

## SHORT REVIEW

# Correlational selection and the evolution of genomic architecture

B Sinervo<sup>1</sup> and E Svensson<sup>2</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA; <sup>2</sup>Section for Animal Ecology, Department of Ecology Lund University, S-223 62 Lund, Sweden

We review and discuss the importance of correlational selection (selection for optimal character combinations) in natural populations. If two or more traits subject to multivariate selection are heritable, correlational selection builds favourable genetic correlations through the formation of linkage disequilibrium at underlying loci governing the traits. However, linkage disequilibria built up by correlational selection are expected to decay rapidly (ie, within a few generations), unless correlational selection is strong and chronic. We argue that frequency-dependent biotic interactions that have 'Red Queen dynamics' (eg, host-parasite interactions, predator-prey relationships or intraspecific arms races) often fuel chronic correlational selection, which is strong enough to maintain adaptive genetic correlations of the kind we describe. We illustrate these processes and phenomena

using empirical examples from various plant and animal systems, including our own recent work on the evolutionary dynamics of a heritable throat colour polymorphism in the side-blotched lizard *Uta stansburiana*. In particular, male and female colour morphs of side-blotched lizards cycle on five- and two-generation (year) timescales under the force of strong frequency-dependent selection. Each morph refines the other morph in a Red Queen dynamic. Strong correlational selection gradients among life history, immunological and morphological traits shape the genetic correlations of the side-blotched lizard polymorphism. We discuss the broader evolutionary consequences of the buildup of co-adapted trait complexes within species, such as the implications for speciation processes.

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## Introduction

Consider the classical example of microevolution elaborated by the British ecological geneticists tradition: industrial melanism and selection on colouration of the Peppered Moth, *Biston betularia* (Kettlewell, 1955; Haldane, 1956; Ford, 1975). During the early part of last century, soot from industrial pollution began to darken trunks and branches of trees (Ford, 1975). Light moths were at selective disadvantage in that they were more conspicuous to avian predators on dark bark. Conversely, melanic moths were at a selective advantage, being less conspicuous relative to light moths. We use this classical example to illustrate a general point about correlational selection that arises from interactions between predator behaviour, prey behaviour, and prey morphology. Prey behaviour plays a critical role in this selective scenario. For instance, consider a black moth that chooses as a resting place the few lichen-covered patches that remain in an industrialized area: its black colour will be a liability because it will be detected and eaten by avian predators. Consequently, there will be selection not only on black colouration, but on combinations of colour and habitat choice. Individuals that choose backgrounds that match their col-

our survive, whereas those with the wrong character combinations die.

When two or more traits affect fitness in an interactive way, selection is correlational (Lande and Arnold, 1983; Phillips and Arnold, 1989). When traits are heritable and encoded by separate sets of loci that interactively affect fitness we also refer to this as fitness epistasis (Whitlock *et al*, 1995). Although correlational selection at the phenotypic level can arise from fitness epistasis at the genotypic level (Brodie III, 2000), correlational selection can occur even if the interacting traits are non-heritable or governed by the same pleiotropic locus. Hence, correlational selection and fitness epistasis are closely connected but not identical phenomena.

When evolutionary quantitative genetics was applied to organisms in the wild, it was assumed that the genetic variance-covariance matrix (**G**-matrix) was constant, even during the course of long-term evolution (Lande, 1976; Lande and Arnold, 1983). Recently, however, the assumption of constant **G**-matrices has been questioned (Turelli, 1988; Zeng, 1988; Wilkinson *et al*, 1990). Here, we describe correlational selection, a process that operates on ecological time-scales, but has profound consequences for **G**-matrix evolution. Correlational selection can alter, destroy, refine or generate genetic correlations between suites of co-adapted traits (eg, Cheverud, 1984; Kingsolver and Wiernasz, 1987; Brodie III, 1989; 1992; Lynch and Walsh, 1998; Sinervo *et al*, 2000b; Svensson *et al*, 2001a). Hence, correlational selection can shape genomic

architecture. We argue that frequency-dependent selection often, if not always, plays a key role in generating chronic correlational selection. The importance of frequency-dependent selection in this context raises questions about sources of selection. The sources arise from external biotic and social environments consisting of predators, parasites or conspecific competitors. We summarize these phenomena under the umbrella of the Red Queen (Van Valen, 1973).

Correlational analysis has focused on continuous variation, but the process is involved in the genesis and maintenance of discrete morphotypic variation. We focus our discussion on male and female morphs of the side-blotched lizard, *Uta stansburiana*, which exemplify processes of correlational and frequency-dependent selection. However, our goal is to elucidate relations between natural history and genetics that underlie all forms of correlational selection. Thus, we review principles of correlational selection with reference to other empirical studies. Natural history consideration of correlational selection begins with techniques for visualizing selection.

#### Detection and visualization of correlational selection

Correlational selection can be detected using analytical techniques first elaborated by Lande and Arnold (1983). They proposed that students of natural selection should use parametric regression techniques to quantify univariate or multivariate selection. Multivariate selection gradients are obtained from regression of relative fitness as the dependent variable, and traits under selection as independent variables that are standardized to mean zero and unit variance (Endler, 1986). A multivariate approach, in which selection gradients rather than univariate selection differentials are estimated, has the advantage that the direct and indirect effects of selection on traits can be teased apart (Lande and Arnold, 1983). However, multivariate analysis is more complicated when fitness is determined by interactions among traits (Brodie III, 1992, 2000). Interaction effects indicate that fitness variation is not merely due to additive effects of single traits, but rather, characters jointly determine fitness and particular trait combinations have higher fitness than others. The correlational selection gradient ( $\gamma$ ) estimates the magnitude of interaction between two traits. The gradient is estimated from a selection model that includes a regression variable which is computed from the product of two traits (Brodie III, 1992; Svensson *et al.*, 2001a).

Schluter (1988) and Schluter and Nychka (1994) have developed techniques to visualize the form of univariate and multivariate selection, respectively. We focus on the multivariate approach, which is relevant for correlational selection. For simplicity, we restrict discussion to two traits ( $x$  and  $y$ -axes) under selection, which are visualized on three-dimensional plots or contour plots with fitness as the  $z$ -axis. It is possible, however, to visualize selection on three traits; interested readers should consult Phillips and Arnold (1989). The multivariate cubic spline (Schluter and Nychka, 1994) is a non-parametric regression technique that aims to find the best fitness surface without *a priori* assumptions about surface topology (eg, it can be linear or non-linear with multiple peaks and valleys). Bivariate fitness surfaces can be parametrized using two linear (directional) selection gradients ( $\beta$ 's), two quadratic (stabilizing or disruptive) selection gradients ( $\alpha$ 's) and a correlational selection gradient between

two traits ( $\gamma$ ) (Phillips and Arnold, 1989). A bivariate fitness surface can take the form of a plane, a saddle with two peaks, a single internal peak, or ridge(s) of high fitness (Phillips and Arnold, 1989). Of the four alternatives, correlational selection is possible whenever there is curvature in the fitness landscape, hence in all cases except a plane (Phillips and Arnold, 1989). Examples of correlational selection (Figures 1 and 2) and selection gradients (Table 1) include escape behaviour and morphology of garter snakes (Brodie III, 1992), flight morphology of sparrows (Schluter and Nychka, 1994), floral traits and phenology of orchids (Maad, 2000), germination date and elongation of the velvet leaf (Weinig, 2000), and our studies of clutch size, egg mass, immunocompetence, and lay date of female lizard morphs (Sinervo, 2000; Sinervo *et al.*, 2000b; Svensson and Sinervo, 2000; Svensson *et al.*, 2001a).

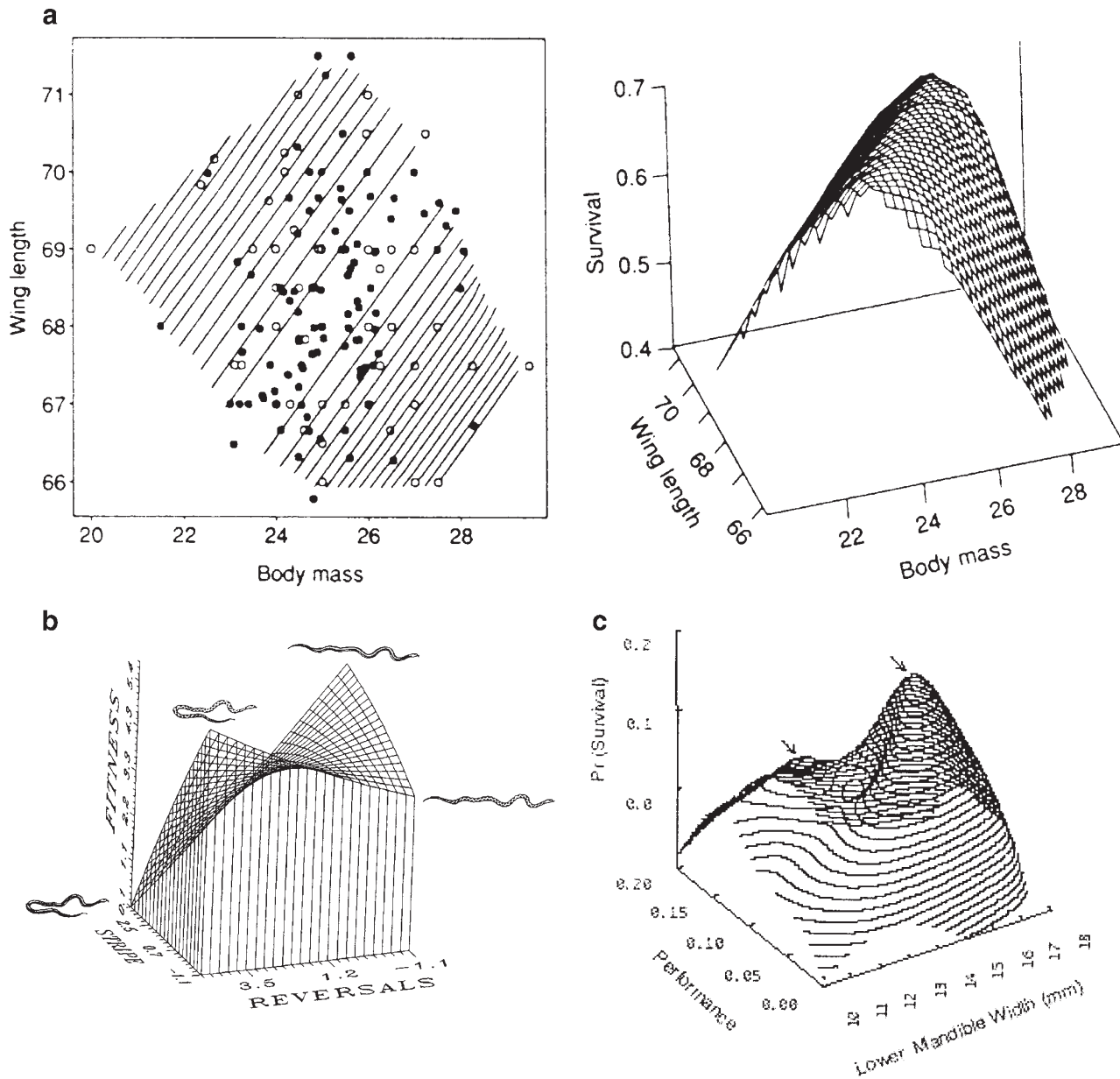
In cases where correlational selection favours different trait values in two or more discrete morphs (see below), correlational selection arises from directional selection within each morph towards alternative optima (Figures 1 and 2). Morphotypic correlational selection is analyzed with analysis of covariance, which estimates differences in the slope of fitness functions ( $\beta$ 's) between morphs (Sinervo *et al.*, 2000b; Svensson *et al.*, 2001a). Even though morph variation is discrete it can become correlated with continuous traits through some kind of fitness interaction.

#### Correlational selection, evolution of discrete morphs, and tradeoffs

What is a morph? A simple adaptational definition of morphs includes the fitness surfaces that either produced the morphs or the surfaces that serve to maintain or refine them. Morphological differences *per se* are not necessary under this process-oriented definition of morphs. Morphs are the byproduct of multivariate disruptive natural selection. Adaptational analysis aimed at identifying and describing morphs should focus on the disruptive selection or the multiple fitness peaks on adaptive landscapes (Wright, 1932; Whitlock *et al.*, 1995).

Visualizing correlational selection on morphs therefore requires a description of how natural or sexual selection operates on the different types. Alleles underlying the expression of phenotypic traits are differentially sequestered into the morphs (see next section). In the case of multivariate selection, coadapted suites of traits of the morphs are refined along performance or life history tradeoffs. Tradeoffs were undoubtedly present before the origin of the morphs, perhaps owing to pleiotropy. Once morphs arise they evolve to peaks on opposite sides of the adaptive surface and morph divergence occurs along genetic constraints imposed by tradeoffs.

For example, the disruptive surface acting on female side-blotched lizards is aligned along the trade-off between clutch size and egg mass (Figure 2a, b). Orange-throated females are selected to lay large clutches of small eggs while yellow-throated females are selected to lay small clutches of large eggs (Sinervo *et al.*, 2000b) (Figure 2c). In male morphs, rock-paper-scissors strategies are involved in signaling and physiological tradeoffs that arises from plasma testosterone (Sinervo *et al.*, 2000a), and also space use tradeoffs of mate acquisition balanced against paternity assurance (Sinervo and Lively, 1996; Zamudio and Sinervo, 2000). Orange males (rock)



**Figure 1** Forms of multivariate selection on continuous traits that can promote correlational selection. (a) Survival selection on body mass and wing length takes the form of a ridge of high fitness on 2d and 3d plots (alive – solid, dead – open; from Schluter and Nychka, 1994). (b) Survival selection on behaviour (number of reversals during escape) and dorsal pattern in garter snakes takes the form of a fitness saddle with peaks of high fitness in opposite corners (blotched snakes that reverse often and striped snakes with no reversals; from Brodie, 1992). Correlational selection has been measured on garter snakes (see Table 1). (c) Survival selection on bill morphs and feeding performance of African seed crackers could promote correlational selection owing to two fitness peaks present on the fitness landscape (from Smith and Girman, 2000).

beat blue males (scissors) with a high stamina and aggressive strategy. Orange is a badge of status (Parker and Rubenstein, 1981; Calsbeek *et al*, 2001; Calsbeek and Sinervo, 2001) used to intimidate blue-throated neighbours. When honest signaling evolves between such intended receivers, it can be exploited by unintended receivers, such as by the female-mimicking yellow males (paper). Yellow males parasitize copulations from females on an orange male's territory, but blue males can thwart the yellow strategy by mate guarding females on their territory (Zamudio and Sinervo, 2000).

Correlational selection acting on trait complexes of other species involves tradeoffs. In garter snakes, striped and blotched morphs may exploit alternative sides of perceptual trade-offs faced by predators: the ability to follow rapidly moving and reversing prey with stripes versus cryptically blotched prey that are stationary (Brodie III, 1992) (Figure 1B). Correlational selection on bill size, morphology and feeding performance of African seed cracker morphs is constrained by performance tradeoffs of efficient handling time on small seeds versus seed-cracking ability on large seeds (Smith and Girman, 2000)

**Table 1** Examples of correlational selection gradients ( $\gamma$ 's) that have been estimated in natural populations of two animals and two plants. The list is not exhaustive

Organism	Traits	$\gamma$	Source
Garter snake <i>Thamnophis ordinoides</i>	Colour patterns and escape performance	-0.268 -0.230	(Brodie III, 1992)
Side-blotched lizard <i>Uta stansburiana</i>	Throat colour and immunocompetence	-0.365	(Svensson <i>et al.</i> , 2001a)
	Throat colour and clutch size on survival of first clutch progeny to maturity	0.397	(Sinervo <i>et al.</i> , 2000b)
	Throat colour and egg mass on survival of later clutches to maturity	-0.487	(Sinervo <i>et al.</i> , 2000b)
	Clutch size and egg mass on survival of first clutch progeny to maturity	-0.306	(Sinervo <i>et al.</i> , 2000b)
	Clutch size and egg mass on survival of female parent to second clutch	-0.261	(Sinervo, 2000)
Orchid <i>Platanthera bifolia</i>	Phenology and flower characters	-0.251 -0.301	(Maad, 2000)
Velvetleaf <i>Abutilon theophrasti</i>	Germination date and timing of elongation	-0.140 -0.170	(Weinig, 2000)

(Figure 1c). Song sparrow flight is constrained by the allometry of wing loading and flight performance (Schluter and Nychka, 1994) (Figure 1a).

### The genetical causes of correlational selection

The potential for tradeoffs hints at the involvement of pleiotropy in generating conditions for correlational selection surfaces. Experimental manipulations of side-blotched lizards indicate that pleiotropy is an important component of correlational selection on side-blotched lizard morphs (Sinervo, 2000; Sinervo *et al.*, 2000b; Svensson *et al.*, 2002). Even in the absence of pleiotropy, natural selection can generate linkage disequilibrium between alleles at separate loci thereby forming a genetic correlation (Endler, 1986; Lynch and Walsh, 1998). Recombination and segregation should reduce most linkage disequilibria within a few generations (Falconer and Mackay, 1996; Futuyma, 1998). Nevertheless, if correlational selection is strong and chronic, substantial linkage disequilibrium can be maintained owing to a balance between recombination, segregation and selection (Hartl and Clark, 1997; Lynch and Walsh, 1998). Thus, correlational selection favours trait combinations that couple underlying alleles at loci. Recombination and segregation erode these effects. In the case of disruptive selection associated with a fitness saddle, disequilibrium is proportional to the depth of the fitness valley. In the univariate case, genetic variance of the population reaches its maximum when the population mean straddles two fitness peaks (Kirkpatrick, 1982a). Morphs of side-blotched lizards reflect such a situation.

At equilibrium, a segregational and recombinational load arises from newly produced progeny phenotypes that are found in the fitness valley at the beginning of every generation. Segregational and recombinational load can be ameliorated if loci are located on the same chromosome and are closely linked (Hurst, 1999). Segregational and recombinational load can be reduced through tight physical linkage, as in pin-and-thrum floral morphologies of *Primula*, a distylous plant (Ford, 1975), or, if loci are further apart on chromosomes, recombination suppression can evolve by chromosomal inversions as typified by the supergenes of *Drosophila* (Dobzhansky,

1970). Alternatively, modifier loci may be selected for which ensure that the optimal trait combinations favoured by correlational selection are expressed in different morphs (c.f. the evolution of allelic dominance through modifiers; Otto and Bourguet, 1999).

Charlesworth and Charlesworth (1975) modeled evolution of supergenes in the context of aposematic mimicry among species of butterflies, but such mechanisms should be general for all morphs. First, traits could originate from a mutation in a regulatory locus of major effect thereby producing a 'hopeful monster' (Goldschmidt, 1940). Subsequently, modifier loci that improve resemblance to the model species are recruited into a supergene. If, by chance, loci happened to be on the same chromosome, only minor recombination suppression would be required to build a supergene (eg, centromeric inversion). Alternatively, favourable mutations at loci on separate chromosomes could be translocated to a single linkage group with recombination suppression evolving later. Charlesworth and Charlesworth (1975) argued that selection favouring mimicry was not strong enough to generate supergenes through such rare events as translocations. (N.B., Subsequent empirical analysis indicates that selection on mimicry and colour patterns is very strong (Mallet and Barton, 1989).) Furthermore, physical linkage is less likely when many loci are involved in the trait complex (eg, wing colour analoga of butterflies; Brakefield *et al.*, 1996). Thus, Charlesworth and Charlesworth (1975) concluded that the most plausible explanation of supergenes was a gene of major effect that was subsequently joined by modifier loci on the same chromosome.

### Supergenes, fitness epistasis, and the origin of morphs

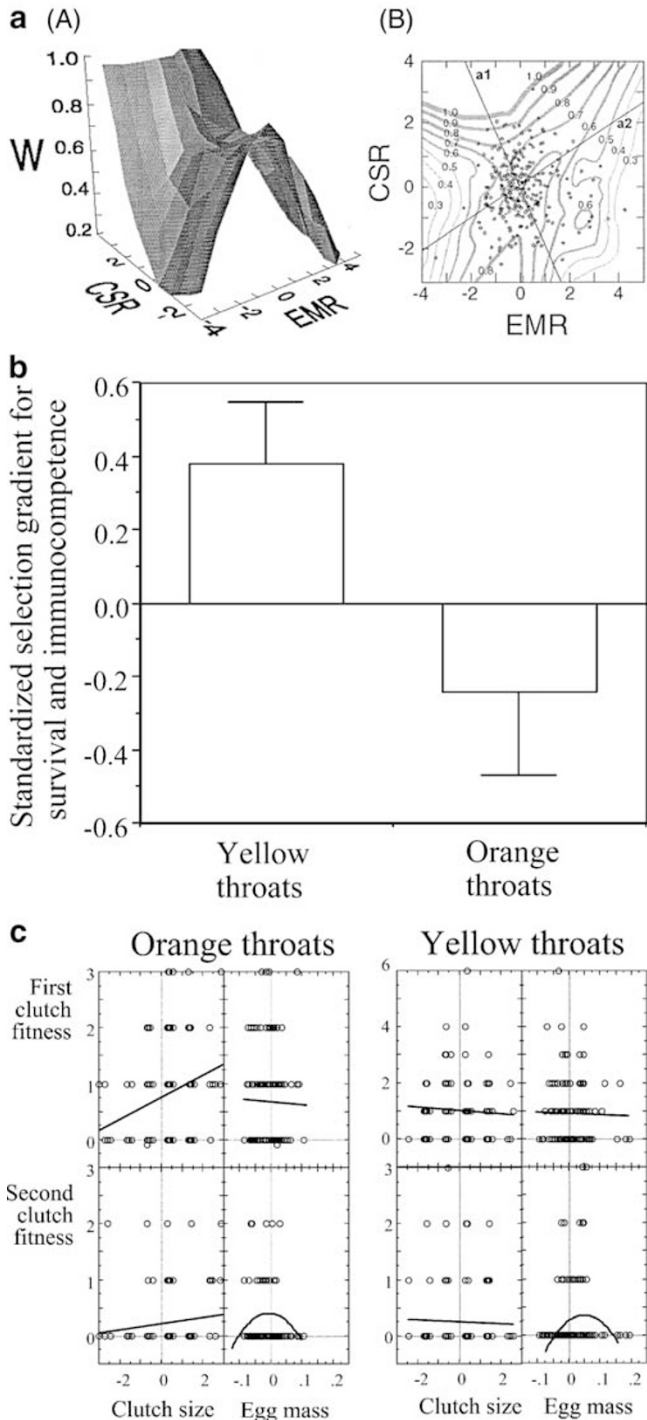
Genes governing hormonal regulation are likely candidates for genes of major effect, owing to the potential for pleiotropic and epistatic effects of hormones on colour, behaviour, physiology and life-history traits (Ketterson and Nolan, 1992; Sinervo and Basolo, 1996; Voss and Shaffer, 1997; Moore *et al.*, 1998; Nijhout and Emlen, 1998; Zera *et al.*, 1998; Svensson *et al.*, 2002). Interestingly, selection for tame behaviour during domestication often leads to correlated responses of colour, hormone profiles and

reproductive traits (Belyaev, 1979). Genomic mapping of floral colour variation indicates that a few genes of major effect contribute disproportionately to phenotypic variation (Schemske and Bradshaw, 1999). Hence, colour patterns may be governed by a few major genes and are often genetically correlated with other traits.

In the case of side-blotched lizards, strong negative genetic correlations among orange, blue, and yellow colours (Table 2), suggests that colours segregate as a single genetic factor, perhaps a supergene (Sinervo *et al*, 2001; Sinervo and Zamudio, 2001). Furthermore, colour

is phenotypically and genetically correlated with many other traits (Sinervo *et al*, 2000b, 2001; Sinervo and Zamudio, 2001; Svensson *et al*, 2001a, b, 2002). However, colours expressed by side-blotched lizards arise from completely different physiological mechanisms (Fox, 1976): orange-yellow colour is due to carotenoid metabolism and blue is due to structural pigments. Given the sheer number of genetically-correlated traits of the lizard morphs and the different mechanisms by which yellow-orange and blue colour are determined, it seems unlikely that all morph variation is due to a single 'morph' locus. Many loci are likely to govern the manifold effects on life history, physiology, morphology, and behaviour. This is more likely given that side-blotched lizards have 20 chromosomes. On the other hand, the Charlesworths' model for the evolution of large co-adapted gene complexes may apply in part to this system, particularly since colour variation is governed by hormone regulation. In particular, orange-yellow colour is activated by progesterone in lizards (Cooper and Greenberg, 1992), while blue colour is related to testosterone (Hews *et al*, 1994; Hews and Moore, 1995). A single endocrine gene controlling progesterone conversion into testosterone (eg, an aromatase) may regulate orange-blue-yellow (OBY) colour expression and have cascading pleiotropic and epistatic effects on behaviour and life history traits. Thus, fitness epistasis associated with correlational selection may arise in part from physiological epistasis between a morph locus of major effect and other endocrine loci that regulate expression of behaviour and life history traits.

When the throat colour locus and quantitative trait loci (QTL) of side-blotched lizards are mapped, we will be able to evaluate the validity of the Charlesworths' model in the *Uta* system. Preliminary mapping studies using nine nuclear microsatellite loci suggest that eight of the nine are coupled to throat colour by strong linkage disequilibrium (Sinervo and Clobert, unpublished data). Thus, by this estimate, the OBY locus involves 81% of all loci in genome-wide epistasis. Recent QTL-studies on pea aphids and sticklebacks have mapped functionally important loci (Hawthorne and Via, 2001; Peichel *et al*, 2002). Both studies indicate a role for genes of major effect and found that functionally integrated traits were governed by a few pleiotropic loci, or a few tightly linked loci, consistent with our model for the evolution of co-adapted trait complexes.



**Figure 2** Forms of correlational selection on side-blotch lizards include: (a) continuous traits and (b–c) discrete morphs with continuous traits. (a) Survival selection on adult females from the 1st to the 2nd clutch is disruptive on clutch mass and stabilizing on egg mass. Correlational selection favours certain combinations of clutch-size and egg-mass (residuals computed about the trade-off between clutch size and egg mass; from Sinervo, 2000). (b) Survival selection on immunocompetence during the same episode. Yellow females with high immunocompetence survive best while orange females with low immunocompetence survive best (from Svensson *et al*, 2000a). (c) Progeny recruited by female colour morphs as a function of life history traits. The difference in selection on the clutch size of orange and yellow females was significant during the first clutch. The difference in selection on optimum egg size of orange and yellow females was significant during the later clutches (from Sinervo *et al*, 2000b). See Table 1 for  $\gamma$  estimates.

**Table 2** Heritability and genetic correlations for various life history and morphological traits that we have measured in free-ranging side-blotched lizards and in controlled laboratory crosses. See Sinervo *et al.* (2001) for further details on additive regression models of colour expression

Trait(s)	Familial relationship	Genetic parameter	Source
Clutch size	Mother-daughter	$h^2 = 0.62$	(Sinervo, 2000)
Egg mass	Mother-daughter	$h^2 = 0.58$	(Sinervo, 2000)
Immunocompetence (Antibody responsiveness)	Mother-daughter	$h^2 = 0.88$	(Svensson <i>et al.</i> , 2001b)
Clutch size and egg mass	Mother-daughter	$G = -0.92$	(Sinervo 2000)
Orange colour (yellow, blue = 0, orange = 1)	Mother-daughter	$h^2 = 0.48$	(Sinervo <i>et al.</i> , 2000b)
Orange colour and clutch size	Mother-daughter	$G = 1.09$	(Sinervo <i>et al.</i> , 2000b)
Throat colour and egg mass	Mother-daughter	$G = -0.84$	(Sinervo <i>et al.</i> , 2000b)
Throat colour and immunocompetence	Mother-daughter	$G = -1.36$	(Svensson <i>et al.</i> , 2001b)
Orange colour in DNA paternity-based pedigrees in the wild	Sire-progeny – son	$h^2 = 1.24$	(Sinervo and Zamudio, 2001)
	Sire-progeny – daughter	$h^2 = 0.88$	
Orange colour scale in lab crosses with field release of progeny	Sire-progeny	$h^2 = 1.06$	(Sinervo <i>et al.</i> , 2001)
	Dam-progeny	$h^2 = 0.86$	
Blue colour scale in lab crosses with field release of progeny (yellow, orange = 0, blue=1)	Sire-progeny	$h^2 = 1.40$	(Sinervo <i>et al.</i> , 2001)
Score on orange scale and score on blue scale	Sire-progeny	$G = -1.01$	(Sinervo <i>et al.</i> , 2001)

## Ecological causes, genetic cycles, and the Red Queen

Correlational selection arises often, if not always, through frequency-dependent interactions between predators and prey, hosts and parasites or conspecifics competing over food resources or mates. Therefore, understanding the ecological causes of selection (Wade and Kalisz, 1990) is necessary to elucidate the origin and maintenance of correlational selection. The biotic environment is a 'moving target' to which organisms adapt. This process was first termed 'The Red Queen' in community ecology by Van Valen (1973) to describe the general belief that organisms are under chronic selective pressure to escape from continually evolving parasites or predators, or in the case of predators and parasites themselves, to exploit evolving hosts or prey. Frequency-dependent selection is an inherent property of Red Queen scenarios. Furthermore, correlational selection on escape behaviour and morphology that is involved in predator-prey dynamics is frequency-dependent because sensory and memory limitations constrain foraging behaviour of predators. Search image of predators promote negative frequency-dependent selection in which rare prey have an advantage (apostatic selection; Dawkins, 1971; Gendron, 1986). The cases of mimicry discussed above involve aposematic selection, which is also frequency-dependent.

Many predators develop a search image for the most common prey and exert apostatic selection on polymorphic prey (Pietrewicz and Kamil, 1979), which should selectively favour the minority prey type. The converse could be also true, in which different morphs in the predators are involved in a frequency-dependent game with their prey. This process leads to a never-ending cycle of adaptation between the predator morphs. Hori (1993) has described an example of frequency-dependent selection involving a scale-eating fish that attacks East African cichlids. The scale-eater attacks the cichlids from behind, either from the left- or the right-hand side. The scale-eater has an asymmetric and discontinuous gape-morphology in that some individuals have a left-facing mouth and attack cichlids from the right-hand side, whereas others have a right-facing mouth and attack cichlids from the

left-hand side. Gape morphology in the scale-eater is heritable and seems to be governed by a Mendelian locus (Hori, 1993). The relative foraging success of the two scale-eater morphs is inversely proportional to frequency because cichlid prey become more wary against attacks from a particular side (right or left). Consequently, the two scale-eating morphs oscillate due to frequency-dependent selection (Hori, 1993).

Red Queen processes are not limited to interspecific interactions, however. Intraspecific arms races between competitors within species are also likely to be common (Rice, 1996; Rice and Holland, 1997). Antagonistic co-evolution between the sexes is a particularly common form of the intra-specific Red Queen, and has been labeled Inter-locus Contest Evolution (ICE) by Rice and Holland (1997). In *Drosophila melanogaster*, males continually adapt to females and evolve toxic seminal fluid proteins to increase mating success in sperm competition, whereas females evolve resistance towards these substances, leading to an evolutionary arms race between the sexes (Rice, 1996). Although Rice and Holland did not explicitly develop this idea, such evolutionary arms races between or within sexes are inherently frequency-dependent. Rare genotypes should experience a minority advantage and rapidly increase in frequency, and subsequently be replaced by other genotypes that exploit a vulnerability of the most common form. It should be quite clear that perpetual antagonistic co-evolution between the sexes is only one special case of intraspecific arms races, and that Red Queen scenarios could also easily arise between different trophic forms (Hori, 1993), sexual and asexual forms (Dybdahl and Lively, 1998) or different morphs within a population (Sinervo and Lively, 1996; Sinervo *et al.*, 2000b).

## Genetical and ecological interactions: self-reinforcing genetic correlations

West-Eberhard (1983) proposed that traits involved in social interactions between or within the sexes should evolve faster than non-social traits; this idea is consistent with the social environment driving evolutionary dynamics of competitors within a species. Consider the cycles

of frequency-dependent selection observed in female and male side-blotched lizards (Sinervo *et al.*, 2000b) (Figure 3). In the female game, orange-throated females are *r*-strategists that produce many small offspring and this strategy has high fitness at low density when the intrinsic rate of growth, *r*, dominates the Lotka-Volterra growth equation. In contrast, yellow-throated females are *K*-strategists that produce a few large offspring and this strategy has high fitness when the population density exceeds the carrying capacity, *K*, and the population crashes in the ensuing generation. After the population crashes to low density the yellow strategy becomes common. These conditions favour orange, which increases in frequency, and the density cycle repeats. Oscillations of density and frequency-dependent selection create a social environment in which chronic selection shapes each strategy. As orange becomes better adapted to recover after a population crash, overshoot of carrying capacity in ensuing generations becomes incrementally greater. Conversely, as yellow becomes better adapted to weathering a population crash, orange females crash to even lower levels in ensuing generations. The cyclical female game recursively refines genetic correlations that contribute to fitness of each evolving morph. As genetic correlation between morph loci and 'strategic' (fitness) loci build, more intense frequency-dependent selection is generated. This further intensifies selection in subsequent generations (Sinervo, 2000; Sinervo *et al.*, 2000b, 2001). This cyclical runaway game has properties that are analogous with runaway sexual selection (see below).

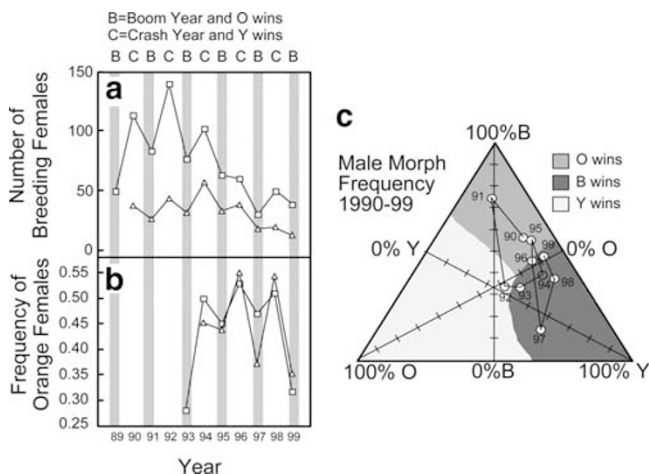
Negative frequency-dependent selection has a key role in the evolution of genomic architecture, apart from its obvious effect in creating and maintaining linkage disequilibria through correlational selection. Frequency-dependent selection could be important in genomic evolution because it will delay fixation of alleles at loci that are subject to strong selection. The maintenance of balanced polymorphisms over an extended period of time through frequency-dependent selection will in turn facilitate indirect selection on modifier (epistatic) alleles to act

over sufficiently long periods of time, rather than being limited to act during the spread of alleles prior to fixation. Frequency-dependent selection might lead to the substitution of alleles with epistatic effects on fitness and thereby reduce segregational load. This could eventually lead to a genetic architecture that allows for the maintenance of multilocus genotypes in sympatry. This view is similar to recent models of evolution of dominance through modifiers (Otto and Bourguet, 1999). In both scenarios, strength of selection favouring modifiers increases when heterozygotes are common (Charlesworth and Charlesworth, 1975; Otto and Bourguet, 1999), which is a property of fluctuating frequency-dependent selection observed in the *Uta* system (Sinervo *et al.*, 2000b).

In addition, random evolutionary forces, such as genetic drift and founder effects, can interact with deterministic forces such as natural selection and result in genetical consequences that would not necessarily be achieved by simple Fisherian mass selection alone (Wright, 1932; Coyne *et al.*, 1997; Wade and Goodnight, 1998). This is evident when animals interact in social neighbourhoods of limited size where sexual selection and natural selection is determined. As animals disperse and settle at reproductive sites, local founder effects displace neighbourhoods from the population-wide frequency. A consequence of random perturbations at a local scale is that no neighbourhood actually attains the equilibrium, even if the population is at equilibrium (Sinervo, 2001b). Such scale-dependent conditions set the stage for chronic frequency-dependent selection of multi-locus genotypes, even when no cycles are present in a species.

Thus, the strength of selection on *Uta* morphs is not merely because the population oscillates but arises as a property of social interactions among local neighbours (Sinervo, 2001a; Sinervo *et al.*, 2001). In both male and female games, fitness is strongly dependent on genotype and on relative frequency of neighbouring genotypes. Small neighbourhood size is an explicit component of our analysis of the frequency-dependence of fitness (Sinervo and Lively, 1996; Sinervo *et al.*, 2000b) and neighbourhood size is built into population genetic models of morph microevolution (Sinervo, 2001a). In these scenarios, local random processes such as meta-population founder effects actually fuel deterministic processes of density and frequency-dependent selection. This generates more linkage disequilibrium in a balance against erosive effects of recombination and segregation, than in a panmictic population (c.f. Lande, 1984). Local subdivision of a meta-population increases inbreeding, lowers effective recombination rate and increases levels of linkage disequilibrium present in each deme (Lande, 1980, 1984; Wade and Goodnight, 1998). Furthermore, small population size enhances probability of peak shifts involved in chromosomal rearrangements of morph supergenes (see above). This view of behavioural evolution by frequency-dependent selection is similar to the shifting balance proposed by Wright (1932). In both models, interactions between local selection and random processes initiate the buildup of co-adapted gene complexes by linkage disequilibrium.

The spatial scale of social neighbourhoods also creates pre-conditions for the origin of morphs. Based on early theory of selection in coarse and fine-grained environments (Levins, 1962a, b), we have predicted that genetic



**Figure 3** (a) Female density and (b) frequency of orange female morphs oscillate synchronously in two demographically-independent populations (squares, triangles). (c) Frequency of male colour morphs from 1990–1999 oscillate with a 5-year periodicity. The frequency of each morph increases from one side (0%) to the opposite vertex (100%).

morphs will be common when the social environment is both temporally and spatially coarse grained (Sinervo, 2001b, Zamudio and Sinervo, 2001). A temporally coarse grained social environment is typical for life histories in which a single or few reproductive season(s) are possible and thus the time to maturity is long relative to reproductive opportunity (eg, salmon (Gross, 1984) or lizards (Sinervo and Lively, 1996)). A spatially coarse-grained social environment is typical where fitness outcomes are contingent upon few social interactors. In contrast, plastically determined morphs will be common in cases when either the spatial or temporal environments are fine-grained. The indeterminate growth of hermaphroditic reef fish leads to fine-grained temporal environment in that individuals experience variation in body size during ontogeny. Given the fitness gains of maleness and femaleness differ with size (Warner, 1984; Warner and Hoffman, 1980), a plastic switch in sex is expected. Furthermore, population size on reefs is often small, social interactions are few, and the social environment is coarse-grained, the situation also favours alternative male strategies of the sneaker and despot. Finally, when both temporal and spatial environments are fine-grained purely plastic strategies are expected to evolve. Future theoretical research should focus on determining how the spatial scale of selection (eg, the role of social neighbourhoods) shapes the evolution of social traits.

## Speciation?

Fisher (1930) formulated a theory of sexual selection that become known as the 'runaway' and which was later elaborated by Lande (1981) and Kirkpatrick (1982b). These models take as their starting point the fact that inter-sexual selection builds a genetic correlation between alleles for female preference and male traits. This correlation is formed by linkage disequilibrium of alleles at female preference and male trait loci, since choosy females will bundle up preference alleles with alleles for male ornamentation (Lande, 1981; Kirkpatrick, 1982b). The genetic correlations between unlinked loci, which are formed during the social runaway selection typified by lizards, build in a fashion analogous to the genetic correlations of runaway sexual selection. The sexually-selected runaway process results from a positive feedback loop between the frequency of alleles for female preference and male traits: as choosy females become common, male traits favoured by these females increase in frequency and vice versa. Hence, male and female traits reinforce each other in a hitch-hiking process, a case of positive frequency-dependent selection. In the case of runaway social games, correlational selection on morphs promotes a recursively refining genetic correlation among the strategic traits that govern the strength of frequency interactions.

To model sexual selection on morphs, we have developed a theory of context-dependent mate choice that is fundamentally different from Fisherian runaway (Alonzo and Sinervo, 2001). Fixed genetic preferences are assumed under runaway, while plastic mate choice is favoured to evolve under context-dependent mate choice. Given oscillations, the future social environment is predictable from the current social environment. A female is strongly favoured to choose mates that maximize progeny fitness, given the context of the progeny's future

social environment. In side-blotched lizards, the fundamental decision rule that is predicted to evolve is to choose a rare sire genotype that maximizes fitness of sons in the context of the male game, or sire genotypes that maximize fitness of daughters in the context of the female density and frequency game (Alonzo and Sinervo, 2001). Females choose mates based on cognitive inputs or physiologically modulated (stress-based) preferences that provide information on the current social environment.

Our initial models of context-dependent mate choice (Alonzo and Sinervo, 2001) did not assume fitness epistasis between morph loci and other traits. Progeny fitness was determined from frequency-dependent gains associated with colour alleles *per se*. An alternative mate-choice theory is to minimize the breakup of co-adapted gene complexes built by correlational selection. Assortative mating of the colour morphs is an obvious solution in such scenarios.

Lande (1984) showed that genetic correlations of large magnitude are facilitated by tight linkage between loci, close inbreeding or assortative mating, and strong selection, whereas in panmictic, randomly mating populations with weak linkage, the genetic correlations are likely to be small. Hence, inbreeding or assortative mating ensure that recombinational or segregational load is minimized and that adaptive genetic correlations can be maintained. Females that mate assortatively ensure that recombinational or segregational load is minimized. Furthermore, assortative mating fuels a buildup of linkage disequilibrium in a sexually-selected runaway process. An obvious end-point to this process would be speciation. Speciation results from fitness epistasis which leads to the buildup of co-adapted gene complexes (Rieseberg *et al*, 1996). In this regard, the co-adapted trait complexes that arise from the evolution of self-reinforcing genetic correlations, may create pre-conditions for speciation. The combined effects of correlational selection and assortative mating favour the buildup and maintenance of linkage disequilibria. Evolution of reproductive isolation is the next critical step. It is noteworthy that side-blotched lizards are basal to the major Sceloporine radiation in western North America and Mexico (Wiens, 2000). An OBY colour locus in a *Uta*-like ancestor may have fueled speciation processes by the combined effects of correlational and frequency-dependent selection on morphs within populations, thereby generating co-adapted gene complexes, a pre-condition for speciation. These scenarios are similar to recent models for sympatric speciation (Dieckmann and Doebeli, 1999); in both cases speciation starts with a buildup of co-adaptive gene complexes within populations, followed by assortative mating and reproductive isolation. Thus, co-adapted gene complexes in *Uta* morphs may be the first step in the causal chain of events that lead to speciation. It is also noteworthy that the African Cichlid radiation includes sibling species with alternative colour types, and that some species are also polymorphic for colour (Seehausen *et al*, 1999). We suggest that cichlid speciation may have taken place by the mechanisms of frequency-dependent correlational selection outlined above. The generality of these ideas will become clear only after we determine whether scale-dependent frequency selection is common in other species. This is obviously the case for African cichlids, which are territorial and restricted to small populations on reefs, and for lizards, which are also terri-



torial. It is perhaps no coincidence coarse-grained social environments are associated with morphotypic variation in both groups. Perhaps these forces have contributed to their speciation.

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