M. C. (1992). Behavioral and hormonal correlates of alternative reproductive strategies in a polygynous lizard - tests of the relative plasticity and challenge hypotheses. *Hormones and Behavior* **26**, 568–585.

Tobler, M., Healey, M. & Olsson, M. (2011). Digit ratio, color polymorphism and egg testosterone in the Australian painted dragon. *PLoS One* **6**, e16225.

Tobler, M., Healey, M. & Olsson, M. (2012). Digit ratio, polychromatism and associations with endurance and antipredator behaviour in male painted dragon lizards. *Animal Behaviour* **84**, 1261–1269.

van den Berg, C. P., Troscianko, J., Endler, J. A., Marshall, N. J. & Cheney, K. L. (2020). Quantitative Colour Pattern Analysis (QCPA): A comprehensive framework for the analysis of colour patterns in nature. *Methods in Ecology and Evolution* **11**, 316–332.

Vercken, E. & Clobert, J. (2008a). The role of colour polymorphism in social encounters among female common lizards. *Herpetological Journal* **18**, 223–230.

Vercken, E. & Clobert, J. (2008b). Ventral colour polymorphism correlates with alternative behavioural patterns in female common lizards (*Lacerta vivipara*). *Ecoscience* **15**, 320–326.

Vercken, E., Clobert, J. & Sinervo, B. (2010). Frequency-dependent reproductive success in female common lizards: a real-life hawk-dove-bully game? *Oecologia* **162**, 49–58.

Vercken, E., de Fraipont, M., Dufty, A. M. Jr. & Clobert, J. (2007a). Mother's timing and duration of corticosterone exposure modulate offspring size and natal dispersal in the common lizard (*Lacerta vivipara*). *Hormones and Behavior* **51**, 379–386.

Vercken, E., Massot, M., Sinervo, B. & Clobert, J. (2007b). Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. *Journal of Evolutionary Biology* **20**, 221–232.

Vercken, E., Sinervo, B. & Clobert, J. (2008). Colour variation in female common lizards: why we should speak of morphs, a reply to Cote et al. *Journal of Evolutionary Biology* **21**, 1160–1164.

Vercken, E., Sinervo, B. & Clobert, J. (2012). The importance of a good neighborhood: dispersal decisions in juvenile common lizards are based on social environment. *Behavioral Ecology* **23**, 1059–1067.

Wellenreuther, M., Svensson, E. I. & Hansson, B. (2014). Sexual selection and genetic colour polymorphisms in animals. *Molecular Ecology* **23**, 5398–5414.

Yewers, M. S. C., Jessop, T. S. & Stuart-Fox, D. (2017). Endocrine differences among colour morphs in a lizard with alternative behavioural strategies. *Hormones and Behavior* **93**, 118–127.

Yewers, M. S. C., Pryke, S. & Stuart-Fox, D. (2016). Behavioural differences across contexts may indicate morph-specific strategies in the lizard *Ctenophorus decresii*. *Animal Behaviour* **111**, 329–339.

Zajitschek, S. R. K., Zajitschek, F., Miles, D. B. & Clobert, J. (2012). The effect of coloration and temperature on sprint performance in male and female wall lizards. *Biological Journal of the Linnean Society* **107**, 573–582.

Zamudio, K. R. & Sinervo, B. (2000). Polygyny, mate-guarding, and posthumous fertilization as alternative male mating strategies. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 14427–14432.

Ziegler, I. (2003). The pteridine pathway in zebrafish: regulation and specification during the determination of neural crest cell-fate. *Pigment Cell Research* **16**, 172–182.

Zucker, N. (1994). A dual status-signaling system - a matter of redundancy or differing roles. *Animal Behaviour* **47**, 15–22.

Zucker, N. & Boecklen, W. (1990). Variation in female throat coloration in the tree lizard (*Urosaurus ornatus*) - relation to reproductive-cycle and fecundity. *Herpetologica* **46**, 387–394.

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