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# Multiple-trait coevolution and environmental gradients in guppies

John A. Endler

Closely related species are often divergent in many different kinds of traits, and particular suites of traits are characteristic of particular environments. This differentiation is best known in life history traits<sup>1,2</sup>, but is also found in physiology, morphology and behavior. Guppies (*Poecilia reticulata*) are one of the few species in which within-species, genetically based, geographical variation is known for many different kinds of traits. Is there any pattern in this variation, and does it have general implications?

Guppies are small poeciliid fishes native to small clear streams in northeastern South America and adjacent islands. Haskins *et al.* were the first to point out their value to evolutionary studies<sup>3</sup>. They noted that predation intensity varies among populations, but females prefer more conspicuous males, so the genetically controlled polymorphic color patterns of any one place could represent a local balance between sexual selection and geographically varying predation<sup>3</sup>. Subsequent work has shown that the color patterns of each population do indeed represent this balance<sup>4–8</sup>, and a similar pattern is

**Guppies show geographical variation in many different kinds of traits. Traits covary with each other, with predation and with other environmental factors.**

**Phenotypic correlations are often assumed to result from genetic correlations, but may also result from covariation among different sources of natural selection and interactions among the traits' functions. This network of interactions could bias the direction of evolution in characteristic ways, and suggests how intraspecific variation may give rise to interspecific variation.**

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also found in guppies living in different predator faunas<sup>6,8</sup>. On average, as one moves from low to high predation intensity, the color patterns become simpler and have less visual contrast than low-predation populations. The changes in visual contrast are achieved with different combinations of genes in different populations, but their phenotypes vary in parallel with predation<sup>3,4</sup>. Seghers<sup>9–11</sup> was the first to document geographical variation in behavior and morphology, and relate it to predation risk. On average, as one moves from low to high predation intensity, the anti-predator defenses increase. Since this pioneering work, there has been an explosion of interesting work on geographical variation in diverse traits in natural populations of guppies. This is summarized in Table 1.

## Covariation between traits and predation

Many different suites of traits covary with each other and with predation intensity (Table 1). Increased predation is usually associated with less conspicuous color patterns, a smaller and more fusiform body (larger length/height

**Table 1. Variation of guppy traits with predation intensity<sup>a</sup>**

Trait	High predation	Low predation	Refs
Number of spots	low	high	4-6
Spot size	small	large	4-6
Color diversity	low	high	4-6
Area of spots	low	high	4-6
Conspicuousness	low	high	3-6,8,12
Body length/Height ratio	larger (fusiform)	smaller (high bodied)	4,5
Tail size	small	large	4,5,32, see below <sup>b</sup>
Body size	small	large	3-5,11
Age at maturity	younger	older	17,18,39, see below <sup>c</sup>
Size at maturity	smaller	larger	16,17,39,40, see below <sup>c</sup>
Lifespan	short	long	4, see below <sup>b,c</sup>
Brood size	large	small	16,17,39,40, see below <sup>c</sup>
Size at birth	small	large	16,17,39,40
Inter-brood interval	small	large	16,17,39,40
Reproductive allocation	large	small	16,17,39, see below <sup>c</sup>
Overall population density	low to medium	medium to high	4,11, see below <sup>b,d</sup>
Sex ratio	more even	female biased	11, see below <sup>b,d</sup>
Feeding rate and tendency to feed when predator present	higher	lower or none	49
Time spent foraging when predator present	less	more	30
Time spent by males foraging relative to courtship <sup>g</sup>	less	more	30
Time spent by males in following females	higher	lower	30
Time spent by females in avoiding males	higher	lower	30
Courtship distance	short	medium to long	see below <sup>f</sup>
Courtship intensity	higher	lower	50
Courtship style of males	more sneaking, less display	less sneaking, more display	30
Courtship style of males, in response to predators	fewer sigmoids	no change	38
Sneaky copulation <sup>h</sup>	more	less	28,46,50,51
Importance of sexual selection	low	high	30, possibly 46
Female preference for males with more, larger and more-reflective colored spots	weaker or none	stronger	31,32,45,52
Female preference for males with more orange	weaker or none	stronger	31,32,45,52,53
Aggression towards other guppies	less	more	54
Adult schooling size, cohesion and orientation (fish predation threat)	high	low	9,38,54
Subadult schooling: parallel orientation	high	low	55
Subadult schooling: nearest neighbor distance	medium	medium	55
Juvenile schooling: cohesion, orientation	high	low to high <sup>h</sup>	38,54,56,57
Change in schooling of juveniles in the physical presence of predators during tests: cohesion, orientation	low (always school)	high	54,56
General anti-predator behavior	stronger	weaker	11,30,38, see below <sup>d</sup>
Response to threat of bird predation	high	low	10
Aquatic predator danger (hunger) assessment <sup>i</sup>	efficient	weak	58
Reaction distance to potential predators	long	short	9,10
Aquatic predator inspection and attack-zone avoidance	high	low	38,56,59
Apparent use of tit-for-tat strategy during aquatic predator inspection	high	low	59
Shallow or cover-seeking in response to predator threat	high	low	see below <sup>d</sup>
Parasite load	higher (lower elevation sites)	lower (higher elevation sites)	60, see below <sup>j</sup>
Allozyme heterozygosity	high	moderate	21,25
Allozyme allele frequency variation	high	high	21,23,25
DNA variation	moderate	moderate	24

<sup>a</sup>With one exception (bird predation) 'High predation' indicates that guppies were collected from populations that were subject to predation by the Cichlid *Crenicichla alta*, as well as other cichlid, characin, and pimelodid predators. 'Low predation' indicates guppies from populations subject to predation from only the relatively innocuous fish predator *Rivulus hartii*, and in some cases also by the weak prawn predator *Macrobrachium crenulatum* (see Ref. 4). (Populations with both *R. hartii* and *M. crenulatum* show different color patterns<sup>4</sup> and life history traits<sup>61</sup> than populations with *R. hartii* alone.) Not all papers note the predation regime of the source populations; this was obtained directly from the authors and verified by the locality name numbers, and Trinidad National Grid references. The results in the body of the table are averages calculated among populations within a particular predation regime. Not all populations show these effects, and the exceptions often provide clues to additional selective<sup>4,6</sup> or historical<sup>22</sup> factors. The color pattern, body shape and size, life history and behavioral changes with predation intensity are also found in field introduction experiments in which predation intensity is decreased or increased<sup>9,10,18,20</sup>, indicating that predation is an important factor affecting the patterns in this table. Nevertheless, some of these patterns may reflect responses to geographical gradients in selective factors that are correlated with predation intensity (see text). Note how in some cases the response to predation is plastic – the pattern is different depending on the physical presence or absence of the predator during the observations (e.g. juvenile schooling) as well as varying with predation intensity in the source population. Criteria for inclusion in this table: (1) Studies using fish from natural populations rather than many-generation laboratory-reared wild-descendants, inbred wild strains, or domestic ('pet-shop') guppies. (2) Studies using the same methods and observers on more than two natural populations of guppies. (3) Experiments using one- or two-generation descendants of wild-caught fish raised under uniform conditions. This implies, but does not prove, heritable geographical variation in these traits. (4) Data from populations where predation or other environmental factors can be unequivocally ranked.

<sup>b</sup> Ender, unpublished; <sup>c</sup>D. Reznick, unpublished; <sup>d</sup>B.H. Seghers, PhD thesis, University of British Columbia, 1973; <sup>e</sup>may result from differences in food density<sup>14</sup> as well as predation<sup>30</sup>; <sup>f</sup>K. Long and G. Rosenqvist, unpublished; <sup>g</sup>partially genetic and partially facultative response to physical presence of predator during tests; <sup>h</sup>higher when *Rivulus hartii* abundant; <sup>i</sup>may be related to age; <sup>j</sup>A.R. Lyles, PhD thesis, Princeton University, 1990.

ratio), more 'r-selected' life history traits (i.e. characteristic of high mortality populations), less female-biased adult sex ratio, proportionally more time spent in feeding than courting when predators are visible, proportionally less time and effort in the highly visible full display, relatively more time and effort in the less-conspicuous sneak copulation, courtship at higher intensities and at shorter distances, weaker female preferences and influence of sexual selection, weaker aggression and stronger schooling, and stronger and more-specific behavioral responses to potential predators. The overall population density is lower but increased aggregation and schooling results in a shorter nearest neighbor distance under high predation. Parasitism is greater in high predation areas.

The observed patterns (Table 1) generally make sense biologically. Less conspicuous color patterns are less likely to be seen by predators, although they may be less conspicuous to potential mates, so the balance between sexual selection and crypsis shifts with predation intensity<sup>4,5,12</sup>. Smaller and more-fusiform fish should be able to flee faster and escape more easily from predators<sup>13</sup>, and optimal foraging theory suggests that smaller fish are less likely to be selected by the large dangerous predators. Larger fish may be less likely to be affected by low food abundance, which is characteristic of the deeply shaded low-predation localities (Refs 4,14 and Endler, unpublished), and larger higher-bodied males would present a larger colored surface to females during the courtship display, which would be particularly valuable in the dark low-predation streams. Field transfer and artificial stream experiments in which predation is varied<sup>5</sup> confirm that predation is a major cause of natural selection of color patterns, body size and shape. Further support is provided by spatial analysis<sup>7</sup> and parallel geographic variation in three different predator faunas<sup>8</sup>.

Guppy life history patterns are very similar to that expected from life history theory<sup>1,2</sup> under these predation regimes. For example, predation accounts for around 70% of the variance in life history traits<sup>15</sup>, and high mortality favors earlier maturity, higher fecundity and greater reproductive allocation. The sex ratio becomes more female-biased in low-predation sites because the weaker predator, *Rivulus hartii*, is gape-limited, and only female guppies can grow above this gape limit and thereby escape predation (B.H. Seghers, PhD thesis, University of British Columbia, Canada, 1973). Field transfer and artificial stream experiments confirm the importance of predation in determining geographic variation in life history traits<sup>16-18</sup>.

Geographical variation in behavior among populations is similar to that expected from behavioral ecology theory and other fish species<sup>19</sup>. Generally, with increasing predation, there is an increase in the frequency and intensity of the use of traits which reduce predation either directly through anti-predator behavior, or indirectly by using less-conspicuous courtship. For example, higher predation is associated with more and tighter schooling, less aggression, more vigilance and predator inspection, more time spent using the relatively inconspicuous mating strategy (sneaking), proportionally less time spent feeding at a higher rate, and more time and effort in all courtship activity. Increased parasitism by *Gyrodactylus* with predation may reflect the shorter nearest-neighbor distance of guppies in high-predation site aggregations, which facilitates interhost transmission of ectoparasites, but this is confounded with variation in elevation, temperature and greater human disturbance in the lower reaches of the streams. The importance of predation in natural selection of behavior is also supported by a field transfer experiment<sup>20</sup>. In summary,

many traits vary with predation intensity, either as a direct consequence of predation, or an indirect consequence of the interactions among various kinds of traits, including those affected directly by predation (Fig. 1).

Some traits are not associated with environmental factors. There is no correlation between predation intensity and allozyme allele frequency variation or molecular genetic variation. This lack of correlation is similar to that found in many other species. This is very convenient because it implies selective neutrality of the loci<sup>21</sup> and therefore allows us to track known dispersal events<sup>22,23</sup>, and make inferences about the history of colonization of Trinidad by guppies<sup>24</sup>.

Although there is no effect of predation on allozyme allele frequencies, heterozygosity increases with predation among populations<sup>21,25</sup>. This is not directly because of predation and is what one would expect from the joint effects of random factors, gene flow and stream geometry. The upstream (low predation) populations are absolutely (by waterfalls) or relatively (fewer tributaries and isolation-by-distance) more isolated than the lowland (high predation) populations, and may, in some cases, also have smaller effective population sizes (so random effects would be greater) leading to relative loss of heterozygosity upstream<sup>21</sup>. In addition, predation intensity increases with stream order (size and number of tributaries). As stream order increases, gene flow will come from more tributaries, hence from more populations. Gene flow from a greater number of source populations will increase gene diversity directly and it will also increase the local effective population size, reducing rates of random loss of alleles. As a result, neutral allele frequencies downstream will be proportional to the average of the upstream source populations, and downstream populations will have greater allelic diversity than upstream populations. The presence of varying numbers of tributaries contributing gene flow also predicts less among-population genetic variation in downstream populations compared to upstream populations, but this has not been investigated (it would require a massive study of at least eight drainages).

It is interesting that of the two river systems studied by Shaw and colleagues<sup>21</sup>, the one with a longer history of human disturbance (Tacarigua) has a lower mean heterozygosity, and there is some evidence for drainage-basin-specific mating behavior. Whether this is due to human disturbance or a greater number of tributaries in the other river (Aripo) is presently unknown. Any study of basin-specific characteristics must account for the variation among basins in the number of tributaries, distributions of stream orders, and the proportion of populations in different habitats and selective regimes.

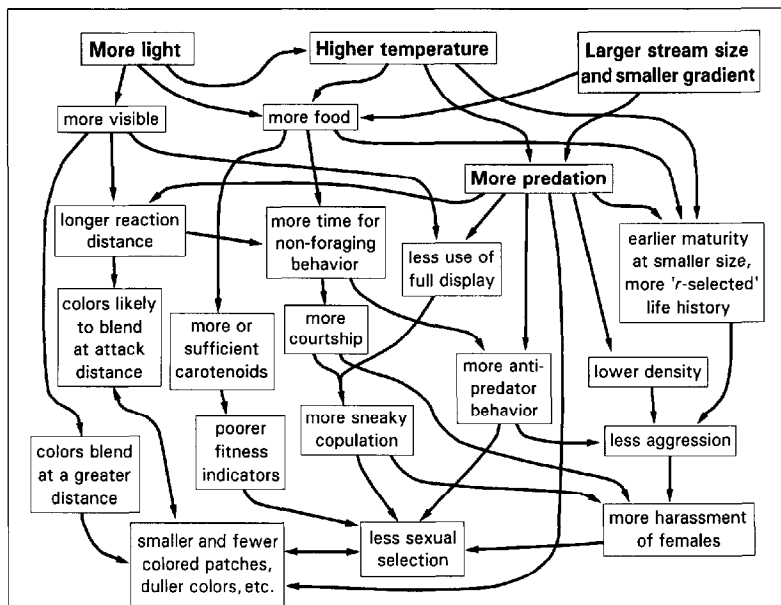
In contrast to allozymes, color pattern diversity decreases with predation<sup>4</sup>, implying that the effects of natural selection (predation) and sexual selection on the local color pattern loci outweighs the effects of gene flow and random factors<sup>4,5,7</sup>. Color pattern diversity is reduced by predation because this is a necessary effect of directional selection and also because as predation intensity increases there are fewer ways to more precisely match the visual background<sup>4</sup>.

#### Interactions among environmental factors and trait suites

Field introduction experiments<sup>4,16,18,20</sup>, artificial stream factorial experiments<sup>4</sup> and spatial analysis<sup>7</sup> show that predation is a major selective factor in the evolution of color patterns, body shape and size, life history patterns and

behavior. However, other environmental factors can have both direct (plasticity) and evolutionary effects on the traits in Table 1. As is common in stream environments, there are correlations between predation intensity and several other environmental parameters. For example, as predation increases, streams become larger, have a lower gradient, the canopy goes from closed to open, light intensity increases, water temperature increases a few degrees, and the benthic flora and microfauna become more productive and abundant (Refs 4,26 and Endler, unpublished). The correlation among guppy traits and predation may be caused by predators using some of these factors as clues in habitat choice, and by waterfalls restricting upstream dispersal of some predators<sup>3,4,6</sup>. These environmental factors have multiple effects on the biology of guppies, and hence may bias the evolutionary direction of the traits in Table 1. Figure 1 illustrates some of these effects, and I will discuss a few of them.

High-predation localities are usually illuminated more intensely than low-predation localities, because there are more and larger gaps in the forest canopy over the stream (Endler, unpublished). These higher light intensities result in increased visibility, compared to low-predation sites. This may allow anti-predation behavior to be initiated earlier and further away from the predators compared to low-light conditions. Both longer-distance visibility<sup>4</sup> and higher predation risk can favor the observed greater reaction distance in high-predation areas<sup>9,10</sup>. Increased reaction distance and reduced visual acuity at greater predator distances allow males to have colors that are relatively more conspicuous at the 2–3 cm courtship distance, but that blend at the greater predator attack distance (Ref. 4 and K. Long, unpublished data). (The colors would still not be as bright as in a low-predation population, just brighter than expected if courtship and predation distances were identical.) Increased reaction distance may also allow more time for courtship and foraging, and less time *per individual* may be needed for predator inspection behavior, especially because schooling involves more individuals in high-predation sites. The combination of increased light and shorter courtship distance means that males are easier for females to see, and a colored spot of a given size subtends a larger visual angle than in low-predation streams. This allows the size of spots to become smaller in response to increased predation and finer background grain<sup>4,5</sup>, without becoming significantly less conspicuous to females (Ref. 4 and K. Long, unpublished data).



**Fig. 1.** The network of functional and evolutionary interactions among various suites of traits and the environment in guppy streams. ('r-selected' is descriptive shorthand for the suite of traits characteristic of high predation localities; see Table 1.) The relationships are shown for high-predation sites relative to low-predation sites. The arrows indicate a functional (use or performance) or natural selection cause-effect relationship, or both. The double-headed arrows indicate that both traits can effect each other's evolution. Not all possible relationships are shown, although an attempt was made to show the known relationships. The direct effects of predation on color patterns, density, life history, and some behavioral traits have been confirmed in field transfer experiments<sup>5,16,18,20</sup>. This diagram is meant to indicate the average effects of each environmental factor and trait functions. Any one locality may not show all of these relationships, nor may a single stream show enough variation in the environmental factors to cause measurable evolutionary changes. Disturbances caused by man have destroyed or changed many of these relationships, especially in the high-predation localities.

Increased light intensity at high predation sites also means increased food productivity<sup>27</sup>, either directly when feeding on diatoms and other algae, or indirectly when feeding on algal-feeding invertebrates and their predators<sup>26</sup>, all eaten by guppies<sup>14</sup>. Increased insolation results in higher water temperatures, which leads to increased food productivity<sup>27</sup>. Even if food productivity were spatially constant, as predation increases, decreasing guppy density should mean increasing food per guppy.

Greater food availability allows more-rapid foraging for shorter times, minimizing predation risk when a guppy's attention is preoccupied by feeding. Increased food abundance at high-predation localities may allow a reduction in foraging time, allowing more time for anti-predation behavior (such as schooling) and courtship. But given that the full display is highly visible and negatively related to light intensity<sup>12,28</sup>, this results in a greater percentage of courtship time spent on sneaky copulation at the expense of full displays<sup>28,29</sup>. This shift is greater for larger males<sup>29</sup>, which are probably more conspicuous and give the predator a greater return per effort than would smaller males. This, in turn, increases rates of harassment of females by males<sup>30</sup>. The net effect is to reduce the effectiveness of female choice, and therefore the importance of sexual selection in high-predation streams<sup>30–32</sup>. In general, interactions between courtship behavior, predator vigilance and foraging can affect the kinds of mating strategy used by male guppies; full displays and female choice in low predation, and sneaking and male-male competition in high predation<sup>30</sup>.

Increased water temperature results in more-rapid metabolism, which favors earlier maturity at a smaller size<sup>33</sup> in high predation localities. Smaller size may aid maneuverability, especially for sneak copulation, and both increased maneuverability and smaller size make guppies a lower-quality food item for predators. But smaller size and earlier maturity are parts of the suite of 'r-selected' life history parameters that are generally favored when mortality is high<sup>1,2,16-18</sup>. Greater food availability with temperature also makes it physiologically possible or easier to produce the larger brood sizes and greater reproductive allocation that are favored by high mortality.

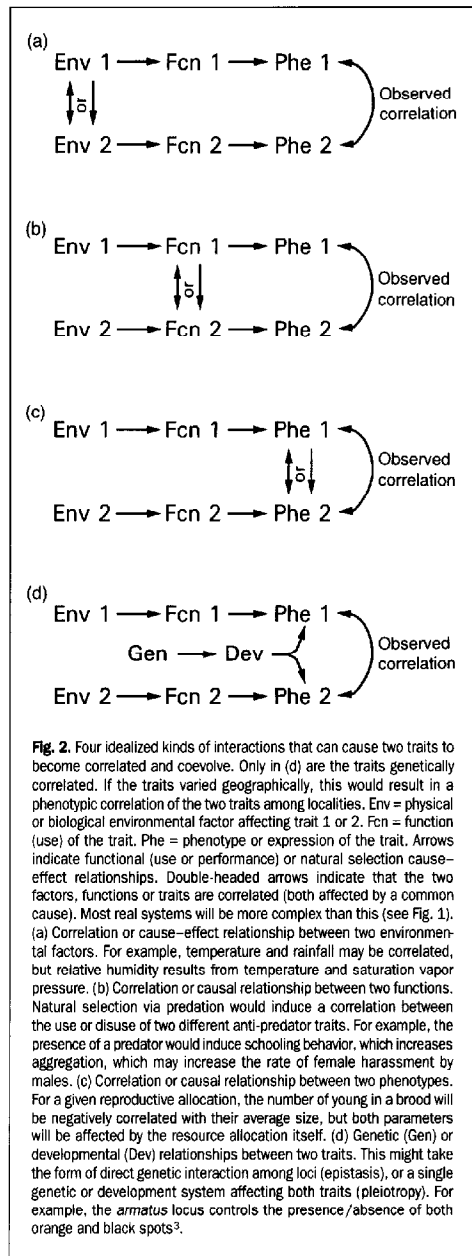
**Evolutionary effects of interactions among traits and the environment**

Figure 1 does not show all possible relationships, but the main point is not the details of the interactions, but the fact that the interactions exist. The interaction network among the traits suggests that traits do not evolve independently, even though they may be genetically independent. These interactions should cause phenotypic correlations among the traits both within and among populations. Among-population covariation may be easier to detect than within-population covariation because the range of causes, and hence their effects, will be greater. This assumes that the same factors work in all populations.

Most discussions of interactions and correlated evolution of traits concentrate on the genetic and developmental causes of correlations among traits<sup>34</sup>. Genetic correlations can be unexpected. For example, aggressive behavior and life history traits covary phenotypically and genetically in poeciliids and sticklebacks because genetic variation in pituitary function affects both<sup>35</sup>. If geographically varying natural selection affects any one or more genetically correlated traits, then there will also be a phenotypic correlation between the traits when measured among populations; concordant geographical variation as in Table 1. However, covariance among traits can also evolve as a result of the correlated effects of natural selection and interrelationships of function among traits<sup>36,37</sup>, as strongly suggested by Table 1 and Fig. 1.

We can conceptually simplify Fig. 1 by considering two logical chains of cause-effect relationships which can lead to correlated phenotypic distributions of two traits in a population (Fig. 2). One kind of chain is environment→function→phenotype (Fig. 2a-c). A trait's function is a description of what a trait does and how it performs during the interaction between the organism and the environment. A trait's function translates environmental factor variation into fitness variation, which leads to phenotypic selection, which, along with heritability, leads to the population's phenotypic distribution. A second kind of chain translates genotype via development into phenotype, so the two chains converge on the phenotype (Fig. 2d). Arnold<sup>36,37</sup> considers all of these components to be in a hierarchy, but given the potential for interaction at all levels, a logical chain or network may be a more useful approach. In addition, some genotypes interact with the environment through development or experience during phenotype construction, resulting in a cause-effect network involving both phenotypic selection and genetics converging on the phenotype. However, the main point here is that each trait is affected by chains of cause-effect relationships, and interactions can occur between the chains of two traits at any link in each chain (Fig. 2).

If two correlated environmental factors cause natural selection on genetically or developmentally uncorrelated



**Fig. 2.** Four idealized kinds of interactions that can cause two traits to become correlated and coevolve. Only in (d) are the traits genetically correlated. If the traits varied geographically, this would result in a phenotypic correlation of the two traits among localities. Env = physical or biological environmental factor affecting trait 1 or 2. Fcn = function (use) of the trait. Phe = phenotype or expression of the trait. Arrows indicate functional (use or performance) or natural selection cause-effect relationships. Double-headed arrows indicate that the two factors, functions or traits are correlated (both affected by a common cause). Most real systems will be more complex than this (see Fig. 1). (a) Correlation or cause-effect relationship between two environmental factors. For example, temperature and rainfall may be correlated, but relative humidity results from temperature and saturation vapor pressure. (b) Correlation or causal relationship between two functions. Natural selection via predation would induce a correlation between the use or disuse of two different anti-predator traits. For example, the presence of a predator would induce schooling behavior, which increases aggregation, which may increase the rate of female harassment by males. (c) Correlation or causal relationship between two phenotypes. For a given reproductive allocation, the number of young in a brood will be negatively correlated with their average size, but both parameters will be affected by the resource allocation itself. (d) Genetic (Gen) or developmental (Dev) relationships between two traits. This might take the form of direct genetic interaction among loci (epistasis), or a single genetic or development system affecting both traits (pleiotropy). For example, the *armatus* locus controls the presence/absence of both orange and black spots<sup>3</sup>.

traits, then a phenotypic correlation will result (Fig. 2a). This is called correlational selection because selection on two or more traits is correlated<sup>36,37</sup>. The correlation arises because some combinations of trait values work much better together and have higher fitness than other combinations of the same trait values. For example, there is a correlation between predation and food density both within and among undisturbed guppy populations. Within populations subject to medium or low predation, the stream bed is a mosaic of shade and sun flecks. The tracks of sun

flecks will have a higher diatom and other food density than areas shaded all day, but guppies in the sun flecks will be more conspicuous to predators<sup>12</sup>. Correlations evolve among populations because higher predation streams tend to have more sun throughout the day than lower predation sites (this is now being drastically altered by human disturbance). In both cases, the correlation between predation and food productivity may cause a phenotypic correlation between age at maturity, colored spot size, and time spent on non-foraging behavior because these combinations are favored by the correlated environmental factors. The correlations may not be strong enough to be detected within populations, but they are obvious among populations (Fig. 1, Table 1).

If a single environmental factor affects two unrelated traits, they will also become correlated. For example, predation alone induces correlations among color patch size<sup>4</sup>, patch numbers<sup>4</sup>, reaction distance<sup>9,10</sup>, predator inspection and schooling<sup>28</sup> (Fig. 1). Large patches and a short reaction distance result in easier detection by predators than the large-long or small-short combinations. The small-long combination would also have lower fitness than large-long or small-short because smaller spots are discriminated against in sexual selection. The advantageous combinations subtend a larger visual angle to females and a smaller angle to predators. The net effect is that there is a correlation between the traits, and this is observed among populations<sup>4,38</sup>.

Correlations between genetically unrelated traits can also arise out of related or jointly constrained functions (Fig. 2b), and this can induce correlational selection. Functions can be correlated because one function is required before another one is performed, as in the stages of a courtship or feeding sequence. Functions can also be correlated because they operate within a common resource. For example, time is an absolute constraint because guppies cannot forage, court or escape predation at the same time. Predation reduces the amount of time that can be spent foraging or courting, while increased food density allows faster foraging for shorter periods, leaving more time for courtship, and causing correlations among these functions (Fig. 1). Within a given total courtship time, the time spent in sneaking reduces the time available for the full visual display, but increased predation and light intensity favors the less-conspicuous sneak attempts. As a result, the traits are negatively correlated (Fig. 2b).

Trade-offs in function can also have a genetic or developmental component which affects the relationships among traits at the phenotypic level (Fig. 2c), as in life history and color-pattern traits. For a given reproductive allocation (which is heritable), if a female produces more offspring, then she will also produce smaller offspring, because her body size is limiting<sup>16,39,40</sup>. This results in a negative phenotypic correlation between brood size (number of offspring) and offspring size when measured among individuals with similar reproductive allocations within populations and among populations with the same predation intensity. It could also result in a positive correlation measured among populations with different predation intensities because greater reproductive allocation is also favored with increased predation intensity. Body size is heritable and constrains the total area of colored spots, so there is a negative relationship between number of spots and size of spots within populations. The main point of Fig. 2 is that both environmental and functional relationships can give rise to correlational selection and correlations among traits, both within and among populations.

These processes may have imposed the relatively consistent correlated geographical variation in many different guppy traits.

Given enough correlational selection for a long enough time, and isolation (or isolation by distance) from populations with different selective regimes, the pattern of genetic variation and covariation among traits in a population will evolve to 'fit' the local selection and correlational selection network, within the constraints imposed by mutation, epistasis and pleiotropy. The net effect will be that traits are genetically, functionally and selectively correlated<sup>36,37</sup>, even if the population is not in equilibrium. There will be an even stronger pattern of geographical covariation of traits among populations. For example, high light intensity is correlated with predation intensity, both geographically and with time of day and weather<sup>28</sup>. This may have led to the behavioral (functional) and evolutionary shift towards more courtship at low light intensities and proportionally more sneak copulation attempts at high light intensities<sup>28</sup>. In turn, this may have resulted in the observed evolutionary shift in courtship style<sup>28,29</sup>, as well as an independent but similar shift in other traits (Table 1), leading to the network of interactions in Fig. 1. In summary, although it is often assumed that correlations among traits arise as a result of genetic or developmental factors (Fig. 2d), correlations and cause-effect relationships among any of the factors in Fig. 2 can lead to correlations among traits (Fig. 2a-c). These factors can induce correlational selection, which would lead to correlated shifts in trait distributions, which can eventually lead to genetic correlations, tying many suites of traits together.

Once environmental, functional and genetic correlations among traits are present, it may be difficult for a population to follow other evolutionary trajectories if large changes in environment or function strongly affect the pattern of correlations in selection<sup>36</sup>. For example, in an artificial selection experiment with mosquitos, in which correlational selection was imposed either similar to or opposite to that of the genetic correlation, the response to selection was rapid when the two were parallel but greatly retarded when they were opposite<sup>41</sup>. The relationships in Fig. 1 suggest that, even if there is geographical variation in environmental factors, the network of interactions among environmental factors and trait functions (Fig. 1) may ensure that correlational selection varies geographically in a characteristic way. Regular and predictable geographic variation in correlational selection will cause suites of traits to evolve together, and populations to diverge along characteristic trajectories, both in phenotype and genotype.

#### Intraspecific and interspecific variation

If the ecological and behavioral interactions shown in Fig. 1 are common, then we would expect to see similar multivariate patterns in other species. Unfortunately, except for sticklebacks (*Gasterosteus aculeatus*)<sup>42-44</sup>, extensive within-species work on the comparative biology of many different kinds of traits in natural habitats is rare. Such work would be most valuable, especially in a greater diversity of orders and phyla. How often do networks of interactions with particular patterns appear in different species? How many of these patterns depend upon the external environment and how many depend upon functional relationships? How often do functional relationships and environmental correlations have similar topologies? How often do genetic correlations evolve to match selective correlations? Such knowledge might enable us to predict the direction of evolution within species.

Although species can be defined by whether or not their member populations can interbreed, congeners generally differ in many different suites of traits, just as do guppy populations on a smaller scale. An understanding of the causes of divergence within species in terms of multivariate variation may provide clues to the early stages of speciation and the likely directions of divergence of the sister species. Unfortunately, guppies are probably not speciating. Although there is female preference for males of their own population over others, it is not strong<sup>32,45,46</sup>, and there is no sign of genetical (postmating) incompatibility among populations. In addition, female preferences vary greatly among populations, even among populations within the same predation regime<sup>32</sup>. We would expect more geographically homogeneous mating preferences within incipient species. Nonhomogeneous preferences would probably prevent populations from differentiating in concert, directly for sexually selected traits, and indirectly for other traits because there would be as much gene flow among habitat (predation) regimes as within them. There are at least three possible reasons for the lack of speciation in guppies, ephemeral habitat gradients, small scale selection regimes, and the reduction of mate preferences in high predation areas.

Speciation may be difficult because guppies live in what may be geologically relatively ephemeral habitats (low order streams). The environmental gradients may not last longer than  $10^4$  years, and the positions of boundaries (waterfalls or extensive riffles) between sets of populations living in different habitats (predation intensity, etc.) may not remain constant longer than  $10^3$  years. This may not allow enough time for strong multivariate differentiation and full speciation to occur. Ephemeral habitat gradients would also reduce the opportunity for consistent selection against hybrids between differentiated groups, further reducing the opportunity for sexual isolation. Freshwater sticklebacks live in somewhat more stable habitats (lakes and larger streams), and have repeatedly diverged from the marine form into two different but sympatric forms (benthic and limnetic). Like guppies, they have diverged into a range of subspecific differentiation among many traits<sup>42,44</sup>, but have not generated many congeners. A possible contradiction to the ephemerality argument is the very rapid response to changed predation intensity in guppy color patterns<sup>5</sup> and life history patterns<sup>16,18</sup> in 2–11 years or 6–40 generations. This suggests that selection for these traits is very strong and response much faster than the longevity of a waterfall or other predator barrier.

The geographical scale of gene flow relative to that of selection determines how strongly groups of populations can differentiate, even under strong selection<sup>47</sup>. The gene flow scale ( $\ell$ ) of guppies is approximately 0.75 km of stream length<sup>47</sup> and the stream drainages are small<sup>4</sup>, so the zones of single selection regimes (particular levels of predation, food density, light, etc.) probably consist of fewer than 100 gene flow units, and may consist of as few as 10, especially in low-predation sites. This means that every guppy population is not very far away (in  $\ell$  units) from other populations that are under different selective regimes. Therefore, although selection for some traits is probably strong, its small spatial scale relative to gene flow may prevent the very strong and spatially large differentiation (compared to  $\ell$ ), which is characteristic of subspecies and species<sup>47</sup>. What does seem to be happening is the repeated but small-scale evolutionary divergence of populations in response to geographically heterogeneous natural selec-

tion. The small geographical scale of habitat gradients may prevent large-scale adaptive radiation and multiple speciation in guppies, and perhaps sticklebacks.

As predation intensity increases among guppy populations, female preferences become weaker<sup>21,31,32</sup>, even though there is a net preference by females for males of their own population<sup>32</sup>. Waterfalls and riffles allow more downstream than upstream gene flow, and downstream (higher predation) populations also receive gene flow from more sources (tributaries) than upstream populations. These effects would prevent or retard downstream divergence and sexual isolation from upstream populations. In summary, possible habitat ephemerality, small areas of uniform selection direction, net downstream gene flow, and reduction of the importance of mate choice downstream, all conspire to retard or prevent speciation in guppies.

If the suites of interactions found in guppies and sticklebacks were characteristic of species living in larger (relative to  $\ell$ ) and more-stable environmental gradients, we might be able to predict where and when speciation can occur, as well as how suites of traits tend to coevolve. For this we need to find species with the following characteristics:

- Convenient and known biology and ecology, short generation time and easy laboratory culture for genetic studies.
- Known genetic variation for a variety of different suites of traits.
- A variety of different traits with known and measurable function and known selective causes.
- Measureable geographical variation in most or all of the known major selective factors.
- Two or more kinds of geographically and geologically relatively stable habitats.
- Geographical ranges of zones of specific selective regimes considerably larger than the gene flow scale, and not intermingled as much (relative to  $\ell$ ) as in guppies. This allows enough isolation-by-distance for large-scale multiple-trait differentiation.
- Some geographical correlations between selective factors, as in guppies. This would probably lead to stronger differentiation among correlated traits over larger areas. It would also be more likely to lead to speciation than uncorrelated geographic variation among factors would; spatially uncorrelated selection gradients would lead to more chaotic geographical variation among traits.
- A stronger link between sexually selected traits and non-mating aspects of fitness may give rise to larger zones of homogeneous preference, encouraging more large-scale differentiation among groups of populations.
- Replicate zones of particular combinations of selective factors provide stronger tests of hypotheses than only two different zones.

Stream organisms have many of these characteristics, but the geographical scales of these species may be too small relative to  $\ell$  to study the larger-scale phenomena. Herbivorous insects may provide the solution; they have large-scale patterns of natural selection that are induced by known distributions of host plants and other selective factors, as in the insect genus *Timema*<sup>48</sup>.

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