Forum

Trait duplication by means of sensory bias

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Trait duplication has played an important role in the origin of species, higher taxonomic groups, and novel traits (West-Eberhard 2003; Carroll 2005; Lynch 2007; Leitch AR and Leitch IJ 2008). Trait duplication involves the duplication of body segments, body parts, genes, and even of whole genomes. These events can promote diversification and novelty by allowing previously evolved mechanisms to acquire novel functions, rather than requiring the machinery for those novel functions to be selected from scratch, mutation by mutation (West-Eberhard 2003; Carroll 2005; Lynch 2007; Des Marais and Rausher 2008). I suggest that a well-known mechanism in behavioral ecology—sensory bias—may foster a process resulting in trait duplication with important consequences for the diversification of mate preferences.

Sensory bias is a process in which preferences originate when responses that evolved in nonsexual contexts or as by-products of sensory systems or other preferences are co-opted by novel displays into favoring as mates the individuals that use the displays (West-Eberhard 1984; Ryan 1990, 1998; Arak and Enquist 1993; Christy 1995; Endler and Basolo 1998; ten Cate and Rowe 2007; Vahed 2007). For example, responses that evolved in ecological contexts may be co-opted, as in water mites in which a predatory response is elicited by a male display (Proctor 1991, 1992). Work with diverse taxa suggests that co-option by sensory bias is often involved in the origin of preferences (West-Eberhard 1984; Endler and Basolo 1998; Rodriguez and Snedden 2004; Gerhardt et al. 2007; Vahed 2007). This process has received various terms—for example, sensory trap, sensory exploitation, preexisting bias—emphasizing different aspects of selection on responses and having different implications for the subsequent evolution of the preference (Endler and Basolo 1998). Furthermore, sensory bias may refer to a feature of the sensory system, to the process of co-option (Ryan 1990), to a product of selection, or to a by-product feature (Arak and Enquist 1993; Endler and Basolo 1998; Arnqvist 2006). Here, I address processes in which a fully formed trait is co-opted either from a different context or from a different range of display values. I refer to the process of co-option as “co-option by sensory bias” and to the response as the “co-opted response.”

Co-option by sensory bias has 2 major consequences, each apparently at odds with the other: 1) It can incorporate a great diversity of traits and modalities of perception into sexual selection (West-Eberhard 1984; Christy 1995; Sakaluk 2000; Arnqvist 2006; Vahed 2007). With traits co-opted from ecological contexts, this amounts to “ecological capture” of diversity (to paraphrase the hypothesis of genic capture in sexual traits; Rowe and Houle 1996). But even with by-products of sensory systems, co-option also enriches the variety of preferences and displays. Sensory bias may thus help fuel rapid and extravagi
tent evolution by sexual selection (West-Eberhard 1983, 1984). 2) However, the long-term course of this process is contested, with considerable debate about the capacity of a co-opted response to coevolve and diverge with a display (Ryan 1990, 1998, 1999; Reeve and Sherman 1993; Ryan and Rand 1993; Basolo and Endler 1995; Christy and Backwell 1995; Shaw 1995; Sherman and Wolfenbarger 1995a, 1995b; Endler and Basolo 1998; Sherman and Reeve 1999; Autumn et al. 2002; Rodriguez and Snedden 2004; Fuller et al. 2005; Arnqvist 2006; Kokko et al. 2006). Nevertheless, there are cases in which it seems that coevolution has followed co-option. For example, moth hearing evolved under selection to evade bat echolocation cries, and in some species it then evolved the function in pair formation involving approach to ultrasonic signals (Greenfield 2002). If initial responses were negative, coevolution must have followed because current sexual responses are positive (Bradbury and Vehrencamp 1998, p. 533). However, it is not clear what mechanisms fostered this trajectory, although categorical perception (Greenfield and Weber 2000; Greenfield and Baker 2003; Greig and Greenfield 2004) and context-dependence (Rodrı́guez and Greenfield 2004) help regulate current responses. The challenge presented by sensory bias is thus to understand the evolution of a co-opted response after co-option.

EVALUATION AFTER CO-OPTION

This discussion is for a preference that originated through co-option by sensory bias, that is, for which there is evidence that it is ancestral to the display and functions in a nonsexual context or can be identified as part of a mechanism with such a function (Basolo 1995; Shaw 1995; Endler and Basolo 1998; Rodriguez and Snedden 2004). There are 4 hypotheses about the subsequent evolution of such a preference (Figure 1). The first 3 have been widely discussed, so I briefly present their main tenets before contrasting them with the hypothesis that co-option by sensory bias may lead to trait duplication.

Costly co-option

This hypothesis posits that a co-opted response is likely be costly because of the manipulation of mating decisions that co-option entails; costs are in turn expected to favor the reduction of the expression of the co-opted response, an outcome sometimes referred to as “emancipation from exploitation” (Reeve and Sherman 1993; Bradbury and Vehrencamp 1998, 2000; Sakaluk 2000; Arnqvist 2006; Vahed 2007). According to this hypothesis, co-option by sensory bias can give rise to diverse preferences, but there will subsequently be a decrease in their expression (Figure 1A) followed by a reduction in the display because costs to the bearer are no longer offset by benefits. Alternatively, there may be cycles of increasing display effectiveness and decreasing responsiveness, as in models of antagonistic sexual selection (Holland and Rice 1998; Sakaluk 2000).

Constrained co-option

This hypothesis posits that co-opted responses are likely to be costly but that selection in the original context favoring their
expression will be stronger than selection in the novel context favoring their reduction (West-Eberhard 1984; Ryan and Rand 1993; Ryan 1998; Fuller et al. 2005; Arnqvist 2006). Because selection in the original context is expected to maintain the response at its optimum, this hypothesis predicts net stabilizing selection on the co-opted response (Fuller et al. 2005) in spite of costs in the novel context. Also, refining discrimination between stimuli across contexts may bring costly errors in the original context (e.g., increased false negatives; West-Eberhard 1984; Christy 1995). Thus, the response is constrained to the form favored in the original context. Here, co-option can give rise to a diversity of preferences, but they will subsequently be evolutionarily static (Endler and Basolo 1998). The display may become more elaborate under selection to better fit the values favored by the preference, but the preference and display cannot coevolve. The preference can be nudged away from stasis only by a change in selection in the original context (Christy 1995; Endler and Basolo 1998).

Synergistic co-option

This hypothesis states that selection in both contexts may favor the same form of the response (Christy 1995; Dawkins and Guilford 1996; Bradbury and Vehrencamp 1998, 2000; Endler and Basolo 1998). For example, co-opted responses may harp on indicators of mate quality, help reduce mate-searching time, or lower the risks of mate searching. This hypothesis also predicts stasis in the preference but because of concordance in selection across contexts. The consequences of a change in selection in the original context differ between this and the constrained co-option hypothesis: A change in one context is likely to detract from the concordance and weaken net selection favoring the expression of the response, approximating the dynamics predicted by either the costly or the constrained co-option hypotheses. However, it is also possible (if less likely) that the change in selection in the original context might strengthen the synergism with the novel context (say, if the new form of the response harps even more squarely on indicators of mate quality or if it further lowers the costs of mate searching).

Trait duplication

This hypothesis recognizes that any of the above forms of selection on co-opted responses may occur. But it further notes that when selection in each context favors different forms of the response there is the opportunity for it to be shaped independently in each context. A difference in selection between contexts is anticipated by all hypotheses except synergistic co-option. When this difference is present, the trait duplication hypothesis recognizes that co-option may often set the stage for the evolution of context-dependent regulation of the response, allowing the novel preference to be modified according to costs and benefits in the mate choice context (rather than be reduced or remain static) while the ancestral response is maintained or evolves separately according to costs and benefits in the original context. As the response acquires context-dependent expression or regulation, it will acquire the ability to diverge in form across contexts, and eventually the result will be trait duplication. This hypothesis is implicit.

Figure 1

Hypotheses about the evolution of responses co-opted by sensory bias, subsequent to the co-option event. (A) The costly, constrained, and synergistic co-option hypotheses view the response as a single trait expressed in 2 contexts. It evolves according to net selection across contexts. (B) The trait duplication hypothesis posits that co-option may set the stage for the evolution of context-dependent regulation of the response, giving rise to 2 traits: the original response and a preference that can be shaped by selection independently, each in its own context.
in some discussions on the costs and benefits of co-opted responses, such as the potential for “emancipation from exploitation” due to an increase in discriminatory ability (Bradbury and Vehrencamp 1998, p. 533, 2000; Arniquist 2006; see also Sakaluk 2000). A comparison with phenotypic plasticity can illustrate the evolutionary potential of co-option by sensory bias. With plasticity, the expression of a trait in a novel environment can expose variation in developmental mechanisms to novel forms of selection (West-Eberhard 2003, 2005; Suzuki and Nijhout 2006, 2008). Co-option also results in the response being expressed in a novel environment, exposing variation in its regulating mechanisms to novel forms of selection. This is because the co-opted response (besides being expressed in its original context) is expressed in a novel environment comprised of 1) external stimuli present in the mate choice context (e.g., displays) and 2) internal physiological stimuli and regulating mechanisms active when the animal behaves in the mate choice context. Expression in the novel context may thus foster the evolution of context-dependent regulation of the response. However, there is an important difference between plasticity and sensory bias. With plasticity, any individual is likely to experience only a subset of the alternative environments (which is what leads to diversity in phenotypes). With sensory bias, every “receiver” individual (in the sense of signalers and receivers) will experience each context (i.e., environment) many times in its life. This means that any diversification in the co-opted response across contexts would occur within individuals rather than between individuals across environments. It is this within-individual nature of the potential for diversification in the co-opted response that leads me to suggest that sensory bias may promote trait duplication.

There is a difference between the standard use of the term trait duplication and the sense in which sensory bias may foster it. In the usual sense, trait duplication begins with an instance of duplication, after which the copies may come to be regulated differently. The sequence of events in sensory bias is the opposite: A trait (say, a foraging response) is first co-opted into the mate choice context. Once it is regulated by factors in both contexts, it may evolve context-dependence and acquire a new form in the novel context.

WHY CONTEXT-DEPENDENCE IS LIKELY TO EVOLVE

Co-option is a derived condition in which a response’s regulating mechanisms are exposed to novel cues, and this may foster the evolution of context-dependence. The contexts would differ in subtle ways, such as levels of hunger or hormone expression or cues present. The neuroethological literature abounds in examples of context-dependent signal processing in which subtle differences are important. For example, awake versus anesthetized birds and awake versus sleeping birds differ in neural responses or in the involvement of brain hemispheres during acoustic stimulation (Schmidt and Konishi 1998; George et al. 2003; Nick and Konishi 2005); signaling versus quiet primates and bats differ in the response of auditory neurons to acoustic stimulation (Muller-Preuss and Ploog 1981; Metzner 1993); flying versus walking insects differ in the signal features they attend to (Doolan and Young 1989; Sergejeva and Popov 1994; Rodriguez and Greenfield 2004); and whether an insect is in contact with the substrate influences the elicitation of escape behavior by auditory interneurons (Ritzmann et al. 1980; Nolen and Hoy 1984; ter Hofstede et al., 2009). Furthermore, in tinguara frogs, natural and experimental variation in hormone levels influences preference strength and sensitivity to sensory modalities (Lynch et al. 2006; Cummings, Bernal, et al. 2008). Finally, the social environment has important effects on the regulation of behavior (see Robinson et al. 2008). For instance, in songbirds, swordtail fish, and tinguara frogs experimental variation in social stimuli influences patterns of hormone concentration and gene expression (Hoke et al. 2003; Ball et al. 2006; Lynch and Wilczynski 2006, 2008; Cummings, Larkins-Ford, et al. 2008). In short, subtle differences in context can be important in the regulation of behavior. The potential for context-dependence may be even greater across the more widely differing contexts involved in sensory bias (e.g., foraging vs. mate choice).

The flip side of the above argument is that when the contexts differ very little, the potential for the evolution of context-dependence may be limited, even if favored by selection. This may be the case with responses co-opted by displays that are used in the same contexts and places as the original stimuli. Examples of this may occur in the fiddler crab and water mite case studies discussed below. Other examples may occur in cichlid fish in which males have evolved egg-mimicking displays that elicit female responses to pick up eggs, which results in the female picking up the male’s sperm and fertilizing her eggs with it (Wickler 1962, 1968, 1997; Goldschmidt 1991); in darter fish in which male egg-mimicking displays elicit the female response to lay eggs in nests that already contain eggs (Porter et al. 2002); and in katydids in which male egg-mimicking genitalia elicit the female egg-fertilizing response of releasing sperm, causing her to eject most of her stored sperm (von Helversen DV and von Helversen OV 1991). In these cases, the original and novel contexts of the response functions are so close in time and space that it may be difficult for context-dependence to arise. However, even here, internal environments composed of regulatory physiological cues may result in differences between contexts.

TESTING THE HYPOTHESES

The costly, constrained, and synergistic co-option hypotheses view the response as a single trait that experiences selection in 2 contexts; these hypotheses differ in the form of selection and the resulting evolutionary pattern they predict. The trait duplication hypothesis recognizes that any of those forms of selection may occur, but notes that if selection in the two contexts were to favor different forms of the response 2 independent traits may evolve because co-option may foster the evolution of context-dependent regulation. Testing the hypotheses may require 2 approaches: 1) estimating the relative strength and direction of all sources of selection on the response or experimentally assessing costs and benefits (Kokko et al. 2002, 2006; Cordero and Eberhard 2003; Fuller et al. 2005) and 2) inferring the course of evolution after co-option. This combination may be necessary because the process may be observed at different stages in different species, with the earliest stage being soon after co-option (Fuller et al. 2005). If enough time has elapsed, tests may involve inferring what already has happened, but if not it may be necessary to estimate costs and benefits. Furthermore, phylogenetic tests of the predicted patterns rely on specific assumptions about the rate of the evolution of preferences and displays and about the rate of speciation and may thus not be useful in some cases (Endler and Basolo 1998).

Costly co-option predicts net costs of expressing the response; that these costs will arise from the novel context; and that there will be a derived decrease in the expression of the response after co-option (Figure 1A). Constrained co-option predicts net benefits of expressing the response due to benefits in its original context and in spite of costs in the novel context; and stasis in the response after co-option (Figure 1A). Natural or experimental changes in selection in the original context should change the response (Christy 1995; Endler and Basolo 1998). Synergistic co-option predicts...
net benefits of expressing the response due to a concordance between the original and mate choice contexts; and stasis in the response after co-option (Figure 1A). Changes in selection in the original context would lead to the dynamics of costly or constrained co-option (assuming that repeat concordance is unlikely). Trait duplication predicts that, if selection in each context favors different forms of the response, there will be derived context-dependent expression of the response (Figure 1B). This prediction can be tested with transposition experiments, in which responses to the original stimulus and to the co-opting display are assessed in each context (e.g., Christy 1995; Christy et al. 2003). Context-dependence would be supported if responses to each stimulus type differ between contexts. A refinement of this test might involve a single set of stimuli (say, synthetic stimuli resembling the original and co-opting stimulus and signal) presented in 2 contexts to generate 2 preference functions. Differences in preference functions across contexts would support context-dependence. In a phylogenetic framework, this test could be further refined with the prediction that context-dependence should be weak or absent in basal species (especially where the co-opting display has not arisen) and stronger in derived groups in which the co-opting display has evolved.

It will be most straightforward to distinguish trait duplication from costly co-option with comparative methods because they predict opposing patterns. Constrained and synergistic co-option predict similar patterns, so estimates of costs and benefits will be required. It will be difficult to distinguish synergistic co-option and trait duplication if there is concordance in selection across contexts because context-dependence might be possible but not favored. If so, the potential for context-dependence could be tested experimentally with transposition experiments. Another difficulty would arise if context-dependence was favored by selection but impossible due to similarity between contexts. Thus, diverse approaches will be necessary to distinguish between the 4 hypotheses.

THREE CASE STUDIES

There have been few comprehensive tests of hypotheses about evolution after co-option by sensory bias. This is in part because it has taken great effort to show that co-option by sensory bias may be widespread (West-Eberhard 1984; Ryan 1990; Arak and Enquist 1993; Christy 1995; Endler and Basolo 1998; Rodriguez and Snedden 2004; Arnqvist 2006; ten Cate and Rowe 2007; Vahed 2007). The study of evolution after co-option must build on this work. Nevertheless, 3 case studies show that this process can have a variety of outcomes: 1) In fiddler crabs, males of some species build pillars or mounds next to their burrows; these constructions help to attract females by exploiting the predator-evasion response of approaching a landmark (Christy 1995). At least in one species, the co-opted response may be favored in the mate choice context because male pillar building is condition-dependent (Backwell et al. 1995). Furthermore, in one species responses to natural objects and male-built hoods neither differ between reproductive and nonreproductive females nor between mate-searching and nonmate-searching females (Christy et al. 2003); in this species and another females regulate their preference as if it were beneficial in reducing predation risk: when perceiving an increased threat of predation they strengthen their preference for male structures (Kim et al. 2007, 2009). 2) In Neumania water mites, males of some species tremble their legs to mimic the vibrations of copepod prey, co-opting the foraging reactions of females, which clutch at leg-trembling males (Proctor 1991, 1992). Hungrier females show the response more often (Proctor 1991). Thus, findings in fiddler crabs and water mites support synergistic co-option and reject trait duplication, as no context-dependence seems to have evolved. 3) In Goodeinae fish, male displays that mimic prey items have co-opted a foraging response, and subsequently its expression has changed independently in the foraging and mate choice contexts (Macías García and Ramirez 2005). Importantly, in species with more elaborate displays responsiveness has decreased in the foraging context (Macías García and Ramirez 2005). This study rejects costly co-option, because it shows the exact opposite evolutionary pattern (Figure 1A), and supports trait duplication, because it demonstrates derived context-dependent expression of the co-opted response (Figure 1B).

CONCLUSION

If co-option can foster the evolution of context-dependence, sensory bias may sometimes permit an uncoupling of the origin of preferences from their subsequent evolution. In the default scenario, genetic variation in the novel preference and display would lead to genetic covariance between the sexes, creating Fisherian runaway selection (Fisher 1958; Mead and Arnold 2004). This has been recognized as likely (Lande 1981; Fuller et al. 2005; Arnqvist 2006), but such “genetic benefits” of mate choice are also expected to be weaker than any costs or constraints (Fuller et al. 2005; Arnqvist 2006). This limitation has applied to any sort of benefit unless synergistic with the original context, if for no other reason than the expectation that individuals will experience the original context (e.g., foraging) more frequently than the mate choice context. The perspective offered by the trait duplication hypothesis is that the evolution of the co-opted response may not depend on a summation of selection across contexts but rather be tuned to each context. If so, the capture of diversity by sensory bias may be reconciled with subsequent change and elaboration by sexual selection.

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