The Developmental, Physiological, Neural and Genetical Causes and Consequences of Frequency-Dependent Selection in the Wild

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Key Words

cognition, correlational selection, interspecific interactions, intraspecific, perception, rock-paper-scissors

Abstract

We outline roles of frequency-dependent selection (FDS) in coadaptation and coevolutionary change. Coadaptation and coevolution occur because correlational selection (CS) and correlated evolution couple many traits. CS arises from causal interactions between traits expressed in two or more interactors, which invariably involve different traits (signalers-receivers). Thus, the causes of CS are due to FDS acting on trait interactions. Negative FDS, a rare advantage, is often coupled to positive FDS generating complex dynamics and FD cycles. Neural mechanisms of learning and perception create analogous routes by which traits are reinforced in cognitive and perceptual systems of interactors, substituting for positive FDS. FDS across all levels of biological organization is thus best understood as proximate causes that link interactors and shape genetic correlations within and among interactors on long timescales, or cognitive trait correlations within interactors on short timescales. We find rock-paper-scissors dynamics are common in nature.

INTRODUCTION

We address causes and consequences of frequency-dependent selection (FDS) in nature. All forms of FDS arise from biotic interactions, therefore, FDS is involved in coevolutionary interactions, including those acting on clones, mating systems, social systems, and ecosystems. FDS links causes intrinsic to interactors with causes extrinsic to interactors in a parsimonious fashion, thereby bridging what Mayr (1993) refers to as proximate and ultimate causation.

We highlight FDS in mating systems, given well-characterized genetics and methods (i.e., payoff matrix) for diagnosing forms of FDS. Analysis of clonal prokaryotes requires pinpointing single base-pair changes that alter invasion dynamics (Elena & Lenski 1997, Remold & Lenski 2004). Molecular change is difficult to track in the context of confounding macroscopic effects of natural systems. For this reason, causes of FDS in clonal prokaryotes are best studied in laboratory settings and we review a few of these studies. We also link higher levels of biotic interactions, such as ecosystems, with a set of principles for positive and negative FDS caused by either genetic changes of Darwinian evolution or memetic changes of cultural evolution.

Characterizing FDS requires analysis of how relative or absolute frequency (e.g., density) of one form, arising from genetic or memetic causes, impacts fitness of other interactors. Fitness gains of replicators, copies of single alleles, often come at the expense of the fitness of individual phenotypes in which replicators reside (Nowak & Sigmund 2004). Thus, elucidation of frequency-dependent (FD) causes are intimately related to levels of selection such as genic, individual, kin, group, and species as well as concepts of altruism, antagonism, and mutualism (Hamilton 1964).

FD causes arise from proximate interactions of traits between interactors. Because traits need not be the same between interactors and often involve different traits for obvious reasons in signaler-receiver interactions, the proximate causes of FDS will generate correlational selection (CS) within individuals (Brodie 1992, Chevrud 1984, Sinervo & Svensson 2002) as well as between individuals (Sinervo & Clobert 2003). CS couples the fates of multiple traits and their underlying genetic or memetic control in a nonlinear fashion, generating correlations at the level of genotype and/or memotype where none existed before.

Given that underlying causes of trait interactions involve behavior or physiology, our pursuit of FD causes delves into neural processes such as perception and learning, the routes by which interactors interpret extrinsic biotic environments, comprised of interactors. Likewise, at a molecular level, consideration of physiology is required to understand how interactions arise in clonal, floral, fungal, and ecosystem dynamics. Physiological causes homologize with neural processes in that molecule and molecular action under FDS are parallel to signaler-receiver interactions. Consideration of behavior and physiology allows generalizations to be made at all biological levels of organization, unifying FD causes and the ultimate consequences of FDS such as CS that drives intraspecific coadaptation or interspecies coevolution.

THE FORMS OF FREQUENCY-DEPENDENT SELECTION AND NATURAL SELECTION

We begin our discussion by defining and referencing forms of FDS to forms of natural selection. Conceptual understanding of the causes of selection (Bock 1977, Lande & Arnold 1983, Wade & Kalisz 1990) has been advanced via a multivariate treatment of traits and cascading effects on fitness (Lande & Arnold 1983). Phenotypic selection analysis decomposes fitness into directional, stabilizing, and disruptive components. CS gradients, which describe synergisms among phenotypic traits, are added to multitrait models (Brodie 1992, Chevrud 1984, Lande & Arnold 1983, Sinervo & Svensson 2002). In the case of mating interactions, CS is substituted by special forms of assortative or dissassortative mating, the nonrandom union of gametes driven by phenotypic traits of signalers and receivers.

These key generalizations, homologies among CS on traits within individuals, CS on traits between individuals, and special forms of CS due to nonrandom mating (sexual selection), will be useful in generalizing FDS to ecosystem interactions. We generalize relations further by noting that social causes of CS and FDS, social selection, arise from trait interactions between individuals, even though efforts to date have ignored CS on traits between individuals (but see Sinervo & Clobert 2003), other than the case of nonrandom mating. This is because a focus on individual selection defines the unit of selection as phenotype, but in FDS the unit of selection is interaction and its effects on phenotype(s). CS on traits between individuals drives coadaptation of trait combinations within species and coevolution between species. CS shapes and intensifies tradeoffs linking multivariate suites of traits (**Figure 1**), which reinforces and refines the FDS acting on subsequent generations. Tradeoffs are implicit to CS and FDS and we point out key tradeoffs.

The CS gradient, which acts on two or more traits, is a higher order description of stabilizing or disruptive selection on a single trait. Forms of FD nonrandom mating arise from either linear or quadratic interactions of two or more traits. Sexual selection generates CS between the sexes via mate preference and within the sexes due to mate competition (McGlothlin et al. 2005) or male cooperation (Sinervo & Clobert 2003). Forms of FD mate success that preserve diversity are possible (termed balancing selection, see Hedrick this volume), including forms associated with the major histocompatibility complex (MHC) of vertebrates, analogues in invertebrates, in which diversifying selection favors mate preference for nonself (Aeschlimann et al. 2003, Grosberg & Hart 2000, Landry et al. 2001, Potts et al. 1991, Reusch et al. 2001) or self-incompatibility systems of plants (Weller & Sakai 1999). Other forms of nonrandom mating based on MHC exert stabilizing selection, in which self-mate preference may arise at contact zones where hybrid unfitness promotes evolution of premating isolation (Howard 1999).

Forms of FDS in predator-prey interactions are referred to as apostatic and antiapostatic selection. Apostatic selection, a rare morph advantage, reflects negative FDS. In other contexts, negative FDS can arise from self-poisoning effects of common forms. Antiapostatic selection, a common morph advantage, reflects positive

Social selection: a form of FDS in which mating or social systems are coupled via signaler and receiver coevolution

MHC: major histocampatibility complex

Apostatic selection: a form of FDS in which rare types have advantages during positive and negative reinforcement of predator-prey detection and learning

Antiapostatic selection: a form of FDS in which the common type has advantages during positive and negative reinforcement of predator-prey detection and learning

a

b

c

d

e

f
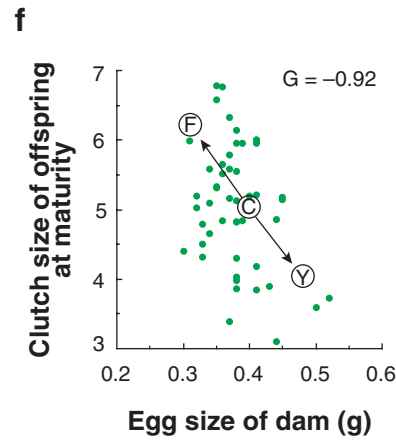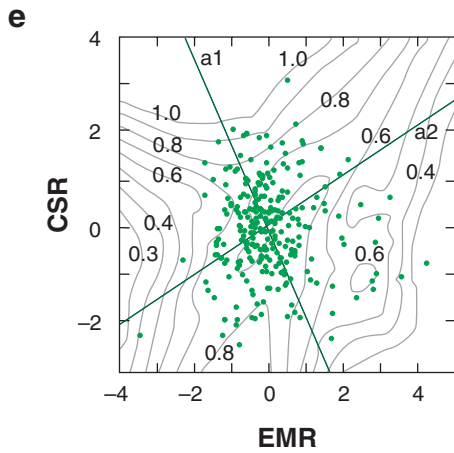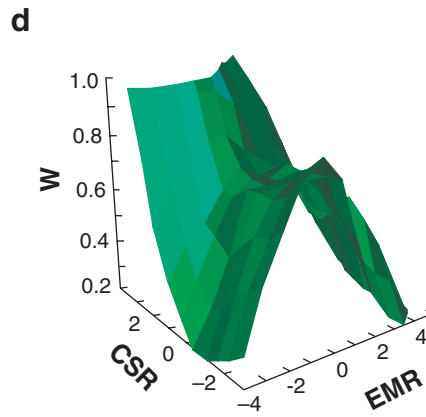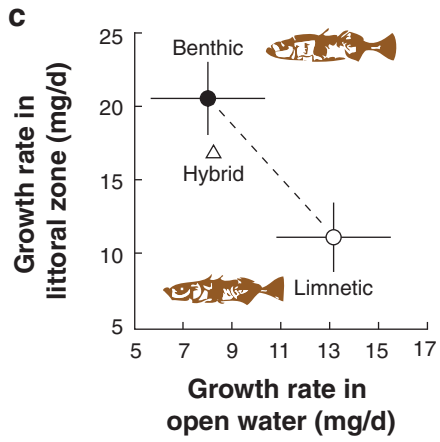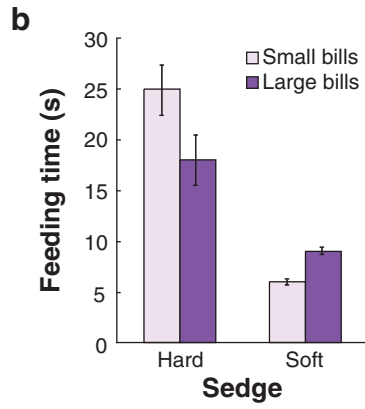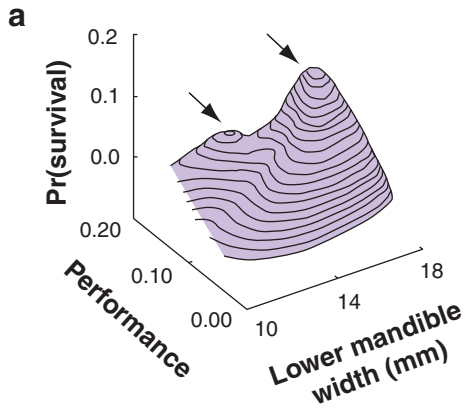
FDS. Positive FDS can be due to Allee effects (Greene & Stamps 2001) in which rarity limits and high density permits interaction, or from aposematic effects where aggregations enhance fitness (Endler & Mappes 2004).

Distinctions between positive and negative FDS can be further subdivided into open-ended versus closed outcomes (cycles: discussed below). Open-ended positive FDS moves trait distributions rapidly in one concerted direction; higher frequencies of traits enhance change in subsequent generations. Depletion of genetic variation places ultimate limits on such processes. Open-ended positive FDS does not arise from unity of FD cause acting on distributions of single traits, but from unity of FD cause that shapes trait frequency distributions in two interactors (signaler-receiver) or, more generally, from any interaction force that links interactors.

The distinction is made clear by Fisherian runaway sexual selection (Fisher 1930), the most celebrated example of open-ended positive FDS (see Kokko et al., this volume). Mate preference for traits in the opposite sex generates positive feedback on genetic correlations. The proximate cause of this runaway is thought to be open-ended perceptual mapping of preference and preferred traits (Lande 1981). Positive FDS occurs because of this invariance of signaler-receiver relations that link preferences and preferred traits. In contrast, balancing selection at the MHC arises from negative FDS in which rare progeny genotypes are advantageous in the context of disease resistance (Reusch et al. 2001), an open-ended diversity-generating mechanism.

Red Queen dynamics: (van Valen 1976) coevolutionary inter- or intraspecific interactions that arise from FDS and generate never-ending cycles of adaptation and counter adaptation

CYCLES AND NEGATIVE FREQUENCY-DEPENDENT SELECTION BETWEEN THE SEXES

Other forms of sexual selection involve evolutionary cycles and Red Queen dynamics. Interlocus sexual conflict, for example, arises when traits have alternative fitness optima in the sexes (Rice & Chippindale 2001). Alleles that move one sex toward one optimum moves the other sex away; this is a rare advantage of strategy and counterstrategy.

Figure 1

(*a*) Survival selection on bill morphology and feeding performance of African seed crackers, *Pyrenestes ostrinus*, will promote correlational selection and alternative fitness peaks (Smith & Girman 2000). (*b*) Tradeoffs in handling time of hard and soft seeds from the sedge *Scleria verrucosa* as a function of bill morph (**Table 1**, Smith 1993). Distribution of seeds varies with rainfall. The tradeoff plays an important role in maintaining the bill polymorphism (with permission from T.B. Smith). (*c*) Tradeoffs in growth of limnetic, benthic, and hybrid forms of the stickleback, *Gasterosteus* spp. in two different habitats (from Schluter 1995). (*d*, *e*) Fitness surface and contour plot of survival of adult female side-blotched lizards, *Uta stansburiana*, from first to second clutch (residuals after removing year are depicted). Disruptive selection on clutch mass and stabilizing selection on egg mass shape a tradeoff between clutch size and egg mass. (*f*) Negative correlation of daughter's clutch size and dam's egg mass is indicative of a genetic correlation (G = –0.92, Sinervo et al. 2000a). Experiments (follicle stimulating hormone [F], follicle ablation [Y], relative to controls [C]) elucidate the physiological basis of the tradeoff.

Sequestering genes on sex chromosomes, evolving sex-specific modifiers or sex steroid control of traits (Rice 1984) can ameliorate such cyclical FDS. Experiments on *Drosophila* supports the importance of X chromosomes for harboring sexually antagonistic variation, given that in each generation two copies are under selection in females whereas only a single copy is under selection in males (Gibson et al. 2002). Thus, sexually antagonistic selection may explain a large proportion of traits that are sexually dimorphic, if dimorphism evolves to limit sex specific costs of sexually antagonistic alleles (Rice 1984). However, sex limitation (dimorphism) of traits may rely on the evolution of modifiers to alter expression of traits initially expressed in both sexes.

Moreover, some sex-limited traits are thought to promote sexual conflict. For example, in *Drosophila* seminal fluid proteins are hypothesized to reduce female remating rates and enhance paternity assurance (Rice 2000). Physiologically naïve females, which have been selected under monogyny and thus not previously exposed to male strains that have evolved under polygyny, suffer higher rates of mortality when mated to polygamous strains compared with polyandrous females that have evolved under polygyny (Holland & Rice 1999). Evolved female resistance to male proteins may be countered by increased efficiency of seminal fluid proteins.

THREE-PLAYER MATING SYSTEM DYNAMICS

Much generalization is afforded from a study of FD mating systems in which genetics of alternative strategies have been elucidated. In mating systems analysis, we highlight the role of CS between individuals in shaping FD interactions (**Figure 2**, and see the **Figure 2** Supplementary Materials; follow the Supplemental Material link from the Annual Reviews home page at **http://www.annualreviews.org/**). Trimorphisms are common in animal and plant mating systems. We argue that mating systems with dimorphisms, sexual dimorphisms included, involve similar forces of FDS, but a reduced subset of those acting in trimorphic mating systems. In animal mating systems, spatial tradeoffs associated with territoriality (despotic strategy) are counterbalanced by paternity assurance afforded by mate guarding (Sinervo & Svensson 2002). Mating system tradeoffs exert survival costs thereby invoking life history tradeoffs. Tradeoffs of social interactions (Sinervo et al. 2006b) generate a third axis along which CS acts. Trimorphic mating systems exhibit sets of multivariate tradeoffs that sustain CS. Increased dimensionality in tradeoffs, such as in mating systems that involve life history tradeoffs, sexually-selected tradeoffs, and socially-selected tradeoffs provide enough dimensionality to sustain cyclical dynamics such as the rock-paper-scissors dynamic.

The trimorphism referred to as the rock-paper-scissors game (RPS) (Maynard Smith 1982) is named for intransitive fitness interactions in which rock beats scissors, paper beats rock, and scissors beats paper. In each pair wise interaction, players are involved in negative FDS of their own type that enhances fitness of another type. However, RPS cycles in biological systems may necessarily involve positive FDS within forms (Sinervo et al. 2006b). When mixtures of negative and positive FDS interact, a system can become destabilized and oscillate. Forces of positive FDS

cause RPS cycles to spiral outward from the attractor, whereas forces of negative FDS cause the RPS to spiral inwards from the absorbing boundaries and toward the attractor.

The simplicity of the lizard RPS mating system (**Figure 2**) also involves complex dynamics of female morphs that sustain density cycles via female life history tradeoffs (**Figure 1**). FDS on female morphs have been addressed with experimental manipulations on large-scale plots of both morph allele frequency and egg-size phenotype frequency (Sinervo et al. 2000a, 2001). Experiments are critical in elucidating causes of FDS and CS (Sinervo & Basolo 1996) and in elucidating the proximate causes of genetic correlations underlying tradeoffs (**Figure 1E**, **F**).

In other mating systems, pure apostasis among three forms is common. For example, trimorphisms of female damselflies found in Europe and North America are maintained by pure apostasis among three female morphs based on equations for FD fitness gains of the damselfly *Ischnura elegans* (Svensson et al. 2005), which we have re-expressed as a payoff matrix (**Figure 2**). Apostatic FDS is thought to arise from search image formation in males for common female morphs (Fincke 2004). Given intense sexual conflict arising from male harassment, rare cryptic female morphs gain higher fecundity, thus involving previously discussed tradeoffs for costs of reproduction, fecundity, polyandry, and sexually antagonistic selection owing to polygyny.

Complex dynamics involving both negative and positive FDS (**Figure 2**) are also exhibited by the marine isopod *Paracerceis sculpta* (Shuster & Wade 1991a,b). Apostatic (female mimic or cryptic) male mating strategies can invade despotic male strategies that guard female harems, however, invasion is synergistically dependent on density of female harems and negative FDS acting on male strategies. Reanalysis of data (Shuster & Wade 1991a) in the form of a payoff matrix (**Figure 2**) indicates that stability of the system is in part determined by apostatic selection.

A tristylous arrangement of anthers and styles in some plant mating systems (Barrett et al. 2004) is thought to promote outcrossing (Eckert et al. 1996), because the rare anther form more efficiently transfers pollen to common stigma types (Oneil & Schmitt 1993). This negative FDS is often not strong enough to preserve all three types and many populations are fixed for combinations of dystyly, a response to genetic drift or founder events (Eckert & Barrett 1992, Eckert et al. 1996, Husband & Barrett 1992). However, reanalysis of frequency and fitness data from Ågren & Ericson (1996) in the form of a payoff matrix (**Figure 2d**) indicates that stability of tristyly in *Lythrum salicaria* arises from more complex FD epistatic interactions (and three-way interactions) among plants and their neighbors (**Figure 2d**, *right panel*), not merely a rare advantage.

ESS analyses (**Figure 2**) indicate that three of the four mating systems exhibit RPS fitness intransitivity, which was first characterized in nature for lizards (Sinervo & Lively 1996). In **Figure 2**, we define evolutionarily stable strategy (ESS) conditions for an apostatic RPS, based on the damselfly mating system:
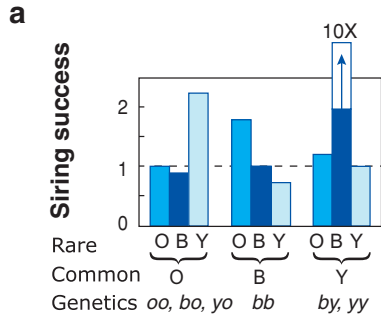
$$\text{WIO, A} > \text{WI, A} > \text{WA, A, WA, I} > \text{WIO, I} > \text{WI, I} \quad \text{and}$$
$$\text{WI, IO} > \text{WA, IO} > \text{WIO, IO.} \qquad\qquad 1.$$

Evolutionarily stable strategy (ESS) analysis: (Maynard Smith 1982) used to analyze the invasion conditions of forms. Often, systems exhibit ESStates of many interactors and cyclical dynamics, maintained by interplay of negative and positive FDS
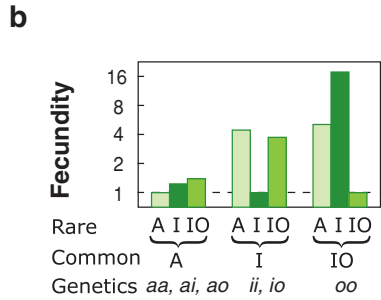
Payoff matrix

a
Siring success

Rare	O B Y	O B Y	O B Y
Common	O	B	Y
Genetics	oo, bo, yo	bb	by, yy

b
Fecundity

Rare	A I IO	A I IO	A I IO
Common	A	I	IO
Genetics	aa, ai, ao	ii, io	oo

c
Siring success

Rare	α β γ	α β γ	α β γ
Common	α	β	γ
Genetics	αα	ββ,βα,βγ	γγ, γα

d
Seed set

2.2X   1.7X

Rare	L M S	L M S	L M S
Common	L	M	S
Genetics	ssmm	ssMm ssMM	SsMM SsMm

Evolutionary dynamic
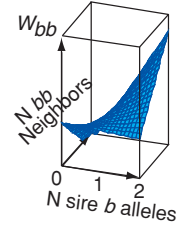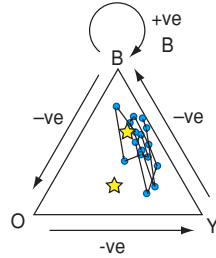
True RPS:
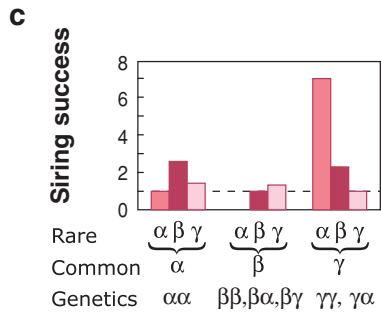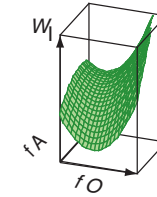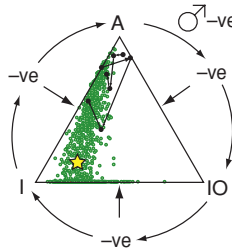
Apostatic RPS:

True & apostatic RPS:
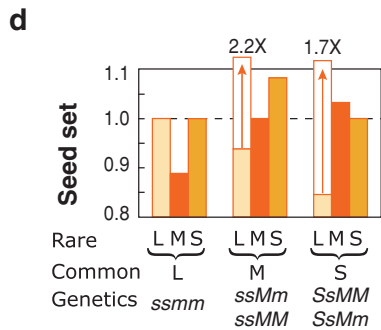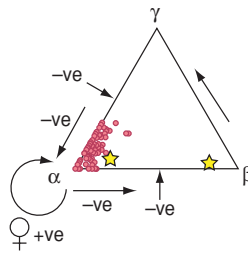
Fisherian sex ratio apostasis:

Correlational FDS
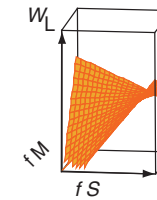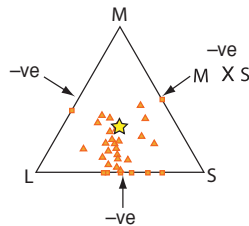
The isopod mating system exhibits a mix of a true RPS and an apostatic RPS:

$$W_{\beta,\alpha} > W_{\gamma,\alpha} > W_{\alpha,\alpha}, W_{\gamma,\beta} > W_{\beta,\beta} > W_{\alpha,\beta} \text{ and } W_{\alpha,\gamma} > W_{\beta,\gamma} > W_{\gamma,\gamma}. \qquad 2.$$

In an apostatic RPS, common strategies lose to rare strategies. In a true RPS each rare strategy loses to one common strategy and each beats one rare strategy (Sinervo 2001), which generates more intense FDS among types relative to RPS apostasis. Nevertheless, RPS fitness intransitivity is common to both the true and apostatic RPS. Prevalence of RPS intransitivity in trimorphic taxa provides a simple avenue for lineage diversification. Loss of morphs during RPS excursions may rapidly fix the systems on degenerate mating systems that lack one or more morphs. These new degenerate mating systems can diverge rapidly, forming new mating systems and species (discussed below).

←——

Figure 2

Diagnosing frequency-dependent selection (FDS) in mating systems with payoff matrices (*left panels*: $W_{rare,common}$), evolutionary dynamics (*center panels*: ternary plots with calculated or theorized attractors, *star*), and correlational FDS (*right panels*: nonlinearity that deviates from linear FD relations assumed if payoffs were purely due to linear and negative FDS). Fitness (W) is shown on the vertical axis. In payoff matrices *a* and *d*, supplementary fitness is illustrated (histograms with *arrows*), and arise from nonlinear and/or three-way interactions that generate correlational FDS. Supplementary Materials (follow the Supplemental Material link from the Annual Reviews home page at **http://www.annualreviews.org/**) provide: methods of payoff matrix construction, derivation of nonlinear equations for FDS, discussion of FD correlational selection, and emergent properties of genetics. (*a*) Data on siring success of side-blotched lizards, *Uta stansburiana* (Sinervo 2001), are nearly consistent with true rock-paper-scissors (RPS) fitness intransitivity in which one rare strategy has high fitness while the other rare strategy has low fitness relative to the common strategy $W_{Y,O} > W_{O,O} > W_{B,O}$; $W_{O,B} > W_{B,B} > W_{Y,B}$ and $W_{B,Y} > W_{Y,Y} > W_{O,Y}$ (it only deviates from a true RPS in that $W_{O,Y} > W_{Y,Y}$, however, payoffs based on overlap show $W_{Y,Y} > W_{O,Y}$, Sinervo 2001). Strong positive FDS on blue male cooperation (positive loop, *center panel*; CS surface, *right panel*) enhances the ability of B to invade the Y sneaker male strategy (Sinervo et al. 2006b). (*b*) FDS (Svensson et al. 2005) on fecundity of the damselfly, *Ischnura elegans*, is consistent with a purely apostatic mating system, which is diagnosed by both rare strategies having higher fitness than each common strategy. However, the payoff matrix also exhibits RPS intransitivity (Equation 1) (*c*) Reanalysis of data (Shuster & Wade 1991a) on siring success and female harems in the isopod, *Paracerceis sculpta*. Isopods exhibit a mixture of true RPS and apostatic RPS (Equation 2). The despotic α morph (R = rock) controls harems, but is self-limiting (*right panel*) at high harem densities, when two cryptic (P = paper) morphs (β, γ) invade. Correlational and stabilizing selection on α−male frequency and female density is due to female copying (Shuster & Wade 1991b). (*d*) Reana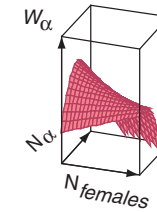lysis of data (Ågren & Ericson 1996) on the tristylous purple loosestrife, *Lythrum salicaria*. A payoff matrix based on linear FD relations indicates that two morphs, M and S, will exist in a stable evolutionarily stable strategy state (ESState), but the third morph, L, cannot invade M or S. However, the negative FDS assumed for tristyly (Barrett et al. 2004) does not entirely stabilize the system. Stability is also conferred by epistatic (nonlinear and three-way) interactions on L, which exhibits two optima, when either M or S is fixed. At intermediate values of M and S, L has low fitness (fitness saddle).

THE ROLE OF COGNITION, PERCEPTION, AND INNATE SIGNALS IN FREQUENCY-DEPENDENT SELECTION

Cognition constitutes three steps (Roitblat 1987):
1. perception—units of information are collected and stored,
2. processing—this data, stored in memory, is analyzed with computational rules built into nervous systems,
3. environmental representations form from data processing—adaptive behaviors are based on these "pictures".

Though cognition promotes negative FDS (e.g., uncommon "picture" advantage), other noncognitive processes can influence FDS. Innate recognition is a genetically codified signaler-receiver interaction. Habituation, sensitization, and input matching supply critical filtering systems in a messy world. For example, habituation of lizards to sinusoidal waveforms (blowing branches) favors mimicry to evolve in snake movement and morphology, thereby thwarting antipredator detection systems of lizards (Fleishman 1986). Learning builds correlations among many interrelated "pictures" of the environment. Cognition and innate neural processes thus contribute to correlations that build among the pictures or memotypes of neural systems (plastic: imprinted, habituated, sensitized, or learned signals; or genetic: innate), much like correlational selection on traits, but through positive and negative reinforcement or through signaler-receiver coevolution.

LEARNING MECHANISMS AND FREQUENCY-DEPENDENT CYCLES

Cognition: neural process involving learning; breaks down into the three phases of perception, data manipulation, and formation of a representation of the external environment

Our goal in this section is to link correlative forces of cognition, perception, and learning (i.e., cognitive representations of traits or memotypes) directly to CS and FDS on genotypes. Apostasis in predator-prey interactions (Cook & Kenyon 1991, Mallet & Joron 1999), analogous to mating system apostasis, promotes evolutionary cycles of highly variable forms.

Learning experiments on *Cyanocitata cristatta* in a virtual-reality environment (Bond & Kamil 1998, 2002), which used many alternative cryptic forms, produced cycles in frequency of computer-generated cryptic prey morphotypes. As *C. cristatta* switched between common type, learning preserved and cyclically generated new variation (**Figure 3**), experimentally confirming the role of prey learning in driving cycles of apostatic selection. Analogous effects with dorsal pattern manipulations have been demonstrated in nature (Forsman & Appelqvist 1998).

Handedness is a common form of FDS, which is hypothesized to become fixes owing to advantages of a bias from bilateral symmetry that allows for rapid stereotyped actions to always commence within the same hemisphere of the brain and propagate through a dominant-handed motor pattern (Propper et al. 2005). Handedness is ancient in origin. Handed attack patterns appear on trilobite prey, owing to their
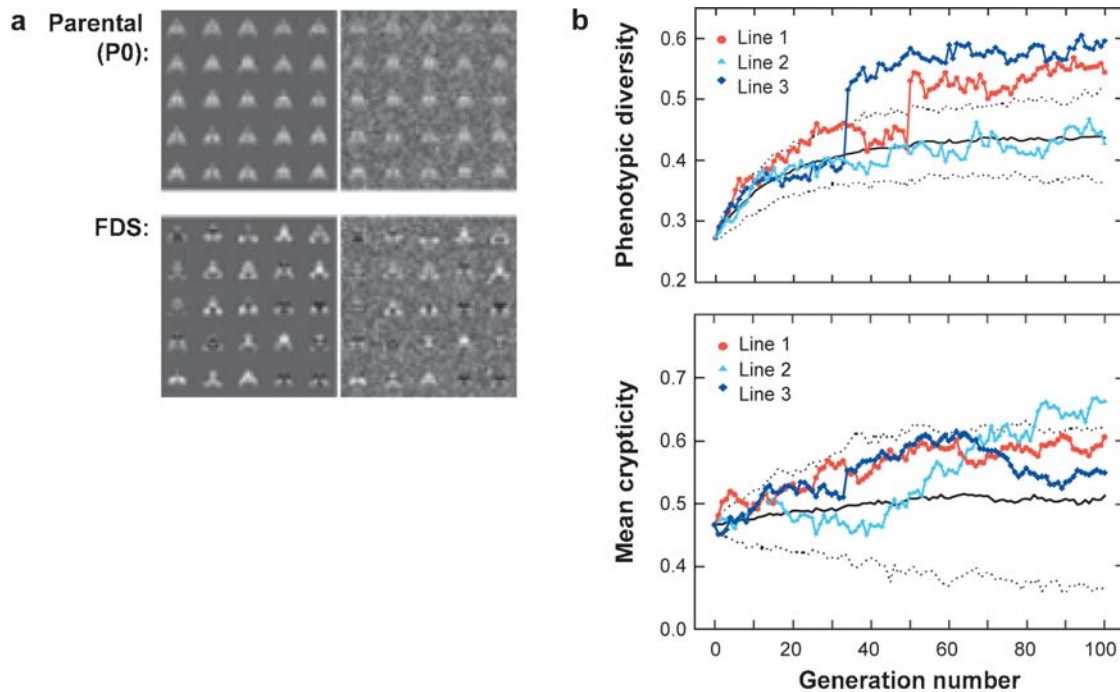
Figure 3

(*a*) Samples of virtual prey (digital moths) for blue jays, *Cyanocitatta cristata*, shown on uniform gray (*left*) and cryptically textured (*right*) backgrounds. Panels show prey items from parental prey population, P0, and from prey populations after 100 generations of frequency-dependent selection (FDS) by jays. (*b*) Moths from the FDS lines were more cryptic than those in the nonselected lines, and more variable in appearance than those in the lines subjected to frequency-independent selection (not shown). Changes in mean crypticity and phenotypic variance across successive generations in three experimental lines (plotted in *color*), contrasted with distribution of values from two sets of control lines (plotted in *black*) (from Bond & Kamil 2002, with permission).

handedly biased predators that hunted Cambrian ecosystems (Babcock 1993). Attack handedness of the scale-eating cichlid, *Perissodus microlepis*, which exhibits right- and left-jawed morphs, drives FD cycles via either learning or sensitization of their prey cichlid species (Hori 1993). Handed feeding polymorphism in crossbills, *Loxia curvirostra*, generates FD advantages (Benkman 1996, Benkman & Lindholm 1991) in opening cones that are either sinistral or dextral with respect to the spiral orientation of bracts.

In humans, the advantage of handedness and other rare behaviors are common knowledge in sports (switch hitting, a form of ambidexterity; south paw in boxing; or regular versus goofy, a footedness advantage to surfing the rare left or right-hand wave depending on breaking surf). The advantage of left-handedness (Billiard et al. 2005), as judged by handedness frequencies in sports (Raymond et al. 1996), is most prominent in close contact sports (e.g., fencing or boxing compared to tennis). A
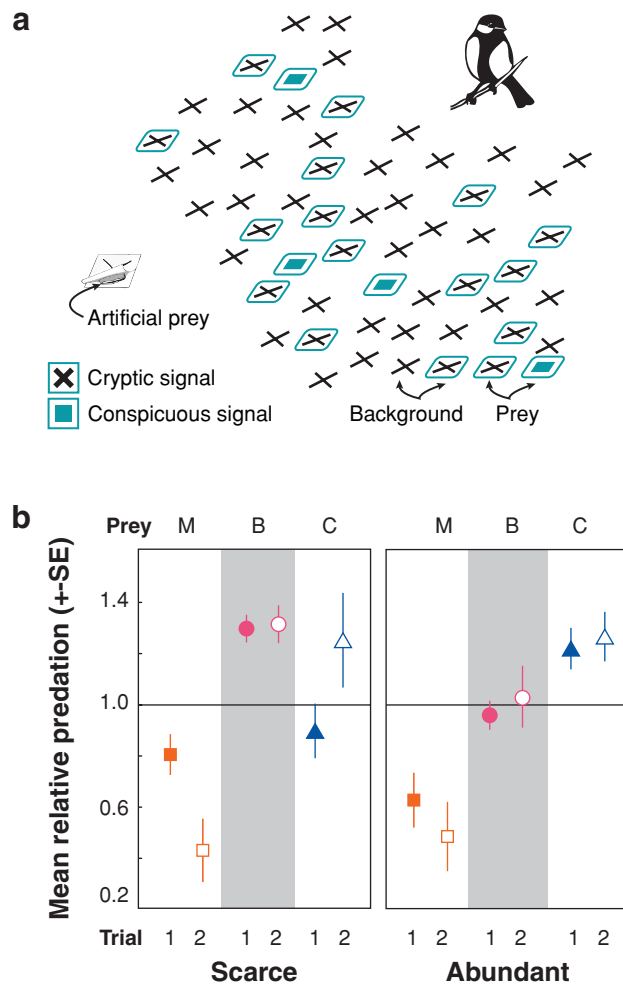
rare left-handed advantage may have first arisen in close contact fighting (Faurie & Raymond 2005). Handedness in humans has a genetic basis (Klar 2005, McKeever 2004). However, learning is involved, because most training partners and contestants are right-handed. Defensive and offensive strategies will always be reinforced in real contests with right-handed opponents regardless of novel training regimes, such as sparring with south-paws.

Invasion of cheaters is also driven by rare advantage. For example, rewardless orchid species evolve conspicuous and colorful flowers but forgo provisioning them with nectar (Gigord et al. 2004). CS on floral morphology has been observed in rewardless orchids (O'Connell & Johnston 1998). As bumblebees emerge to feed in spring, they often visit rewardless orchids, which have evolved color mutations with rare advantage. Bumblebees visiting common floral types are negatively reinforced, and subsequently avoid that color (Smithson & Macnair 1997).

Aposematic selection, which favors conspicuous prey signals coupled to noxious or lethal defenses, involves learning or innate recognition. Fisher (1930) realized that a kin benefit in prey would favor evolution of aposematism if kin were aggregated, a form of positive FDS (Endler & Mappes 2004). Death of an individual that reinforced predator learning would benefit nearby kin. A constraint on studying origins of aposematism is a universal innate predator aversion to certain colors, which in avian systems are usually yellow or red (Brodie & Janzen 1995). Thus, extant bird species share innate aversion to feeding on certain colors, reinforced over eons of interactions with prey that have all converged on yellow or red aposematic signals.

To circumvent this constraint, ingenious learning environments involving novel worlds (Lindstrom et al. 2001) allow abstract geometrical shapes to be substituted for aposematic colors (**Figure 4**). Early experiments (Mappes & Alatalo 1997) confirmed Fisher's idea that gregarious aposematic prey gain an advantage through single-trial learning of predators, in which clustered and obvious but noxious forms have a survival advantage over dispersed noxious forms. CS makes origin of warning signals contingent on prey behaviors or life history traits that aggregate signals. Aposematism is common in butterflies (Langham 2004), which often evolve to lay eggs in batches, thus establishing kin aggregations. Extensions of the novel world approach (Mappes et al. 2005) demonstrated advantages of Mullerian forms that are conspicuous but not necessarily aggregated. Other studies demonstrated that aposematic forms are anti-apostatic (Lindstrom et al. 2001), further underscoring impacts of rarity on origin of aposematism. Use of three morphs also confirmed the role of cryptic forms in maintaining imperfect Batesian mimicry (**Figure 4**). Batesian mimics evolve to resemble a noxious or toxic aposematic model and gain FD protection (rare advantage) from attack even though they lack defense, provided that cryptic forms are common.

Additional constraints and tradeoffs involved in perceptual systems of predators can drive CS and FDS on alternative antipredator prey traits such as escape behavior and dorsal patterns (Brodie 1992, Niskanen & Mappes 2005). For example, predators attacking a moving snake with stripes often miss because moving stripes appear stationary. The alternative tactic, freeze, becomes coupled to cryptic patterns. Though speed is often coupled to stripes, differential crypsis can arise through either pattern matching a background (e.g., spots on fine backgrounds, bars on bark),

a

Artificial prey

☒ Cryptic signal
■ Conspicuous signal

Background   Prey

b

or disruptive patterns like large spots that break up the prey outline (Ruxton et al. 2004).

Coevolved strategies of hosts and brood parasites are also coupled by FDS (Soler et al. 2003). Brood parasites lay eggs in nests of conspecifics or other species, to be cared for by hosts. To reduce reproductive costs of brood parasitism (Payne et al. 2001), hosts evolve defenses including refined recognition of parasitic eggs and chicks, nest defense (Amundsen et al. 2002), or egg counting (Lyon 2003). Brood parasites, counterselected to combat host defenses, evolve refined egg mimicry (Soler et al. 2003) and signals to enhance host feeding (Lyon et al. 1994).

Viduine finches provide a dramatic example of mimetic evolution. Indigo birds, *Vidua chalybeata*, learn songs of host species, and as adults, males attract females with songs of foster parents (Payne & Payne 1994). Mutual production and preference of mimetic host songs in both sexes reflect sexually and parasitically-selected traits.

Host-song imprinting of female brood parasites as chicks attracts them to mates and back to the nests of specific hosts in a culturally selected runaway (Payne et al. 2000). Positive FDS may be held in check by negative FDS and counterstrategies of specific hosts that limit specific memetic lineages of Viduine finches. Other brood parasites such as cowbirds have innate songs (divergent from their hosts), which results in a more generalized niche in which they parasitize diverse species (Garamszegi & Aviles 2005).

GENERALIZING THE CORRELATING MECHANISMS OF COGNITION AND PERCEPTION

In preceding examples, neural processes are potent correlating agents by which cues or signals become coupled to preference or performance. Positive- or negative-reinforcement learning couples signals and conditioned response in a FD fashion, thereby coupling memotypes. Likewise, perceptual biases or innate behavior couples alternative attack behaviors in predators with alternative dorsal patterns and escape behavior of prey, thereby coupling genotypes. In other cases, signals attain universal meaning among predator guilds via powerful aposematism.

A second point merits mention. The examples of neural processes (either innate or conditioned), including mating system apostasis, involve negative (rather than purely positive) FDS. This is no coincidence. Observing FDS requires variation in behaviors, which is only preserved by negative FDS. As noted above, positive FDS (like runaway) rapidly fixes populations on single behavioral types. In the mating system examples (**Figure 2**), negative FDS maintains types and in those cases with positive FDS, cycles arise through interplay of these two forces. Thus, negative FDS in one interactor (prey, predators, or hosts) is maintained in the context of the FD of learning or cultural processes of another interactor (predators, prey, or parasites). Learning and imitation have positive correlating effects on memotypes, analogous to CS on multitrait genotypes. Thus, negative FDS on variation is held in check by positively conditioned signals underlying self-reinforcing neural processes such as: reinforcement learning, rehearsal, imitative learning, innate recognition, habituation, and/or sensitization.

Are there examples of pure positive FDS that involve learning? Many cases of positive FDS are present and of great import for theories of memetic evolution. Consider populations of naïve birds in which novel behaviors arise, which have net benefits on all interactors. As the behavior spreads through imitation and learning, there are more teachers available to spread the behavior in a culturally selected runaway process. The clearest example is a rapid spread of milk bottle cap opening within and then among species of passerines in England (Lefebvre 1995).

Analogies between the positive FD of learning and imitation and sexual selection are germane. In light of this analogy, links between perceptual bias and other theories of FD sexual selection, such as sensory bias (Ryan & Rand 1999) are obvious. Positive FDS has made both processes difficult to study with extant forms because endpoints are rapidly attained. For converse reasons, we often observe negative FDS in nature. A reciprocal rare advantage of two forms or RPS fitness intransitivity of three forms

preserves variation. In mating systems, positive FDS would fix morphs were it not for the fact that positive FDS is cyclically held in check by negative FDS. Phylogenetic solutions provide recourse to the dilemma of identifying cases of pure positive FDS. The phylogenetic approach used to study positive FDS underlying receiver perceptual (sensory) bias (Ryan & Rand 1999) could be applied to test whether ancestral perceptual bias of receivers has driven positive FDS in culturally selected systems. Paradigms of novel worlds could also be used to identify rules for neural processes in a potential case of pure positive FDS. In light of these analogies, learning polymorphisms and animal personalities (Sih et al. 2004), which involve observational (imitative) types, provide key linkage to FDS on culture.

INTERPLAY BETWEEN NEGATIVE AND POSITIVE FREQUENCY-DEPENDENT SELECTION, SELF-RECOGNITION, AND SPECIATION

RPS mating systems (**Figure 2**) have important implications for speciation. Interplay among positive FDS in both sexes and negative FDS is clear in the context of RPS mating systems (**Figure 2**, **5**). Positive FDS in the lizard RPS is the result of cooperative behavior (Sinervo & Clobert 2003) not merely positive FD mate preference. Signaler-receiver relations of cooperation and sexual selection share many runaway properties because both promote a buildup of genetic correlations among signalers and receivers. Recent gene mapping studies (Sinervo et al. 2006b) indicate that genetic factors for male self-recognition and the OBY color signal locus, named for the throat colors orange, blue, and yellow, generates true greenbeard altruism (Sinervo et al. 2006b). When orange-throated male despots invade the cooperative blue-throated strategy, the blue allele confers an altruistic benefit among unrelated blue males: blue males next to orange lose competitions for paternity to the orange, but this altruistic male buffers his unrelated territorial partner from orange male aggression. In contrast, when cooperative blue males invade yellow the blue alliance is mutualistic. Thus, RPS social dynamics drive an evolutionary cycle of altruism and mutualism (**Figure 5a** and **5b**).[1]

Altruism exhibited in RPS systems may also predispose such mating systems to socially mediated speciation (Hochberg et al. 2003), a theory of speciation involving FDS and social behaviors like true altruism (**Figure 5a**). This is because the same genetic factors governing blue male self-recognition are also expressed in females and drive mate preference (Sinervo et al. 2006b), a form of positive FDS for self-mating. The dual action of positive FDS in mating and male-male cooperation may rapidly eliminate strategies other than blue (**Figure 5a**). Speciation requires both assortative mating and hybrid unfitness. Hybrid unfitness arises under social selection because self-recognition loci and loci that promote cooperation are distributed across the

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[1]The concepts of altruism, mutualism, competition, and spite form a key framework for Hamilton's (1964) ideas on genic selection. Altruism $(-,+)$, mutualism $(+,+)$, competition $(+,-)$, and spite $(-,-)$ form fitness relations among interactors expressed in terms of the costs and benefits of interaction (Hamilton 1964).
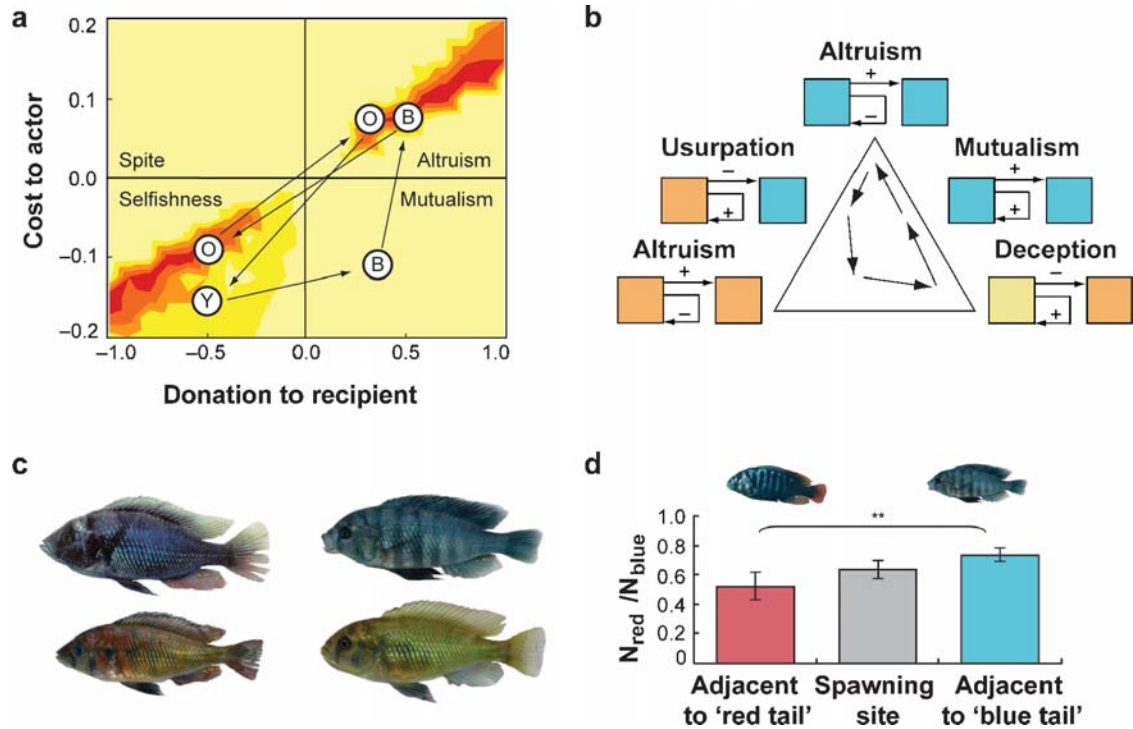
Figure 5

(a) Results from a simulation model of socially mediated speciation (Hochberg et al. 2003) with fitness payoffs (measured in nature, Sinervo et al. 2006b; Sinervo & Clobert 2003) from rock-paper-scissor (RPS) cycles of side-blotched lizards superimposed. The speciation model indicates that reproductive isolation is likely (*red*) when alternatively tagged altruists that donate to self, or usurpers that take from nonself, interact on spatially structured landscapes. Speciation is unlikely (*yellow*) for mutualistic or spiteful social interactions. (*b*) The RPS mating system traverses these social domains during the five-year cycle (superimposed on *panel a*): B altruists are invaded by O (Sinervo et al. 2006a); when O becomes common, O altruists must disperse and pay costs of dispersal (Sinervo & Clobert 2003; Sinervo et al. 2006ab); Y selfishness invades O, and B mutualists invade Y, driving the system to a point where O can reinvade. Thus, the lizard RPS mating system is susceptible to processes of socially mediated speciation: B females exhibit self-preference for B sires (Sinervo et al. 2006b) and B male cooperation also generates positive FDS. For example, elimination of Y should fix the system on B and O or on B alone, a system of true altruism. (*c*) Socially mediated speciation may have arisen from negative FDS on Cichlids. Left panel: Representative "blue" and "yellow–red" male nuptial-color types of two species of Lake Victoria Cichlids: *Lithochromis rubripinnis* (*top*) and *Lithochromis* spp. "red dorsum" (*bottom*). Right panel: two nuptial-color morphs from a single population (Makobe Island) of *Neochromis omnicaeruleus*. (*d*) Under-representation of a territory owner's own coloration among the males that occupy adjacent territories. White bar, the mean ratio *n* ("red tail")/*n* ("blue tail") among territorial males on a spawning site (256 m^2) at Makobe Island (Lake Victoria). Colored bars, the same ratios among territories adjacent to territory owners with a "red tail" (*Neochromis rufocaudalis*) or a "blue tail" (*N. omnicaeruleus*) (*c–d* from Seehausen & Schluter 2004).

genome (Sinervo et al. 2006b); any mixing of this variation with alternative strategies such as usurpation (orange) or parasitism (yellow) breaks up the coadapted gene complex of cooperation.

In this regard, self-recognition of either true or kin altruism may parsimoniously arise from the MHC (Aeschlimann et al. 2003, Grosberg & Hart 2000, Landry et al. 2001, Potts et al. 1991, Reusch et al. 2001). Thus, MHC self-recognition may, in some social systems, serve as a key signal-recognition complex that maintains coadapted gene complexes of social behavior. However, selection favoring self-mate preference produces self-similar progeny, which should tradeoff with the nonself mating benefits of MHC in the context of disease resistance (see above).

Although links between the positive FD of sexual selection and speciation have been made (Lande 1981), the explicit role of negative and positive FDS of social systems and speciation has received little empirical attention (however see Seehausen & Schluter 2004, **Figure 5c**), even though mating system examples (**Figure 2**) and theory (Dieckmann & Doebeli 1999, Hochberg et al. 2003) suggest an important role in diversification. Self- versus nonself-recognition systems like MHC may underlie self-mate preference at hybrid zones between species where reproductive isolation is forming (Howard 1999). Similarly, memetic forms of self-recognition, such as song imprinting among male and female Viduine finches and their host species, provide analogous social avenues for speciation that involve interplay between cultural and biological evolution.

ECOLOGICAL INTERACTIONS AND FREQUENCY-DEPENDENT SELECTION

The FDS of RPS mating systems (**Figure 2**) and social interactions like altruism, mutualism and antagonism (**Figure 5a** and **5b**) have properties directly related to ecosystem-level interactions. The roles of FD learning in ecosystem interactions (see above) make these homologies explicit. Indeed, aposematism can be thought of as a greenbeard (Guilford 1988) in which reinforcement learning of a signal benefits unrelated individuals that merely share alleles for the conspicuous signal. Links between RPS cycles and altruism are further exemplified by a bacterial RPS. Colicins are bacterial plasmids carried by some strains of *E. coli*. Col plasmids code for production of both a toxic protein called colicin, and one of several immunity factors against that toxin (Kerr et al. 2002). Col plasmids are costly, reducing growth rates of col strains relative to those lacking the plasmid. However, col bacteria can invade most noncol strains; cells of the col strain that contact other strains lyse and release colicin, a kin altruistic act clearing the way for self. Other mutant strains evolve colicin resistance, even in the absence of col plasmids (Feldgarden & Riley 1999, Kerr et al. 2002). When the three strains are grown in spatially structured environments, theory suggests (Durrett & Levin 1997), and in vitro (Kerr et al. 2002) and in vivo studies (Kirkup and & 2004) show that they are maintained by an RPS. This example reinforces the analogous roles of physiology in mediating negative FDS. Molecules that can be detoxified by specialists are of great significance to interspecific

allelopathy in plants (Thijs et al. 1994) as well as for plant-fungal mutualism and parasitism (Bruns et al. 2000, Taylor et al. 2004) (**Figure 6a**).

At the ecosystem level (**Figure 6b**), fitness surfaces are shaped by interactions among many species [e.g., host-parasite (Ewald 1983), competition, and predator-prey (Bolker et al. 2003), intra- and interspecific brood parasitism (Lyon 2003)]. Interspecific dynamics often reflect Red-Queen escalation (van Valen 1976), in which selection acting among interactors amplifies the variance in traits as individuals evolve counter-adaptations. For example, interactions of hosts and pathogens involve disruptive selection on both interactors (**Figure 6b**). Host genotypes are under selection for rare immune responses that have no countertactic in pathogens, whereas pathogens are under FD selection to evolve couteradaptations to common resistance genotypes of hosts. In the case of MHC molecules at Class I and II loci, there is a perfect physiological analogy between evolution of novel surface proteins that escape detection by the evolving host, and signaler and receiver evolution (Bernatchez & Landry 2003, Piertney & Oliver 2006). The phenomenon of immune system memory forges the analogy with neural mechanisms of learning.

Multi species interactions and proximate mechanisms that generate FDS, when embedded in rich ecosystem interactions, characterize FDS at higher levels of biological organization. Thompson (2005) has formalized these ideas in the tripartite

$\longrightarrow$

Figure 6

Summary of two-way, three-way, and multiway interactions discussed in the review. Arrows with straight lines indicate negative frequency-dependent selection (FDS), whereas circular arrows indicate positive FDS or analogues for positive FDS in learning, innate behaviors, or immune recognition and memory in the major histocomopatibility complex (MHC). (*a*) The bacterial rock-paper-scissor (RPS) is hypothesized (Kerr et al. 2002) to generalize to allelopathy in higher ecosystem interactions. If so, additional frequency-dependent FD detoxification interactions or cheater dynamics might involve coevolutionary interactions and positive and negative FDS between plants and fungal mutualists or parasites (Bruns et al. 2000, Taylor et al. 2004). (*b*) The simple coevolutionary dynamic involving a host's immune system (e.g., MHC) and a foreign pathogen. The immune system, which retains immunity from cross reactivity, is susceptible to invasion by rare mutant pathogens that beat the immune system. (*c*) Coevolutionary arms race between a toxic newt, *Taricha torosa*, and a snake predator, *Thamnophis elegans* (Brodie et al. 2005), generates a coevolutionary hotspot in Northern California that coincides with a Batesian mimic, *Ensatina eschscholtzii xanthoptica* (Kuchta 2005). In addition, alternative cryptic prey found in the ring species of *Ensatina* (Wake 1997) are hypothesized to be maintained by either background matching or two alternative forms of disruptive coloration. This complex of mimicry and crypsis may serve to exert reinforcement learning on avian predators (**Figures 3** and **4**) in an RPS dynamic. The complete predator-prey dynamic is actually best visualized as a tetrahedron, rather than two RPS triangles (*c*, *lower left*). The predator resides at the apex, aposematic model (and Mullerian forms) at one vertex, Batesian mimics at the other vertex, and cryptic forms at the third vertex. (*d*) Indirect effects are hypothesized to govern three-way interactions between a predator and two-prey species (Bolker et al. 2003). An RPS may arise from competition among three competitors, which is set up by tradeoffs among exploitative and interference competition, and additional tradeoffs from either cooperative competitors or competitors under other forms of positive FDS. Alternative predator behaviors such as individual versus group foragers might generate tradeoffs and negative and positive FDS respectively.
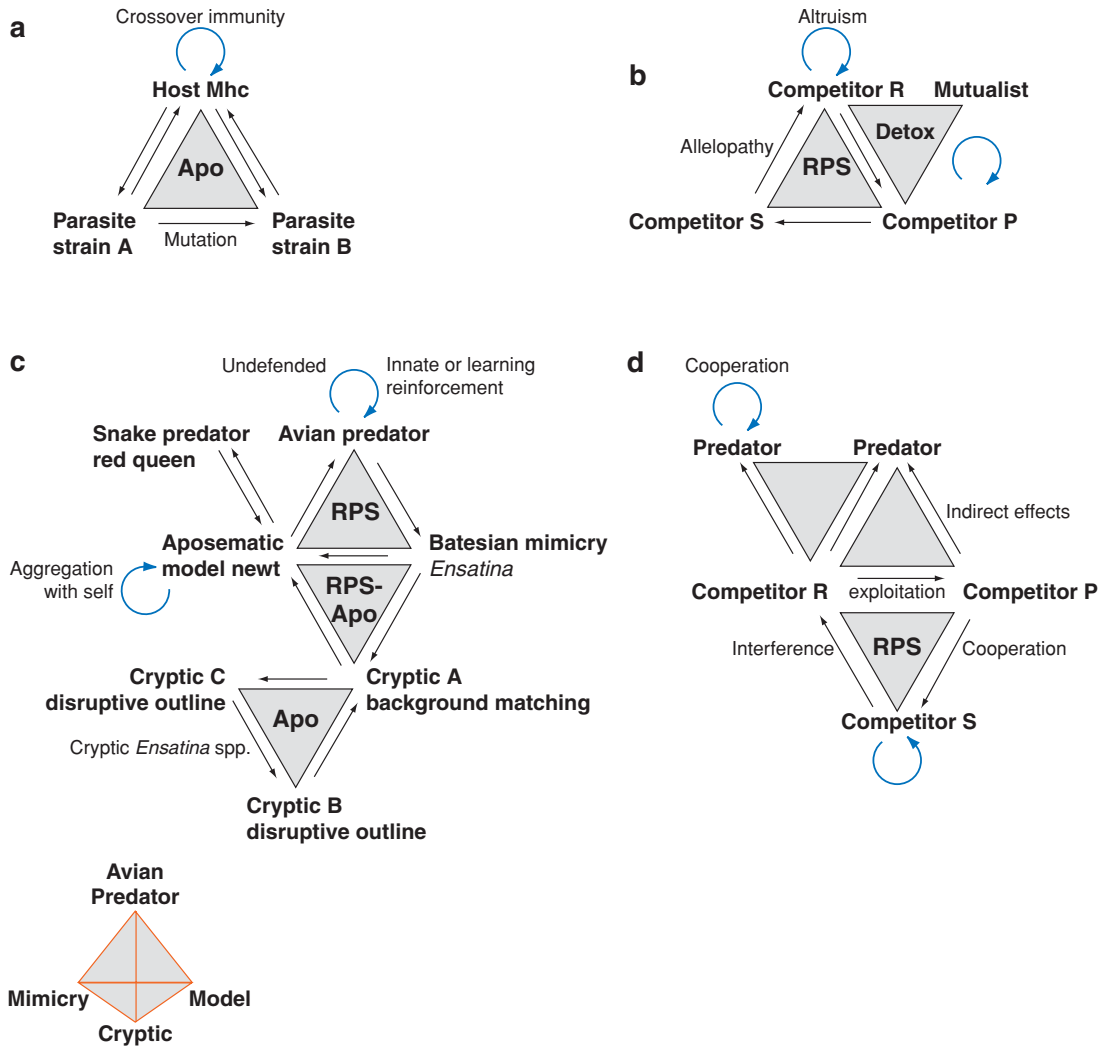
Geographic Mosaic theory of ecovolution. In brief, populations are geographically structured on landscapes and forms of FDS vary in space and time creating hotspots of reciprocal selection acting between species, and evolutionary coldspots, where selection is not reciprocal. Finally, connectivity among spatially structured populations (i.e., gene flow) mixes traits that are locally adaptive in one population but not in another. A geographical hodge podge of locally adapted/maladapted populations results, constantly evolving alternative solutions to similar problems under FDS.

For example, the moth *Greya pollitella* pollinates flowers of the woodland star, *Lithophragma*, as an incidental byproduct of oviposition behavior. *Greya* larvae feed on some seeds produced by the flower, imposing a reproductive cost. A geographic mosaic across both species' ranges arises from parasitic costs and mutualistic benefits

of *Greya* moths pollinating *Lithophragma*, relative to more neutral pollinators like flies (Thompson & Pellmyr 1992).

Coevolution between garter snakes and toxic newts in western North America provides another example of a geographic mosaic (**Figure 6c**). Garter snakes in the genus *Thamnophis* are predators of newts in the genus *Taricha*. These newts produce a paralytic toxin (tetrodotoxin; TTX) whose potency is an effective deterrent against all predation except that by *Thamnophis* (Brodie et al. 2005). Though garter snakes can detoxify TTX, resistance comes with locomotor tradeoffs (Brodie & Brodie 1991). Newt toxicity and snake TTX resistance are geographically variable and closely matched in nature. Moreover, a Batesian aposematic mimic (Kuchta 2005), *Ensatina eschscholtizii xanthoptica*, straddles two coevolutionary hotspots in the newt-garter snake dynamic—the San Francisco Bay Area and central Sierras of California—intensifying the arms race. Other cryptic *Ensatina* salamanders complete a ring species of western North America (Wake 1997). The contact zones and hybrid unfitness in the *Ensatina* ring species are thought to arise from CS on alternative antipredator coloration in *Ensatina* subspecies. If so, *Ensatina* salamanders provide another example of negative FDS in speciation, discussed above. Thus, an arms race (**Figure 6c**) with the attributes of strong FDS has shaped a geographic mosaic of coevolution between predator and prey, perhaps intensified by invasion of mimics.

ON THE NUMBERS TWO VERSUS THREE IN SPECIES INTERACTIONS

Rather than focusing on two-way interactions it will become necessary to shift our focus to three-way interactions of FDS, arising from interplay between positive and negative FDS (**Figure 6c**). Three players and RPS dynamics may be a common Red Queen dynamic in coevolutionary hotspots. We suggest that a system with model, mimic, and cryptic forms is RPS if ($W_{rare,common}$):

$$W_{mimic,model} > W_{model,model}; W_{cryptic,mimic} > W_{mimic,mimic}; W_{model,cryptic} > W_{cryptic,cryptic}$$
$$3.$$

Such RPS conditions are entirely plausible given results of learning experiments in novel worlds (**Figure 4**), and if the model pays costs of defense, which is likely in the case of chemical defense like TTX. Costs of defense, a tradeoff ignored in learning experiments, could reduce growth or delay maturation, thereby allowing mimics to invade, particularly at low frequency and when alternative cryptic prey are common. At high frequency, Batesian mimics should lose against rare cryptic forms, particularly because crypsis is under apostatic selection. To invade, models with weak defense should be aggregated, and common cryptic and edible prey must also be present.

In the case of a model, a mimic, and generalist predator (Kokko et al. 2003), it is difficult to equate fitness of predator and alternative prey. We propose a modification to standard game theoretic approaches (e.g., Equation 3) and introduce the idea of rare versus common cognitive representations developed in predators. A common aposematic form in a predator's search image depresses a predator's fitness, which would otherwise be able to feed on mimetic forms. Conversely, predator fitness is

elevated when Batesian mimics are common in its search image. Thus, this system is an RPS in which: (*a*) mimic beats model and applies selection to model—mimic pays no costs of defense but gains signal benefits, (*b*) predators pay costs of mistakes and learn quickly to recognize and eat imperfect mimics or evolve refined discrimination or learning, (*c*) ongoing predator mistakes with models cause models to chase away from mimics and refine the signal or add greater defense. The RPS cycle repeats endlessly (**Figure 6c**), further refining each player via powerful CS in a runaway cycle, or when the Batesian mimic itself evolves defense and is converted in a more mutualistic Mullerian form. We substitute a cognitive representation of frequency (i.e., memotype), predator{mimic} versus predator{model}, for genotype frequency, model versus mimic, to define ESS conditions under which the three-player dynamic is RPS:

$$W_{mimic,model} > W_{model,model}; W_{predator\{mimic\},mimic} > W_{mimic,mimic};$$
$$W_{mimic,predator\{model\}} > W_{model,predator\{model\}} \qquad 4.$$

Recent advances in our understanding of FD ecological interactions highlights a role for three players even if such interactions are not RPS players. Trait-mediated interactions, in which the outcome of competition and trophic interactions depend on individual traits and density (Bolker et al. 2003), begin to address FDS on ecosystem interactors. For example, apparent competition is an ecological interaction that is couched in terms of three players: two competitors (or herbivores) that compete for the same resource, which are controlled by FD predation (**Figure 6d**), provided that predators exhibit functional responses to prey frequency (Bolker et al. 2003). Competition often involves a behaviorally dominant species that exerts interference competition, whereas the other competitor exerts effects via exploitative competition, each type carrying a set of tradeoffs.

Inferences from FDS in mating system dynamics and the dimensionality of tradeoffs implies that a true RPS competition might be similarly structured in terms of a third tradeoff owing to social interactions. For example, group foraging (cooperative) or learned foraging strategies of the third competitor (Sih et al. 2004) may generate additional social tradeoffs that are necessary for RPS intransitivity (**Figure 6d**). Moreover, our broader definition of RPS intransitivity developed for mating systems (**Figure 2**), which involves either a true RPS or RPS apostasis, broadens this theory of FDS. Many other ecological interactions may involve RPS intransitivity that generates ESS conditions for a three-player Red Queen dynamic, which sustains self-reinforcing CS.

Coevolution in ecological interactions might not involve genetic change, but may involve induced plasticity or learning polymorphisms (Sih et al. 2004). Theoretical models on the value of induced predator defenses, costs of defense, and reliability of inducing cues can be found in Lively (2005). For example, inducible feeding morphs under FDS within a species can lead to ecological character displacement (Dayan & Simberloff 2005, Pfennig 1992) and divergent selection pressures that alleviate competition for common resources (Pfennig & Murphy 2003).

For example, divergent selection favors a limnetic form of sticklebacks, *Gasterosteus* spp., which is specialized on zooplankton, and a benthic form, which is specialized for

the edges of postlacial lakes in North America. Experimental studies (Schluter 2003) demonstrate that fitness costs paid by different morphs (**Figure 1***c*) are greatest when competitors are similar in phenotype, a form of FDS. New genomic methods have begun to pinpoint genetic factors involved in divergence of sticklebacks (Colosimo et al. 2005). Alleles responsible for alternative phenotypes are selected differentially in the benthic form relative to the ancestral marine form, suggesting roles for CS and negative FDS in driving this radiation during the last 20,000 years.

CORRELATIONAL SELECTION AND LINKAGE DISEQUILIBRIUM

It is often assumed that because different species do not exchange genes, no linkage disequilibrium (LD) can arise from interspecific FD interactions. However LD forms among longitudinally transmitted parasites found in alternate hosts that vary genetically in susceptibility (Lively et al. 2005). Likewise, if host specificity or parasite preference arises from culturally heritable behaviors, this sets up analogues of LD (memotypes with genotypes) owing to CS on interactor traits, even if interactors reside in different species (e.g., Viduine finches and host lineages). Coevolutionary relations arise from these analogues of LD, byproducts of correlational FDS and neural systems. CS refines traits in each player generating coevolutionary runaway.

In this regard, genomic approaches for understanding correlated trait evolution (Colisimo et al. 2005) and CS (Sinervo & Clobert 2003, Sinervo et al. 2006b) will become more important in expanding these ideas to other systems. In the case of genetic variation within species, strong CS owing to FDS will generate LD among even unlinked loci (Chevrud 1984, Lynch &Walsh 1998). LD equilibrates when a balance is struck between the force of CS that builds LD and recombination and segregation that destroys LD. Cycles, driven by strong FDS (**Figure 2**), generate LD that is detectable with marker loci. For example, LD associated with FD male cooperation in the lizard RPS was used to map the color signal locus and loci for self-recognition (Sinervo et al. 2006b). LD analysis of genes controlling alternative behaviors in humans (Ding et al. 2002) has likewise identified genes likely to be under FDS (Harpending & Cochran 2002). Similarly, the approach to detecting balancing selection on the MHC is explicitly marker based (see Hedrick, this volume). Though direct measures of CS gradients would be very useful in studying evolution in ecological processes like character displacement, such methods may be impractical. In this regard, genomic approaches to studying consequences of FDS on CS and correlated trait evolution alleviate this difficulty at higher levels of biological organization.

SUMMARY POINTS

1. FDS often involves CS given that it arises from interactions between interactors. Different traits in interactors are coupled by functional relationships (e.g., signaler-receiver, etc.).

2. Tradeoffs are often, if not always, a component of CS associated with FDS. Identifying tradeoffs is useful in elucidating proximate causes of FDS and functional axes along which CS modifies trait correlations to generate functional integration.

3. The payoff matrix provides a succinct way to diagnose the forms of FDS (apostasis, RPS, negative or positive FDS) and these analogies are useful at diverse levels of biological organization, particularly those involving Red Queen dynamics.

4. In learning or perception, correlations between cognitive representations in one interactor may serve as positive agents, which can substitute for genetic CS. In other cases, such representations are codified by selection as innate signal recognition.

5. Thus, roles of rare and common cognitive representations, memotypes, in many interactions (e.g., predator) substitute for rare and common genotypes in ESS analysis.

6. Systems exhibiting FDS across all levels of biological organization often involve a complex interplay between both negative (apostatic, rare advantage, common disadvantage) and positive FDS (aposematic, cooperation, learning, sexual selection).

7. Ecosystem dynamics and stability are often governed by three-way interactions that arise from FDS among three interactors, owing to homologous sets of the rules elaborated for mating system and social system evolution such as the true RPS or apostatic RPS.

FUTURE ISSUES

Much research is based on the premise that simple pair-wise relationships can describe FDS. Lessons from ESS analyses of mating systems (with well-characterized genetics), FDS, and payoff matrices indicate this assumption is rarely met. Nonlinear and three-way interaction drives FDS. Given the prevalence of RPS in trimorphic mating systems, is the RPS common in systems that even lack morphs?

Though positive FDS is built into some speciation models, the pervasive role of negative and positive FDS in mating systems implies that explicit models are required to capture dynamics of evolving mating systems, at contact zones between diverging species or in sympatry. Self-recognition loci should be common in the origin of reproductive isolation.

Few experiments link FDS in ecological systems. Experiments will be required to understand the complex biological interactions of FDS in ecosystem interactions.

Though spatial dynamics are an implicit or explicit component of most ecological systems with FDS, few studies are replicated across a broad geographic framework to test whether interaction strength changes from the center to the edge of a species range or between contact zones of diverging species. The critique also holds for mating and social systems.

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