Commentary

Cliff swallows and the power of behavioral ecology

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It may metaphorically be said that natural selection is daily and hourly scrutinizing, throughout the world, the slightest variations; rejecting those that are bad, preserving and adding up all that are good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the lapse of ages.

—Charles Darwin (1)

The study of adaptive behaviors lies at the very heart of behavioral ecology. Although there is certainly no lack of debate about what constitutes an adaptation (2), most researchers in the field probably would not quibble with the statement that adapted traits are those that are the product of natural selection. Evidence for adaptive behavior then can be found only when the criteria for the process of natural selection to operate are met, namely: (*i*) variation in the trait of interest, (*ii*) fitness differentials across variants of the trait in question, and (*iii*) a means by which the trait is transmitted across generations.

Meeting all three criteria is hardly simple, even for easily quantifiable traits (e.g., certain morphological traits) and gets even more dicey when we start talking about behavioral traits (3). The task becomes more and more daunting when the behavior becomes more and more socially mediated. So, when Brown and Brown (4) in a recent issue of PNAS claim to have found evidence that preference for group size differs among cliff swallows (*Petrochelidon pyrrhonota*), and that this preference is heritable, it's big news.

Since its inception, behavioral ecology and sociobiology have had something of a love/hate relationship with animal group size. Group size seems so fundamental to an animal's well-being—in terms of foraging, predation, disease transmission, mating opportunities, etc.—that it seems reasonable to posit that natural selection should operate in ways to modulate group size according to ecological, genetic, and social circumstances (5). Many studies have, for example, manipulated group size in a given population to examine group size effects on antipredator behavior and foraging (6). In addition, between-population comparisons of group size in a given species often suggest that group size varies as one might expect from a cost/benefit analysis (e.g., ref. 7). Putting together all of the pieces necessary to demonstrate that animals modulate their group size via some heritable preference function, however, has turned out to be incredibly difficult. Yet Brown and Brown demonstrate that with the right system, a detailed knowledge of the biology of the animal in question, and almost endless patience, it can be done.

Brown and Brown have been studying cliff swallows for more than 20 years (8), and their long-term study has proven to be a treasure chest that behavioral ecologists will be drawing from long into the future. What makes their work so powerful is that the vast majority of it takes place in the field, under natural circumstances. And so it should come as no surprise that this is precisely how they opted to study the heritability of group size preferences. That being said, one can't underestimate how difficult studies of heritability in nature genuinely are. It was only with a very meticulous protocol involving many subjects, careful experimental manipulation, and a deep understanding of cliff swallow behavior (the sort of understanding that only emerges after decades of interaction with subjects) that Brown and Brown could have pulled off studying the heritability of complex traits in the wild.

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In experiment 1, using five clusters of cliff swallow colonies, Brown and Brown tackled group size preference and its heritability in two ways. With an impressive sample size of 2,581 birds, the group size of individual swallows was found to be statistically similar to the group size in which their parents lived. This was true for birds that bred at the same site of their parents and birds that emigrated, suggesting that the correlation between parent and offspring was not a function of a common environment.

Using nestlings from two large and five small colonies, Brown and Brown also undertook a classic cross-fostering experiment with cliff swallow young. About half the young from the hundreds of nests in the large colonies were removed, and young from small colonies were placed in their stead. Similarly, half the young in small colonies were replaced by young from large colonies. In all manipulated nests then, Brown and Brown had offspring from large and small colonies. Of the 1,968 birds in their cross-fostering experiment, 721 were recaptured, and the results were as clear as one could hope for. Cross-fostered birds chose breeding colonies that were similar in size to their place of birth. More to the point, Brown and Brown were able to make some fascinating heritability comparisons from their cross-fostering data. The heritability of group size preference for swallows that remained in their natal nests was positive and similar to that of experiment 1. When examining the preference for group size, a parent-offspring heritability analysis showed a significant positive relationship between group size preference in offspring, when the biological parent of such offspring were considered. When the "foster" parent and cross-fostered offspring's group size preference were regressed against each other, a negative heritability was uncovered (birds avoided breeding in group sizes that were similar to those in which they were raised). Further, in all of the analyses run by Brown and Brown, father-offspring heritability estimates were higher than mother-offspring heritabilities, suggesting that maternal effects did not play a large role in group size preference.

One of the many lessons that behavioral ecologists and sociobiologists have learned since E. O. Wilson's classic *Socio-*

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biology (9) is that social behavior in nonhumans is clearly much more complex than was originally thought. Both empiricists and theoreticians now recognize that social behavior in animals often involves complex "if-then" rules, choice of partners and even choice of social environments. Although some of this complexity may well be due to cultural transmission of behavior (10, 11), much of it likely will be the result of natural selection acting on such complexity.

What Brown and Brown show us so eloquently is that even when the trait in question is complex, it might still have a heritable basis. Wherever he may be, Darwin is probably smiling right about now. We may not be able to observe the "slow changes in progress" that often may be associated with behavioral evolution, but we certainly can study them with the empirical, theoretical, and conceptual tools now available to behavioral ecologists (12).

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