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There is no special sauce: a comment on Beekman and Jordan

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> "No one supposes that all individuals of the same species are cast in the same mould. These individual differences are of the highest importance to us, for they are often inherited."
>
> Charles Darwin, *Origin of Species*, Chapter 2, Subsection on "Individual differences"

Beekman and Jordan (2017) raise some criticisms of the study of animal personality that are worth considering. They also voice some popular misconceptions, so this series of papers and commentaries have an opportunity to clear things up. But Beekman and Jordan (2017) also got a few things wrong, including their claim that Darwin (1859) was not interested in individual differences (see above).

One of the authors' misunderstandings is their failure to appreciate why the maintenance of heritable variation in behavior is of such interest to personality researchers. An outstanding question in evolutionary biology is how and why genetic variation is maintained within natural populations over generations. The central problem is that natural selection typically removes variation within populations, rather than maintains it. So when among-individual variation in a behavioral trait is heritable (which is likely to be true for many behavioral traits) and related to fitness, that immediately raises questions about why the variation persists. While a number of mechanisms have been proposed (variable selection, mutation-selection balance, tradeoffs, negative frequency dependence, etc.), theory predicts that the conditions under which these mechanisms are effective are rather restrictive (Hedrick 2006). Moreover, convincing empirical evidence for any of these processes in natural populations is rare and hard to obtain.

Beekman and Jordan (2017) also illustrate some popular misconceptions about the term "personality," much of which reflects baggage from the fact that the term was borrowed from the human personality literature. One of their misunderstandings is that personality implies a "higher psychological process" and is therefore not parsimonious (i.e., Morgan's canon). It is likely that this misunderstanding reflects the way the term "personality" is used in the human personality literature, where it refers to consistent ways of thinking, feeling, and behaving. As observers of nonhuman animal behavior, we have little access to our subjects' thoughts and feelings, and animal personality researchers simply focus on consistent ways of behaving. And the way we study animal personality is really quite simple: we measure the same individuals more than once and quantify within- and among-individual (co)variances. We do not assume any kind of higher-order sophisticated cognitive or emotional processing when interpreting the patterns; *there is no special sauce*. We are agnostic about the sources of variation (genetic, environmental, state dependent) and for how long the differences endure (although it seems reasonable to suppose that correlations that are relatively enduring are more likely to have ecological and evolutionary consequences). This is generally irksome to some people, but there are several reasons why researchers repeatedly measure the same individuals that are well described elsewhere (Sih et al. 2004).

Another problem with the term "personality" is that it has come to be used interchangeably with major axes of behavioral variation, for example, boldness. For example, papers have titles such as "Personality affects *X* (mating success, learning ability, etc.)," when the key result is that an axis of behavioral variation (often boldness) is correlated with *X*. This problem could reflect the way we use the term in the popular vernacular—when we say that something affects our personality we mean to say that we become less extraverted or more conscientious as we get older, or after an experience. But I also think that this problem reflects a bias toward viewing behavioral variation along just a few axes (boldness, aggressiveness, neophobia, exploratory behavior, sociability), an idea originally proposed by (Réale et al. 2007). However, in reality, we know that there is repeatable intraspecific variation in all sorts of behaviors (Bell et al. 2009), and we simply do not yet know whether personality within a given species fits a 5-factor model, much less whether that same 5-factor model is deeply conserved (more on this point next). Indeed, there are other good criteria firmly grounded in the best of behavioral ecology that we can use to help decide which behavioral traits are of most interest, for example, their ecological and fitness relevance (Bell 2007).

The study of animal personality has been criticized by behavioral ecologists for being too descriptive, rather than hypothesis-driven. I think it is worthwhile to consider an alternative perspective, though, which is that studies of animal personality are not descriptive enough (Uher 2008)! From the point of view of human personality psychology, which has spent the last 30 years debating the best way to describe major axes of variation in humans, it might be premature for us to start asking questions about the evolution of personality because we have not yet comprehensively described the phenomenon. I think this line of reasoning should be taken with a grain of salt because unlike human personality psychologists, we study lots of different types of critters, and comprehensively understanding all the relevant axes of variation in literally millions of species is simply not going to happen.

That being said, I do agree with the authors that documenting variation is just the first step and is relatively easy compared to all the hard work that needs to be done to understand its underlying causes and evolutionary consequences. We should be encouraging better and more thorough studies, rather than telling students to give up altogether simply because the topic is popular.

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Insights for behavioral ecology from behavioral syndromes: a comment on Beekman and Jordan

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"It's like déjà vu all over again"- Yogi Berra

My comment will focus on Beekman and Jordan's (BJ17) fundamental criticisms that: the animal personality field is largely descriptive, that it does little that was not already being done, and that it has offered little in terms of novel insights. Most of my points (and indeed, many other points of rebuttal that I could address given more space) were discussed in earlier papers cited by BJ17 (Sih et al. 2004; Sih and Bell 2008), but apparently bear repeating, hence my quoting the great Yogi.

NOTHING NEW IN WHAT WE DO?

Contrary to BJ17, in major areas of behavioral ecology, the study of behavioral syndromes fundamentally changed what we do, the questions we ask, and thus the insights gained. For example, fifteen years ago, a typical behavioral ecology study on prey responses to predation risk used the following design. The behaviour (e.g. activity, refuge use) of 6 groups of 10 fish exposed to predator cues was compared to the behaviour of 6 other groups of 10 fish held in the absence of predation risk. For statistical independence, a rigorous study would use *different* fish for the 2 (or more) treatments. If the investigator faced a shortage of study subjects, she/he might use the same fish in multiple treatments, but would have to make excuses for doing so. Few studies explicitly tracked the same individuals across 2 or more treatment conditions and even fewer tested (and tracked) the same individuals repeatedly in each of the treatments. Of course, repeated assaying of individuals often in multiple treatments is now the norm in the study of animal personalities. Doing so has opened numerous questions that were not previously addressed by most predator–prey behavioural ecologists: are some individuals consistently bolder than others? *Why* are some bolder than others, how stable are these differences over ontogeny, and how do these consistent individual differences affect fitness and aspects of predator–prey ecology? Some studies addressed issues that animal behaviourists were accustomed to addressing (e.g. genetic basis of boldness), but other questions were new (e.g. why are individuals consistent at all in their behaviour when having a (bold or shy) personality is associated with suboptimal behaviour in some circumstances? How does personality dependent dispersal influence invasion ecology?).

Behavioural ecologists studying mating or social behaviours have historically been more likely to track individuals, but still often drew conclusions based on a group's average behaviour testing each individual only once. For example, in studies of female mate choice, one might test 30 guppy females once each to see whether a particular population prefers larger or redder males. A few studies in "standard" behavioral ecology took the step of quantifying individual differences in female choice, but the animal personality field suggests testing numerous other questions about individual differences: are differences in mate choice related to other aspects of personality, or for that matter, to choosiness or choice about other options. Are the same fish (or humans) that are choosier about mates also choosier about habitats, diets or social groups?

More broadly, 15 years ago, behavioral ecology studies tended to focus on behaviour in a particular context during one portion of the individual's overall life cycle. An insight from the study of behavioral syndromes is the potential importance of carryovers across contexts and across different parts of the life cycle. Does aggressiveness in male-male competition carryover to be associated with unnecessary aggressiveness towards females, poor parental care, or a tendency to be bolder than appropriate (perhaps months later during the nonbreeding season) with predators present? How is the exploratory tendency of great tits related to their mating or assortative mating, parental care, dispersal or learning behaviour? While a few earlier studies addressed these behavioral syndrome issues, they were not the norm in behavioral ecology.

An exception, as noted by BJ17, is the long-standing recognition that individuals with distinct "morphotypes" (eusocial insect castes, alternative reproductive morphs, or males versus females) often exhibit consistent differences in suites of behaviours. The relatively new insight was that individuals often exhibit behavioral syndromes even when they do not exhibit overt morphotypes. Indeed, a topic that remains under-addressed is personality differences within morphotypes. The larger point is that the study of animal personalities has guided the field to new questions (and new experimental designs and statistical methods) that are exciting and important.

IT'S ALL DESCRIPTIVE?

Yes, early on, the field was largely descriptive. However, because the field was asking new questions, many descriptive studies yielded new, surprising results about patterns of *variation* in animal personalities or behavioral syndromes that stimulated ongoing study. For example, while several earlier, classic studies showed that boldness and aggressiveness are positively correlated, follow-up work revealed the intriguing fact that this correlation is not always significant, but instead depends on the population's history of exposure to high predation risk (Dingemanse et al. 2010). Neither this issue nor this result was, to my knowledge, on the radar for standard behavioral ecology. As is the norm in any developing field, this result and others describing *variation* in personality patterns stimulated new frameworks, ideas, theory and empirical directions (e.g. Sih et al. 2015).

NO CONCEPTUAL ADVANCES?

Although early on, much of the excitement revolved around the discovery of new, sometimes surprising patterns, a growing interest has been in exploring novel frameworks for explaining these patterns