

Behavioral syndromes versus darwinian algorithms

Bryan D. Neff¹ and Paul W. Sherman²

¹Department of Biology, University of Western Ontario, London, Ontario, Canada, N6A 5B7

²Department of Neurobiology and Behavior, Cornell University, Seeley G. Mudd Hall, Ithaca, NY 14853, USA

In a recent paper in *TREE* [1], Sih *et al.* suggested that populations and species ‘often exhibit behavioral syndromes; that is, suites of correlated behaviors across situations.’ They argued that interindividual consistency in behavior is due to genetic constraints on plasticity, which ‘can explain behaviors that appear strikingly non-adaptive in an isolated context.’ By contrast, others have argued that, when a genetic correlation imposes enough of a fitness cost in one situation, selection will favor genetic modifiers that limit the expression of the behavior in the costly context, thus decoupling the behavior across situations [2,3]. Here, we highlight some well studied examples of adaptive behavioral plasticity as counter-examples to behavioral syndromes, and discuss how we could test whether behavioral correlations, when they occur, represent adaptive darwinian algorithms as opposed to nonadaptive genetic constraints.

At the crux of behavioral syndromes is the notion that genetic constraints prevent individuals from adaptively altering their behavior in different situations. Consider the following example: parental investment theory predicts that parents should adjust their caring behavior according to the reproductive value of their brood whenever there are other investment options that potentially yield greater fitness [4]. For example, if variations in the behavior of males are adaptively plastic, they should adjust their parental behavior based on information about their own paternity and their other reproductive options, sometimes increasing or decreasing brood defense when paternity changes across situations. By contrast, the syndrome framework predicts that all males will adjust their behavior similarly based on evolutionary predispositions (see [5]) about mean paternity across situations – increasing or decreasing defense when perceived paternity typically has increased or decreased across situations through evolutionary time.

How common are behavioral syndromes versus adaptive variation in plasticity? In contrast to the implications of Sih *et al.* [1], many animals use situation-dependent darwinian algorithms to adjust behavior adaptively. For example: in bluegill sunfish *Lepomis macrochirus*, paternity varies owing to the occurrence of sneak spawning. We have shown that care-providing males can assess their paternity based on odor cues emanating from fry but not from eggs. When fry odors were manipulated by swapping eggs between the nests of males shortly after spawning, no difference in egg defense was observed between experimental and control males (whose eggs were

not exchanged) [6]. However, after hatching, experimental males significantly decreased, and control males increased, their levels of defense. These changes imply adaptive variation in behavioral plasticity across situations (before and after eggs hatch) based on whether ‘cuckoldry’ occurred rather than on behavioral syndromes.

In another example, some spadefoot toad tadpoles *Scaphiopus bombifrons* develop into a carnivorous morph whereas others remain omnivores until metamorphosis. Pfennig *et al.* [7] reported that cannibalistic tadpoles nip at unfamiliar conspecifics, and then either consume them if they are unrelated or release them if they are siblings. However, when the same cannibalistic individuals were starved for 48 h, they were equally likely to consume siblings and non-siblings. These changes in behavior indicate adaptive plasticity in cannibalistic aggression across situations (hunger levels) rather than behavioral syndromes.

As noted by Sih *et al.* [1], some populations do display behavioral correlations across situations. For example, in streamside salamanders *Ambystoma barbouri*, Sih *et al.* [8] discovered a genetic correlation between activity levels during the night and day, across risky and safe situations (presence versus absence of a fish predator). They postulated that selection for increased nocturnal activity, which increases the chance that individuals will drift out of fish-containing pools, has led to correlated increases in daytime activity (i.e. time spent out of refuge). However, in this case, it is unclear whether the behavioral correlation is maladaptive. All individuals decrease diurnal activity in the presence of fish, but individuals that are more active in the absence of fish remain more active in the presence of fish (their rank order is maintained). Possibly these ‘overly’ active individuals are physically better able to attack prey (night and day) and escape predators (day). Thus, they might be maximizing their fitness by being active in both situations.

How might we test between the adaptive behavioral correlation versus nonadaptive syndrome hypotheses? For streamside salamanders, the most straightforward experiment involves splitting family groups in half, and restricting one half of each group to a safe refuge during daylight hours, thereby suppressing their activity level below what the genetic correlation would otherwise permit. The behavioral syndrome hypothesis predicts that the restricted family members should have higher fitnesses (i.e. be more likely to survive to metamorphosis) than should their unrestricted siblings, whereas the behavioral plasticity hypothesis predicts the opposite.

Corresponding author: Bryan D. Neff (bneff@uwo.ca).

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The outcome of split-sibship experiments on this and other species will help decide whether behavioral syndromes can, as Sih *et al.* [1] claim 'limit behavioral plasticity and explain non-optimal behavior.'

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Letters Response

Reply to Neff and Sherman. Behavioral syndromes versus darwinian algorithms

Andrew Sih¹, Alison M. Bell² and J. Chadwick Johnson³

¹Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA

²Department of Environmental and Evolutionary Biology, Graham Kerr Building, University of Glasgow, UK, G12 8QQ

³Division of Life Sciences, University of Toronto at Scarborough, 1265 Military Trail, Toronto, Ontario, Canada, M1C 1A4

In their comment on our *TREE* article [1], Neff and Sherman [2] contrast adaptationist versus behavioral syndrome views on behavioral plasticity. Below, we clarify our views on these concepts.

Neff and Sherman [2] present two examples of sophisticated, context-dependent, adaptive behavioral plasticity [3,4]. The implication is that this plasticity is incompatible with syndromes; that is, the syndromes imply maladaptation and lack of plasticity. However, our view is that, although syndromes can explain suboptimal behavior in a particular isolated context, they do not necessarily result in maladaptation, and do not conflict with sophisticated plasticity. Instead, we suggest that syndromes and sophisticated plasticity are complementary rather than opposing views.

Consider their two examples. Neff [3] showed that, on average, male bluegill sunfish *Lepomis macrochirus* altered their parental defense in response to experimental changes in paternity. This implies adaptive behavioral plasticity. However, as with most behavioral studies, Neff [3] found variation among individuals in their response to reduced paternity. Some males abandoned their nests, whereas others stayed and defended the mixed brood. The syndrome view asks whether this behavioral variation might be correlated to behavior in other contexts. Do males that stay and defend the brood aggressively (even when paternity is reduced) also defend particularly aggressively when paternity is high? Are these males also particularly aggressive toward other males during the courtship phase, or toward potential predators? If these behavioral correlations exist, then selection on aggressiveness in other contexts might carryover to

explain some of the variation in brood defense observed when paternity is low.

In a second example, Pfennig *et al.* [4] showed that, if cannibalistic tadpoles are not too hungry, they avoid cannibalizing siblings, but if starved for 48 h, they are equally likely to consume siblings and non-sibs. Neff and Sherman [2] conclude that 'these changes in behavior indicate adaptive plasticity...rather than behavioral syndromes.' Again, however, the tadpoles exhibited considerable individual variation in cannibalistic tendencies. The syndrome view asks whether individual variation in the tendency to cannibalize kin was positively correlated across different hunger levels. In that case, the adaptive benefit of being voracious (non-selective) when starved might spillover to explain some cannibalism of kin even when not too hungry. Interestingly, although Pfennig *et al.* [4] had the data to quantify the key behavioral correlation, they did not show this calculation, presumably because their paper preceded the emergence of the syndrome view.

A more recent study on cannibalism guided by the syndrome framework found that the tendency to engage in pre-copulatory sexual cannibalism (female consumption of courting males) in fishing spiders *Dolomedes triton* was positively correlated to feeding voracity on other prey in both the juvenile and adult stages, and to boldness after exposure to simulated risk (J.C. Johnson, PhD Thesis, University of Kentucky, 2003). Individual females altered their cannibalism rates depending on the availability of males [5]; that is, they showed context-dependent adaptive behavioral plasticity. However, given the syndrome, selection favoring high voracity in other contexts conceivably spills over to cause maladaptive, excess sexual cannibalism by some females.

Corresponding author: Andrew Sih (asih@ucdavis.edu).

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Neff and Sherman [2] also suggest an experimental approach to test the adaptiveness of a behavioral correlation. We agree with their basic idea but note that, in our case, the proposed experiment seems unnecessary. Space limitations preclude detailed discussion, but in essence, larvae outside of refuge suffered very high mortality, whereas those in refuge were safe [6,7]. In more-subtle cases, the proposed experiment might still not provide a definitive test. Even if prey forced to be completely inactive suffer reduced fitness, this would still leave the possibility that control larvae would do better with reduced activity (but not reduced to completely inactive). To test definitively whether behavior is optimal, one must know the optimal behavior. That is no small task, particularly if the optimal behavior is either state or frequency dependent.

An alternative approach for evaluating constraint versus adaptation involves examining the stability of behavioral correlations. Recent work showed that syndromes are not necessarily stable over ontogeny [8] and that populations can differ in their behavioral syndromes [9]. These studies show that the correlations are not absolute constraints. An adaptive framework might explain why behaviors are correlated in some groups (certain ages or populations) but not others. Further work

is needed to understand proximate and ultimate (including adaptive) mechanisms underlying behavioral syndromes.

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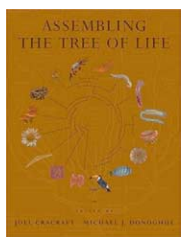
Book Reviews

Putting life in its place

Assembling the Tree of Life edited by Joel Cracraft and Michael J. Donoghue, Oxford University Press, 2004. US\$59.95/£51.99 hbk, £32.99 pbk (592 pages) ISBN 0195172345/0195172353

Andy Purvis

Department of Biological Sciences, Imperial College London, Silwood Park campus, Ascot, Berkshire, UK SL5 7PY



No evolutionary ecologist can have failed to notice the explosion in phylogenetics research over the past decade. As editors Joel Cracraft and Michael Donoghue note, we can now envisage a complete tree of life. Such a phylogeny promises to provide a central organizing principle for all of biological knowledge, and an invaluable framework for the study of diversity, whether pure or applied. So how much progress has been made towards The Tree? In this breathtakingly ambitious book resulting from a 2002 conference, Cracraft and Donoghue have harnessed the expertise of an impressive set of authors to give us an update.

The 26 chapters that form the core of *Assembling the Tree of Life* – mostly synthetic reviews, with some new analyses – is a powerful whirlwind tour of The Tree so far, highlighting areas of consensus and of conflict. All life is here, somewhere, although most of the 561 pages are understandably devoted to the small parts of The Tree where we have given the creatures names. The

organization seems a mite traditional – microbes, then plants, fungi and animals, with vertebrates having the luxury of a chapter per class. However, recent findings from morphological, molecular and genomic analyses illuminate the structure and content at every stage. Inevitably, the less charismatic taxa are dealt with only briefly: one introduction states ‘We cover 15 phyla.’ Most chapters focus on clades, but, sensibly, some treat paraphyletic or polyphyletic assemblages to avoid glaring gaps. Some contributions focus very much on The Tree, but most also use it as a basis for discussing character evolution or macroevolution. *Assembling the Tree of Life* does not dwell on methods – excellent reviews are available [1] – but it does contain thoughtful critique of our ability to find The Tree in the face of problems such as long-branch attraction, and of the concept of a tree in groups with significant lateral gene transfer. Topping and tailing the book are eight short chapters explaining why we should care what The Tree is; these outline clearly its value to science and to society as a whole. Standards of writing and production are high throughout.

The book provides a fascinating status report but, in spite of its title, does not really try to map out a route to

Corresponding author: Andy Purvis (a.purvis@imperial.ac.uk).

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