

animal Behavior

How and Why
Animals Do the
Things They Do



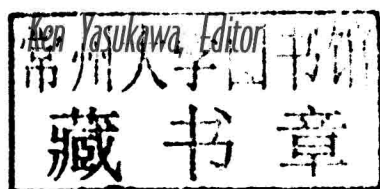
Volume 3 | Integration and Application with Case Studies

Ken Yasukawa, Editor

Animal Behavior

How and Why Animals Do the Things They Do

Volume 3: Integration and Application with Case Studies



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Contents

1. Integrated Studies of Stickleback Behavior	1
<i>Alison M. Bell</i>	
2. Friends and Enemies: How Social Dynamics Shape Communication and Song Learning in Song Sparrows	33
<i>Michael D. Beecher and Çağlar Akçay</i>	
3. A Tale of Two Spiders: Investigating Communication in Two Unique Model Species Using Video Digitization and Playback	63
<i>George Uetz and David Clark</i>	
4. Studying Lifelong Male-Male Partnerships in a Tropical Bird	99
<i>David B. McDonald</i>	
5. Be Loved, Be Prey, Be Eaten	121
<i>Rachel A. Page, Michael J. Ryan, and Ximena E. Bernal</i>	
6. Siblicide in Birds	153
<i>Douglas W. Mock</i>	
7. Referential Signals: A Window into Animal Minds	175
<i>Carolynn L. Smith and Christopher S. Evans</i>	

8. Cotton-top Tamarins: Research for Conservation and Understanding Human Behavior	209
<i>Charles T. Snowdon</i>	
9. Avian Brood Parasitism: How to Spot a Foreign Egg in the Nest?	249
<i>Mark E. Hauber and Jason Low</i>	
10. How Animals Remember Places and Find Their Way Around	269
<i>David F. Sherry</i>	
11. Cognitive Repertoire, Cognitive Legacies, and Collective Reasoning: The Next Frontiers in Conservation Behavior	289
<i>Guillermo Paz-y-Miño-C</i>	
12. Beauty in the Eye of the Beholder: Potentially Adaptive Individual Differences in Human Mate Preferences	311
<i>Lisa M. DeBruine, Benedict C. Jones, S. Craig Roberts, Anthony C. Little, and Christopher D. Watkins</i>	
<i>Glossary</i>	349
<i>About the Editor and Contributors</i>	361
<i>About the Editorial Board</i>	365
<i>Index</i>	367

Integrated Studies of Stickleback Behavior

Alison M. Bell

INTRODUCTION

Threespine sticklebacks (*Gasterosteus aculeatus*) have taught us a great deal about animal behavior. This chapter starts with a tribute to sticklebacks, explaining why this small fish has proven to be such a fascinating subject for studies of animal behavior. Although there are many stories to tell about sticklebacks, this chapter focuses on individual differences in behavior as a case study to illustrate an integrative approach to studying animal behavior. The chapter concludes with a forecast of what new genomic technologies are likely to add to our understanding of individual differences in behavior and to the study of animal behavior in general.

OVERVIEW OF STICKLEBACK BIOLOGY AND BEHAVIOR

The threespine stickleback is a small (adult size is 3–8 cm standard length) teleost fish that is widely distributed throughout the northern hemisphere. The species includes three fundamental life-history types: marine, anadromous, and freshwater (Wootton, 1976; Baker, 1994). For many years, sticklebacks have been a model organism in animal behavior, due in large part to the important role they played in the development of ethological theory (Tinbergen, 1940). Niko Tinbergen was awarded a Nobel Prize, which he shared with two other prominent *ethologists*, Konrad Lorenz and Karl von Frisch, due in no small part to the important discoveries that he and his collaborators made using this small fish.

The reproductive behavior of male sticklebacks has been particularly well studied both in the laboratory and in the field. During the breeding season, male sticklebacks develop red *nuptial coloration* on the belly and blue around the eye. They are highly aggressive toward their neighbors and vigorously defend nesting territories. In the field, territorial male sticklebacks are frequently confronted by intruders, and they are especially aggressive toward other male sticklebacks—they chase and attack male sticklebacks that intrude into their territory. Early ethological studies of sticklebacks emphasized the role of *sign stimuli*, such as the male's red belly, as elicitors of aggressive behavior (Tinbergen, 1951). Besides these highly energetically demanding defensive activities, territorial male sticklebacks actively court females and provide all of the parental care to the developing offspring, from fanning the eggs to defending the nest and retrieving fry that stray from the nest. Therefore, breeding male sticklebacks engage in a variety of activities, all of which are important to reproductive fitness, but some of these activities are potentially contradictory, even though they are not always temporarily or spatially separated from each other. Sticklebacks have been a model system in ethology for understanding how animals resolve conflicting demands, and early ethological theory of "drives" and "motivation" were inspired by studies of sticklebacks (Tinbergen & van Iersel, 1947). For example, high aggression (aggression drive) might compromise a male's courting ability (sex drive) and might also reduce the quality of parental care (parental drive). Despite the solid role that sticklebacks have played in studies of animal behavior, we do not yet understand the molecular mechanisms underlying their rich behavioral repertoire. However, this situation is likely to change in the near future aided by emerging genomic tools, including a full genome sequence (Kingsley & Peichel, 2007), described below.

In addition to their distinguished history as ethological subjects, sticklebacks have also become favorites for the study of *ecological speciation* (Rundle et al., 2000) and *phenotypic evolution* (Peichel et al., 2001; Cresko et al., 2004; Colosimo et al., 2005). Freshwater populations of sticklebacks exhibit dramatic population-level phenotypic variation, and all freshwater populations are the descendants of marine or *anadromous* (fishes that spend most of their lives in the sea and migrate to fresh water to breed) stickleback, which are widely distributed in the Holarctic. Despite their wide geographic distribution, marine sticklebacks are relatively uniform with respect to *morphology* (Walker & Bell, 2000). Whereas the large marine populations are likely to have changed relatively little over the last 7 to 12 million years (Bell & Foster, 1994), the derived freshwater populations have undergone a dramatic diversification (Foster, 1995; McKinnon et al., 2004).

This *radiation* offers several unique opportunities for studying evolutionary processes. For example, much of the phenotypic variation that we observe among freshwater populations is naturally replicated across independent sets of populations. Freshwater populations rapidly evolved *convergent phenotypes* in response to similar selective pressures, and they did so independently by multiple colonizations of different freshwater drainages. Therefore different populations of sticklebacks with convergent phenotypes are independently derived from the marine ancestral type and are therefore biological replicates. In other words, the radiation is a naturally replicated experiment. Because much of the phenotypic variation among populations is adaptive and a response to selection pressures in local environments, comparing across populations can provide clues about the important ecological factors affecting the evolution of traits.

One of the most important selective factors shaping the biology of this small fish is *predation pressure*. Sticklebacks often provide a primary food source for a diverse assemblage of predators including predatory birds, fishes, and some insects. Sticklebacks have *lateral plates*, which are rigid, bony plates along the side of the body that offer some protection from toothed predators such as predatory fishes, and there is tremendous variation among populations in lateral plate morphology, often associated with predation regime (reviewed in Reimchen, 1994). Similarly, variation in predation pressure has also shaped the evolution of behavioral variation among stickleback populations. Sticklebacks from areas where there are high levels of predation tend to show heightened sensitivity to predators when compared to their counterparts in relatively low-predation environments (Huntingford & Coulter, 1989; Huntingford et al., 1994; Walling et al., 2003, 2004; Messler et al., 2007).

CASE STUDY: THE BOLDNESS-AGGRESSIVENESS BEHAVIORAL SYNDROME IN STICKLEBACKS

In a classic study, Felicity Huntingford showed that individual sticklebacks varied along a “shy-bold” continuum. Some individuals were relatively bold toward predators when they were young, while others were more timid. The individuals that were relatively bold as juveniles grew up to become the individuals that were especially aggressive toward *conspecifics* later in life, as adults. In other words, there was a positive correlation between boldness and aggressiveness, or what we might call a boldness-aggressiveness *behavioral syndrome* (Huntingford, 1976).

Part of the reason why this initial study is significant is that we tend to think that behaviors in different contexts are independent of one another.

My favorite example to illustrate this point is that standard animal behavior textbooks often have separate chapters devoted to, for example, foraging behavior, aggressive behavior, and territorial behavior (Bell, 2007). But there is growing evidence for some unexpected correlations between behaviors, or behavioral syndromes. These correlations are especially unexpected when they are between behaviors that occur in very different contexts—it is not too surprising that the time spent attacking a conspecific is correlated with the number of bites delivered to a conspecific during a fight, for example. It is more surprising to think that time spent attacking a conspecific correlates with how an individual (imagine a male red-winged blackbird [*Agelaius phoeniceus*], for example) behaves in a flock or during competition for resources, or with how it parents. These kinds of correlations are unexpected because we tend to assume that how an individual behaves in a particular context is independent of how that same individual behaves in other contexts, and we tend to assume that individuals do not have much trouble switching to the appropriate behavior when situations change. In other words, a common assumption in behavioral ecology is that there is no carryover between behaviors in different contexts and that behavior is instantaneously plastic and changes according to the immediate circumstances (Sih et al., 2004). But one of the interesting things about behavioral syndromes is that if individuals have a tendency to behave a certain way, then individuals might not be able to behave optimally in all contexts; they have a behavioral type that limits their behavioral flexibility, and a behavioral syndrome can be a constraint on optimal behavior (Sih et al., 2004). In what follows, I describe two sets of experiments with sticklebacks to test whether the previously identified boldness-aggressiveness syndrome might act as a constraint over either developmental or evolutionary time.

ARE BEHAVIORAL SYNDROMES CONSTRAINTS OVER DEVELOPMENTAL TIME?

Huntingford (1976) found that male sticklebacks that were relatively bold toward predators were also relatively more aggressive toward conspecifics. Does this apply to sticklebacks throughout their entire development? In other words, is a bold and aggressive fish always constrained to be bold and aggressive from a young fry all the way through adulthood?

We can think about the stability of behavior through development in a variety of ways (Stamps & Groothuis, 2010), but for our purposes here, we are interested in whether rank-order individual differences in a single behavior are stable over time (*sensu* differential stability [Stamps & Groothuis, 2010]). Imagine we measure a behavior, say behavior Y, at three points in time on five different individuals, each represented by a different line in Figure 1.1.

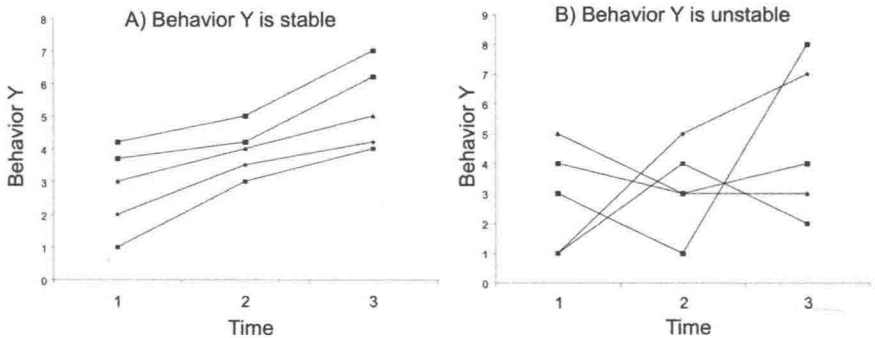


Figure 1.1. The stability of a single behavior. Each line represents the behavior of a different individual, measured at three different points in time. Rank-order differences between individuals are stable in (a) but not in (b).

A stable behavior is one in which the rank-order differences among individuals are preserved through time—the individual that showed the highest levels of behavior Y at time 1 also showed the highest level of behavior Y at time 2. So according to this type of stability, we are not asking whether behavior does not change—it can go up or down in magnitude. Instead, we are asking about whether the rank order of individuals changes. An unstable behavior is one in which individuals might be relatively low on a behavior at one age and then very high at another, so that we are not able to predict how an individual will behave at time 2 if we know how the individual behaved at time 1.

The scenario described above just considered the stability of one trait at a time rather than an entire syndrome or correlation between behaviors. Again, we can use hypothetical data to distinguish between a stable versus an unstable syndrome. Imagine we observe a group of animals, and we measure boldness and aggressiveness on each individual at two different ages. If at age 1 there is a positive correlation between boldness and aggressiveness and at age 2 we also see a positive correlation, we could infer that the syndrome, or the correlation, is stable (Figure 1.2).

If, on the other hand, there is a positive correlation at one age but not at another, then the syndrome is unstable. It is important to note that a stable syndrome does not require stable single behaviors because we might observe the same relationship between two traits at two ages, even if individual behavior changes over time.

To study the development of a behavioral syndrome in sticklebacks, Judy Stamps and I (Bell & Stamps, 2004) reared the offspring of 11 full-sibling families from two populations (Putah Creek and the Navarro River) of

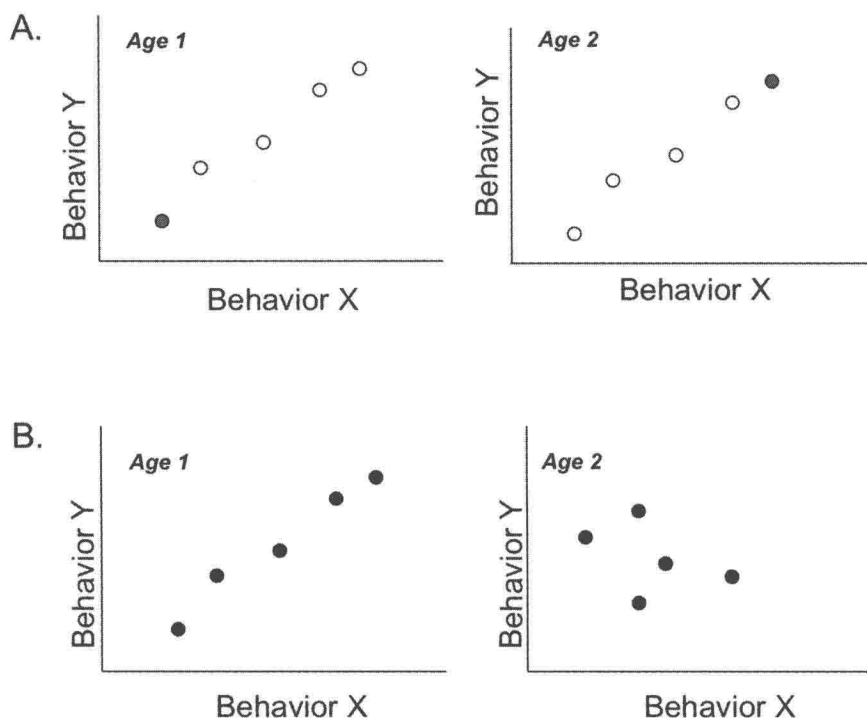


Figure 1.2. The stability of a behavioral syndrome. Individuals are indicated with different data points. (a) A syndrome is stable when we observe the same correlation between behaviors at different points in time, that is, at different ages. Note that a stable syndrome does not necessarily imply stable single behaviors (the individual represented by the filled circle showed the highest levels of behaviors x and y at age 1 but the lowest levels at age 2). (b) A syndrome is unstable when behaviors are correlated at some ages but not others.

sticklebacks in the lab and measured each individually marked individual's aggressiveness and boldness on three occasions during development. Therefore, for each fish, we had a record of its aggressive behavior and boldness at three points during development. To measure aggressiveness, we introduced a conspecific of the same size and sex and from the same population into a transparent cylinder and recorded the response of the focal individual to the conspecific (Figure 1.3).

To measure boldness, we measured each individual's reaction to a predator. We used different techniques to measure boldness toward a predator for each of the different ages in order to simulate the different types of predators experienced by different age classes (Figure 1.4).

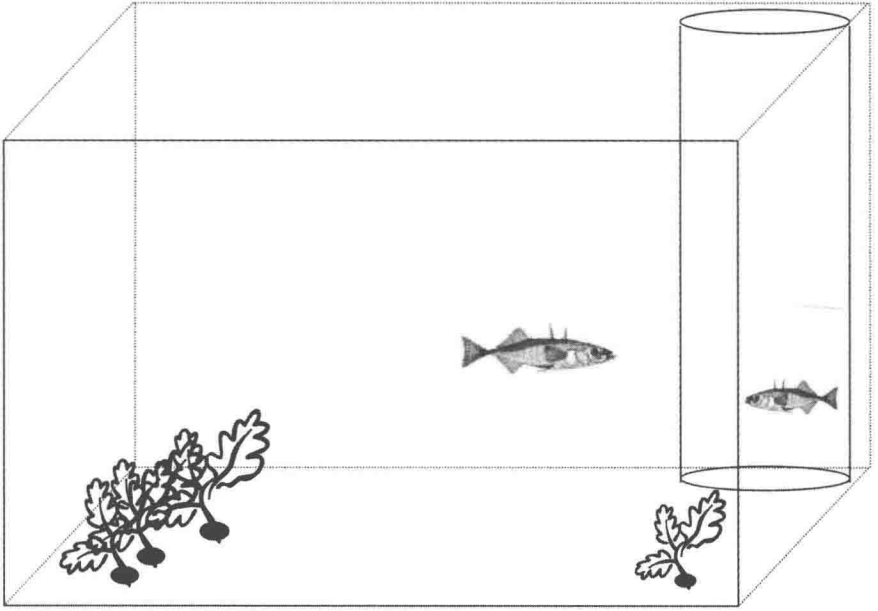


Figure 1.3. Measuring aggressiveness in sticklebacks. The focal fish is presented with an intruder confined to a flask.

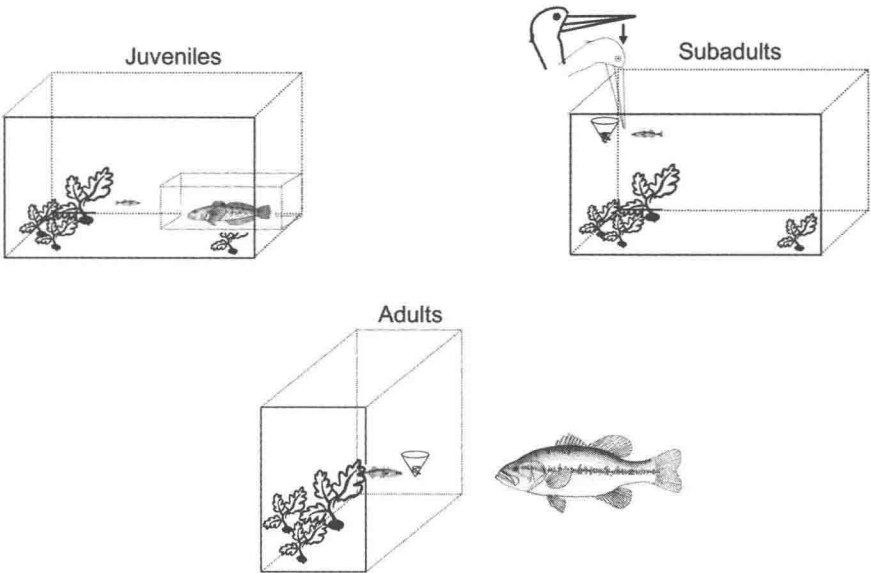


Figure 1.4. Measuring boldness, see text for details. (From Bell, 2005)

This approach was adopted from *developmental psychology*, in which there is a tradition of using different tasks to measure the same behavior at different ages. For example, one might measure inhibition in children in different ways at different ages—in an infant, you might measure inhibition as attachment to the mother, while in a toddler you might measure inhibition by reaction to peers. The basic idea in all of these observations, though, was the same—to record the response of the fish to predation risk—and we interpreted behaviors such as predator inspection behavior, foraging under predation risk, and high levels of activity after a simulated predator attack as “boldness.” On juveniles, we measured each individual’s reaction to a live coast range sculpin (*Cottus aleuticus*). On subadults, we measured each individual’s willingness to forage under predation risk after a simulated attack by a great egret (*Ardea alba*), and on adults we measured their willingness to forage under predation risk by a live largemouth bass (*Micropterus salmoides*).

We found that neither boldness nor aggressiveness were stable over time (Bell & Stamps, 2004); individuals that were bold as a juvenile did not necessarily grow up to become a very bold adult, or vice versa. Similarly, a very aggressive juvenile was not necessarily a very aggressive adult. But that was just one trait at a time. The results for the boldness-aggressiveness syndrome are in Table 1.1, which show the correlation coefficients between boldness and aggressiveness for each population at each age.

In the Navarro population, boldness and aggressiveness were significantly positively correlated with each other at all three ages. That is, as juveniles, subadults, and adults, individuals that were more bold were also more aggressive. For the Putah population, though, boldness and aggressiveness were related to each other in juveniles but not in subadults or adults. In other words, in the Putah population, the syndrome changed over ontogeny. However, in the Navarro population, the single behaviors were unstable, but the syndrome was stable. That is, boldness and aggression were positively correlated at all

Table 1.1. Correlation coefficients between boldness and aggressiveness at three different ages in two populations. Note that in the Navarro population, boldness and aggressiveness were positively correlated with each other at all three ages (Bell & Stamps, 2004).

Population	Juvenile	Subadult	Adult
Navarro (<i>N</i> = 35)	0.56**	0.45**	0.60**
Putah (<i>N</i> = 28)	0.43*	0.12	0.18

P* < 0.05 *P* < 0.01

three ages, so that fish that were more bold were also more aggressive, but a fish that was bold as a juvenile did not necessarily grow up to become a bold adult. However, if a fish was bold as a juvenile, it was also aggressive as a juvenile.

Altogether, these results suggest that correlations between behaviors do not necessarily mean that an individual who started out as one behavioral type, for instance very bold and aggressive, is destined to grow up to be bold and aggressive. On the one hand, this can be interpreted as a lack of *developmental constraint* because there was some flexibility of behavior. However, the pattern that we observed in the Navarro population was that behaviors tended to change together in a coordinated fashion, which means that an individual could not be both shy and aggressive at the same time. Therefore some phenotypic possibilities were limited. The reversible coordinated shift of an entire suite of behaviors in concert with each other is similar to other familiar behavioral transitions, such as the reversible shift between different alternative mating types. For example, when a male cichlid obtains a territory, he becomes brightly colored, very aggressive, and courts females. But this shift is reversible and if that male loses his territory, the entire suites of traits changes back in a coordinated way (Hofmann et al., 1999).

ARE BEHAVIORAL SYNDROMES CONSTRAINTS OVER EVOLUTIONARY TIME?

As described above, sticklebacks exhibit tremendous population-level variation in behavior and morphology. The radiation is a powerful natural experiment because there were independent colonization events and tremendous divergence among populations. If we return to the previously identified boldness-aggressiveness syndrome in sticklebacks (Figure 1.5), we might envision that the traits are correlated in a hypothetical marine ancestor of sticklebacks.

If the correlation between boldness and aggressiveness were to act as a constraint, we can hypothesize about how we would expect the two traits to be related to each other in descendant populations in different selective environments, such as streams that were independently colonized by a marine ancestor and then underwent divergence.

If the two behaviors are genetically correlated and if selection were to favor, for example, high levels of aggressiveness in one population (open circles) but not in another population (gray circles), then over a few generations we might expect the individuals from the population depicted with open circles not only to be more aggressive but also to be more bold so that the entire population shifts up along the correlation. In other words, if the correlation between

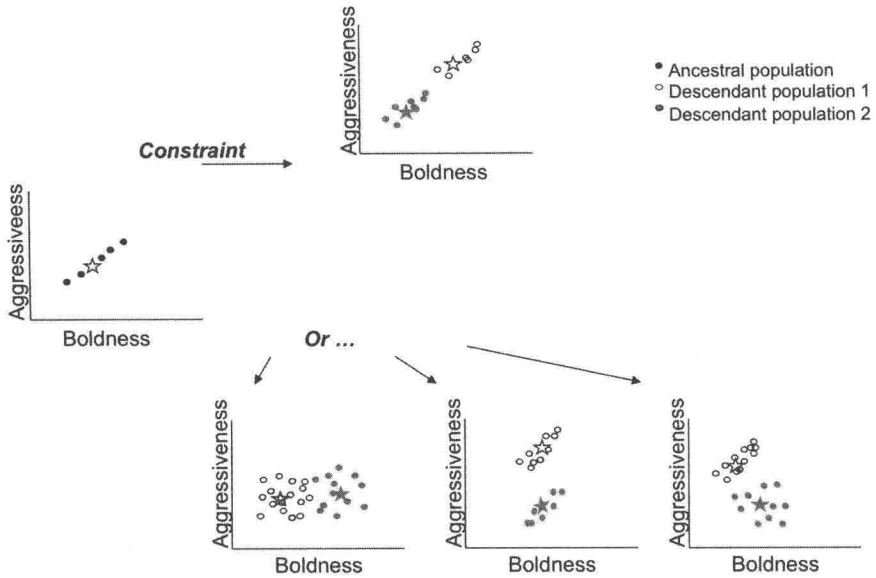


Figure 1.5. The evolutionary fate of correlated traits. Each data point represents a different individual, coded by population; population means are designated with stars. See text for details. (From Bell, 2005)

boldness and aggression acts as a constraint, we would expect to see the behavioral syndrome in different populations, and we would expect the means of the two populations, designated by stars in Figure 1.5, to also lie along the correlation.

Alternatively, if the correlation between boldness and aggression is not constrained by a genetic correlation, or if the correlation can be uncoupled, we can envision a variety of possible outcomes. Perhaps the correlation is broken apart in different populations. Or perhaps the mean level of one of the traits, such as aggression, differs between the populations, but the syndrome is present in both—the intercept is simply shifted up, but the slope is the same. Or maybe the correlation is broken apart in one population but not the other. My point in going through these scenarios is to point out that comparing the relationship between behavioral traits in different populations can tell us whether a behavioral syndrome is acting as an evolutionary constraint.

To test this hypothesis, I collected wild-caught adults from the Navarro River and Putah Creek. I brought the adults into the lab, and I measured boldness and aggressiveness on each individual, using the methods described earlier (the subjects were actually the parents of the fish described in the previous section). The results for the wild-caught adults are in Figure 1.6.

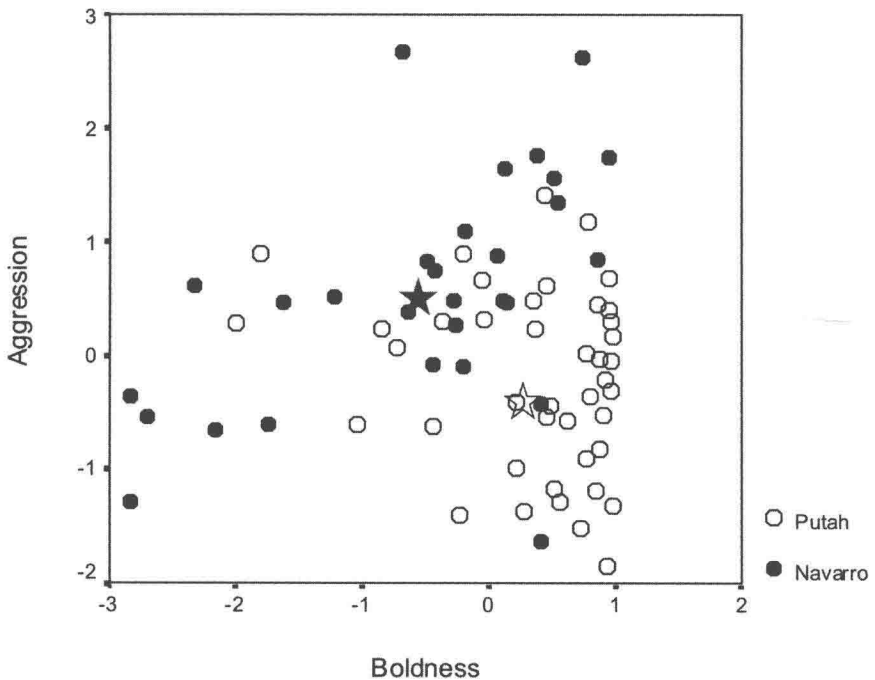


Figure 1.6. Aggressiveness is on the y axis, and boldness is on the x axis. These results show principal component scores. The means are indicated with stars. Boldness and aggressiveness were positively correlated in one population but not the other (Navarro $r = 0.52$, $N = 29$, $P < 0.01$; Putah $r = 0.13$, $N = 42$, NS). (From Bell, 2005)

The first thing that was most obvious—to me, at least—when watching the fish is that Navarro fish were very timid around the predator—while Putah fish boldly foraged under predation risk, the Navarro fish spent most of their time hiding, and this was a statistically significant difference between the means of the two populations. The other thing that was immediately obvious was the Putah fish were much *less* aggressive than Navarro fish. Again, the difference in population means is statistically significant. So means of the populations, although they are just two data points, do not support the idea that the positive correlation between boldness and aggressiveness can act as a constraint because the population that was more bold (Putah) was actually less aggressive.

When we look closer at the actual individual values—each of the dots represents a different individual, coded by population—we found that across individuals from the Navarro River, there was a significant positive correlation between boldness and aggressiveness, so that the most aggressive fish were also

the most bold. So the boldness-aggressiveness syndrome appears to be a general or robust feature of the Navarro population—it characterized wild-caught adult Navarro fish; it was stable through development; it was maintained in the lab; and, moreover, based on quantitative genetic analyses using both parent-offspring regression and full-sibling analysis, there was a strong genetic correlation between boldness and aggression in the Navarro population (Bell, 2005). In the Putah population, though, the two traits appeared to be independent of one another. So the fact that boldness and aggression are not always related to each other in different populations of stickleback, as well as the fact as the means are actually *negatively* related to each other between the two populations, suggests that this syndrome can be readily broken apart.

All in all, these results show that boldness and aggressiveness do not always go together: boldness and aggressiveness are not always related to each other at different ages or in different populations. These results beg the question as to why behaviors might be packaged together in some groups but not others and encourage us to develop proximate and ultimate explanations for why behavioral correlations should occur sometimes but not always (for progress on that front see (Stamps, 2007; Wolf et al., 2007; Dingemanse & Wolf, 2010; Wolf & Weissing, 2010). In what follows, I describe a series of experiments approaching this question empirically from both an *ultimate* and a *proximate* perspective. From an ultimate perspective, we can approach the issue from the top down by asking if the syndrome can be adaptive and how it is shaped by selection. From a proximate perspective, we can ask whether boldness towards predators and aggressiveness toward conspecifics share a common neuroendocrine link that might couple them together (Figure 1.7).

IS THE BOLDNESS-AGGRESSIVENESS SYNDROME ADAPTIVE UNDER PREDATION RISK?

Are there ecological differences between the two populations that might give some insights into why boldness and aggressiveness were positively correlated with each other in the Navarro River population but not in the Putah Creek population (Bell, 2005)? Indeed, the populations differ in several respects, but one of the ways that is most striking is with respect to predation pressure. When I present this work in a talk I always like to ask the audience to guess: Which population do you think is the high-predation population? Is it the one where the two behaviors were correlated, or the one in which the two behaviors were not correlated? Almost always there are votes for both sides. Part of the point in asking the audience to consider this question is to