

Review

Future directions in behavioural syndromes research

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A behavioural syndrome occurs when individuals behave in a consistent way through time or across contexts and is analogous to ‘personality’ or ‘temperament’. Interest is accumulating in behavioural syndromes owing to their important ecological and evolutionary consequences. There are plenty of opportunities in this burgeoning young field to integrate proximate and functional approaches to studying behaviour, but there are few guidelines about where to start or how to design a study on behavioural syndromes. After summarizing what we do and do not know, this brief review aims to act as a general guide for studying behavioural syndromes. Although the array of possible behavioural combinations can seem overwhelming, there are at least four different strategies that can be used to choose which behaviours or contexts to study in a behavioural syndromes view. I describe the strengths and weaknesses of these non-exclusive strategies, and then discuss the methodological and statistical issues raised by such studies.

Keywords: plasticity; correlated traits; personality; coping styles

1. INTRODUCTION

Individuals of the same size, sex and from the same population often differ in how they behave (Clark & Ehlinger 1987; Magurran 1993; Wilson 1998). For example, some individuals are generally more aggressive than others. Behavioural syndromes occur when such individual differences are consistent across contexts (Sih *et al.* 2004a,b) and are analogous to ‘personality’ or ‘temperament’. A behavioural syndrome refers to the correlation between rank-order differences between individuals through time and/or across situations and is therefore a property of a population. In contrast, a ‘behavioural type’ refers to the particular configuration of behaviours that an individual expresses and is therefore a property of an individual (figure 1).

Recently, there has been a surge of interest in behavioural syndromes due to both empirical (Verbeek *et al.* 1994; Drent *et al.* 2003; Reale & Festa-Bianchet 2003; Dingemanse *et al.* 2004; Bell 2005) and conceptual advances (Sih *et al.* 2004a,b). Rising interest in behavioural syndromes is encouraging a different perspective on animal behaviour. The prevailing model in behavioural ecology has been that natural selection has favoured different optima in different contexts, and we generally study behaviour in different contexts as though they are independent of one another. The table of contents of animal behaviour textbooks illustrates this point well, with separate chapters devoted to territoriality, foraging behaviour, mating, antipredator defences, etc. In contrast, the behavioural syndromes view emphasizes carryovers across these contexts, and it suggests that new insights will emerge from considering behaviour in a more holistic way.

In particular, there are at least two important ecological and evolutionary implications of behavioural syndromes that have already been identified (Sih *et al.* 2004a,b). First, consistent individual differences in behaviour can represent limited plasticity if individuals have a ‘tendency’ to behave a certain way generally. If an individual cannot instantaneously modify behaviour optimally according to the immediate circumstances, then that individual’s behavioural type might effectively restrict the range of behavioural possibilities open to that individual. Therefore, behavioural syndromes might be able to account for deviations from the ‘optimal’ behaviour (Sih *et al.* 2003). Second, correlations among traits can act as evolutionary constraints because genetic correlations between traits can cause a correlated response to selection on non-target traits (Lande & Arnold 1983). This insight, long appreciated in evolutionary biology, warns us that we will be misled if we focus on one behaviour at a time because some traits evolve together as packages.

Therefore, this is an exciting time in this new area of study and unexplored arenas of investigation are opening up, providing many opportunities for innovative research. However, this potential does not come without peril, and there are few guidelines for navigating through the vast array of syndrome possibilities and for avoiding common pitfalls, i.e. type 1 error. After summarizing what we do and do not know about behavioural syndromes, this paper aims to provide a brief guide to strategies for studying behavioural syndromes, followed by a brief discussion of methodological and statistical issues.

2. WHAT DO WE KNOW? WHAT DO WE NOT KNOW?

The observation that individuals often differ consistently in how they behave has been appreciated by some

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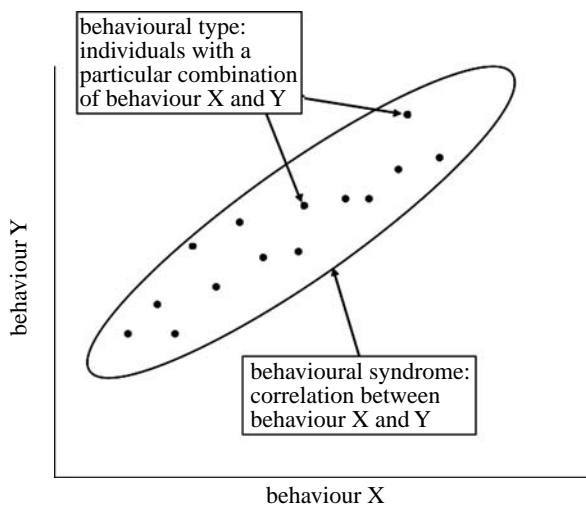


Figure 1. Definitions of behavioural type and behavioural syndrome. Each data point represents a different individual in the population.

observers of animal behaviour for a long time (Huntingford 1976; van Oortmerssen & Bakker 1981; Clark & Ehlinger 1987; Riechert & Hedrick 1990; Magurran 1993; Suomi *et al.* 1996; Wilson 1998; Gosling 2001). More recently, there is accumulating evidence that behavioural syndromes are not restricted to higher vertebrates (Riechert & Hedrick 1993; Sih 1993; Verbeek *et al.* 1994; Coleman & Wilson 1998; Drent *et al.* 2003; Sih *et al.* 2003; Bell & Stamps 2004; Brodin & Johansson 2004; Bell 2005; Quinn & Cresswell 2005; Sinn & Moltschaniwskyj 2005; Stapley & Keogh 2005; Aragon *et al.* 2006), often have underlying physiological or neuroendocrine correlates (Koolhaas *et al.* 1999; van Riel *et al.* 2002; Carere *et al.* 2003; Feldker *et al.* 2003; Sluyter *et al.* 2003; Veenema *et al.* 2003; Overli *et al.* 2006) and can be heritable (reviewed in van Oers *et al.* 2005). Recent studies have also shown that an individual's behavioural type is related to fitness (Reale & Festa-Bianchet 2003; Dingemanse *et al.* 2004; Dingemanse & Reale 2005; Smith & Blumstein submitted), which suggests that this variation does not simply reflect noise around a maximally adapted mean. In addition, some studies have shown that behavioural syndromes might help explain why apparently maladaptive behaviour persists in a population (Sih *et al.* 2003; Johnson & Sih 2005). Therefore, behavioural syndromes are proving to be widespread, sometimes causally linked together and important for fitness. When combined with what we know about the evolutionary and ecological importance of correlated traits and tradeoffs (Roff 1992; Stearns 1992; Lynch & Walsh 1998), it is not surprising that interest in this subfield is booming.

Some of the deepest unanswered questions on the horizon concern behavioural syndromes themselves. For example, why do behavioural syndromes exist in the first place? In an ideal world, individuals would be maximally plastic and adjust their behaviour to whatever situation they find themselves in, but behavioural syndromes imply limited plasticity through time and across situations, perhaps because plasticity is costly (DeWitt *et al.* 1998). Similarly, why are certain packages of behaviours put together but others are not? For instance, boldness and aggressiveness are often correlated with each other, but other behaviours are context-specific. In general, there is

a need for theory to explain when, why and in what form we might expect syndromes to occur.

These important questions can be tackled from the same perspectives that we use to study any other kind of behaviour, i.e. proximate, developmental, functional and historical (Tinbergen 1972). For example, a proximate explanation for why certain behaviours are correlated could involve a common causal connection between traits, in which either the same genes (pleiotropy) or the same hormones act on several targets (Ketterson & Nolan 1999). There are also developmental explanations for behavioural syndromes. For example, early differences in environmental conditions might set individuals out on different trajectories, exposing them to microenvironments that shape entire suites of behaviours (Stamps 2003). From a functional perspective, a behavioural syndrome might occur because certain combinations of behaviours are favoured by correlational selection. Alternatively, the syndrome might be inherited from an ancestor, reflecting shared history. We presently have relatively little idea about the frequency of these non-exclusive processes for producing behavioural syndromes.

3. STRATEGIES FOR STUDYING BEHAVIOURAL SYNDROMES

In principle, a behavioural syndrome might include behavioural tendencies exhibited in any functional context such as feeding, antipredator, mating, competitive contest, cooperative, parental care and dispersal. Studying multiple contexts requires either less effort devoted to studying each context in detail or having the resources to conduct a substantially larger overall project. A fundamental issue for the study of behavioural syndromes is thus the problem of choosing which behaviours or contexts to study. In what follows, I describe the strengths and weaknesses of four different strategies that are currently being used to choose which behaviours or contexts to study in a behavioural syndromes view. These strategies are complementary and the description here is meant to help guide empirical approaches for researchers interested in including behavioural syndromes in their research programme.

One approach for studying behavioural syndromes starts with a puzzling behaviour. For example, precopulatory sexual cannibalism is mysterious from an evolutionary point of view because females eat their potential mates before mating with them, and therefore might produce unfertilized clutches. Based on a suggestion by Arnqvist & Henriksson (1997), Johnson & Sih (2005) hypothesized that precopulatory sexual cannibalism was a 'spillover' of aggressiveness from a context in which it is beneficial. They showed that female spiders differed in their tendency to behave cannibalistically before copulation, and the females that showed this behaviour were also the individuals that were especially voracious towards food items as juveniles, resulting in faster growth and increased fecundity. Therefore, the benefits of high levels of voracity during the juvenile period might outweigh the costs of excessive aggressiveness later in life. The potential for behavioural spillovers across contexts to result in suboptimal behaviour is well illustrated by several other studies (e.g. Sih *et al.* 2003; Quinn & Cresswell 2005; Sih & Watters 2005; Duckworth 2006).

The strength of the 'puzzling behaviour' approach for studying behavioural syndromes is that it can potentially provide a satisfying explanation for a mysterious behaviour. This approach is probably best undertaken when a behaviour has benefits in some contexts but costs in others. In the case of the spiders, aggression is favoured when resources are scarce, but has obvious costs in terms of exposure to risk and enemies.

The second approach for studying behavioural syndromes involves looking for relationships between behaviours that have already been shown to form part of a syndrome in other animals ('the candidate behaviour approach'). For example, individual differences along the shy–bold axis (Wilson *et al.* 1993, 1994; Coleman & Wilson 1998) and the proactive–reactive axis (Koolhaas *et al.* 1999), as well as individual differences in 'aggressiveness' (Huntingford 1976; Benus *et al.* 1991; Riechert & Hedrick 1993), neophobia (Cavigelli & McClintock 2003; Keltikangas-Jarvinen *et al.* 2004) and exploratory behaviour (Verbeek *et al.* 1994) have all been documented in a diverse array of organisms. The advantage of this approach is that it allows us to build upon knowledge gained from other organisms, and could potentially reveal if there are fundamental axes of variation common across species and that affect behaviour in predictive ways. For example, individual differences in rates of processing information, from careful and attentive to cursory and fast, are probably widespread among animals. This fundamental axis might explain why, in many species (Benus *et al.* 1991; Koolhaas *et al.* 1999; Steimer & Driscoll 2003; Ebner *et al.* 2005; Overli *et al.* 2005), fast explorers are also quick to attack others and readily form routines.

The disadvantage of this approach is that it can be difficult to identify different manifestations of the same behavioural tendency, and the way in which a particular behaviour can be measured might vary greatly across different types of organisms. For instance, several different behaviours have been termed 'bold', such as predator inspection behaviour (Dugatkin 1992), behaviour in an open field (Gosling 2001) or feeding under risk (Bell 2005), but it is an open question as to whether each of these behaviours are equivalent and correlated with other behaviours in the same way. Similarly, established protocols for measuring exploratory behaviour (e.g. Verbeek *et al.* 1994) might not be appropriate for all organisms. That is, the relevance of what we perceive as the same situation might not be the same for different kinds of animals, and the behaviours might be incommensurable across species, i.e. the 'jingle-jangle fallacy' (Gosling 2001).

A third approach for studying behavioural syndromes is from the proximate perspective; this approach is from the 'bottom-up' and starts with systems (neuroendocrine or genetic) that integrate environmental stimuli and have pleiotropic effects, and then looks for relationships between behaviours that we suspect are affected by those systems. For example, the manifold consequences of testosterone for male birds are well appreciated: testosterone affects aggressive behaviour, singing, courtship, spermatogenesis and parental care (Ketterson & Nolan 1999). Other important pathways such as hormones involved in the stress response (Romero 2004) or genes with strong pleiotropic effects (e.g. Sokolowski *et al.* 1997) are promising links that could tie together packages of

behaviours. The bottom-up approach is particularly powerful because it not only can explain why syndromes occur (because the behaviours share a common mechanism) but also makes clear predictions about which behaviours are likely to be correlated (the ones that share the same causal connection). The disadvantage of this approach is that it overlooks correlated behaviours that affect fitness but that do not share a common mechanism, where the correlation results from linkage disequilibrium rather than pleiotropy (Conner 2002). As such, the bottom-up approach might inadvertently guide the course of research away from adaptive suites of trait that are the outcome of coordinated selection on independent traits.

In fact, some of the most intriguing behavioural syndromes occur when the constituent behaviours are, to the scientist's knowledge, neither functionally nor mechanistically related. For example, male crickets that produce long songs, which are attractive to both females and predators, are more cautious in a novel environment (Hedrick 2000). An unexplored but potential explanation for this behavioural syndrome is that it is the product of correlational selection, which occurs when certain combinations of traits are favoured over others. That is, attractive and cautious males might have higher fitness than attractive and bold males or unattractive and cautious males, because they reap the benefits of increased mating success while also minimizing the costs of exposure to predation. While the fitness consequences of certain behavioural types have been documented (Reale & Festa-Bianchet 2003; Dingemans *et al.* 2004; Dingemans & Reale 2005; Smith & Blumstein submitted) and we know that correlational selection can favour certain combinations of morphological and behavioural traits (Brodie 1992; Forsman & Appelqvist 1998; Sinervo *et al.* 2001; McGlothlin *et al.* 2005), no study (to my knowledge) has yet explicitly measured correlational selection for a behavioural syndrome. This is a promising area for future investigation.

One of the strongest arguments for how behavioural ecologists can contribute to the study of animal personality and temperament is that, as a discipline, we are especially attuned to the relevant ecological factors affecting an organism and are therefore well situated to take a functional approach (Reale *et al.* submitted). This sensitivity can point to behaviours that are most relevant to the ecology of the species and that have fitness consequences. Therefore, the fourth approach for studying behavioural syndromes starts with the particular details of the ecology of the species in question ('the ecological approach'). For example, perhaps sexual conflict is really strong, or predation pressure is very high, or the animal is a cooperative breeder, but individuals vary in how they behaviourally respond to these pressures. An ecological approach to studying behavioural syndromes asks whether there are correlated behaviours that might help explain individual variation in these fitness-related traits. Arguably, behavioural syndromes are most interesting when they are surprising or non-intuitive. It might not be surprising, for example, that an individual's level of aggressiveness might be related to its dominance rank (Huntingford & Turner 1987), but it is more unusual to think that individual differences in mating behaviour might be related to individual differences in cooperative tendency, for example.

The advantage of this approach is that it is, by definition, studying traits that are ecologically important, and it automatically prompts interesting questions about what is maintaining variation in these fitness-related traits. The disadvantage of this approach is that if we start looking for relationships between all the ecologically relevant behaviours for a given species that we can think of measuring, we could spend a lot of time on a 'fishing expedition', looking in the wrong direction and prone to type 1 errors. However, until theory can predict when and why certain behaviours should be correlated, we should entertain the possibility that some correlations are going to be unexpected and that new insights will emerge from considering relationships among behaviours rather than focusing on them one at a time. This point is well illustrated by evolutionary genetic studies that have found unexpected genetic correlations between seemingly unrelated traits, such as sperm motility and lung capacity (Henderson 1990) or between coat colour and fearfulness in foxes (Trut 1999).

4. ANALYSIS AND METHODS

A study on behavioural syndromes must meet two conditions. First, there must be behavioural variation. Second, individuals need to be measured more than once. The basic procedure, then, is to provide individuals with a set of standardized challenges, and then determine whether individual differences are consistent across challenges.

There are some relatively straightforward ways to incorporate these procedures into existing protocols. For example, if the study is investigating female mate choice in two different kinds of situations such as in the presence and absence of predation risk or at different densities (reviewed in Jennions & Petrie 1997), the same females could be used in the different treatment groups. Therefore, this is an efficient method for measuring both treatment effects and behavioural syndromes. Another simple way to consider behavioural syndromes is to collect data on other behaviours that are expressed during the course of the study, even if they are not the main one of interest. For example, individual differences in response to handling (Reale *et al.* 2000) proved to be reliable predictors of behaviour in other situations and were related to fitness differences in bighorn sheep.

A major practical issue that comes up during studies which attempt to quantify behavioural syndromes is the large number of correlation statistics that are computed, opening up the possibility that a correlation will be detected by chance alone (type 1 error). A possible solution to this problem is to perform a factor analysis or another data compression technique on the entire dataset, and then determine whether behaviours measured in different contexts load on the same factor, which would suggest that they are correlated with each other. This is the basic approach of psychological studies on humans, which have produced five major factors (the 'Big Five') that summarize the major axes of personality variation (McCrae & Costa 1999). The problem with this approach is that if the investigator is comparing different treatment groups or different populations or species, for example, they will need to verify that the factor structure is equivalent in the different groups so that factor scores are comparable with each other. Fortunately, analytical tools for comparing factor and matrix structures have been

developed in both psychology (McCrae & Costa 1997; Church 2001) and evolutionary biology (Steppan *et al.* 2002). These are especially promising methods for behavioural syndrome studies, because one of the most interesting questions about behavioural syndromes is whether behaviours are always related to each other in the same way (Bell 2005). In general, an unexplored issue is how differences among groups (treatments, populations, species, etc.) in behavioural syndromes are manifested: whether in average behavioural type (some groups are more bold and aggressive than others), differences in one but not both behaviours (some groups are more aggressive than others, but do not differ in boldness), or covariance (the strength of the relationship between boldness and aggressiveness differs across groups). Characterizing this variation is an important task for future work.

There are several more sophisticated statistical tests other than simple correlation analysis and that hold promise for analysing behavioural syndrome data. For example, one approach is to use path analysis combined with structural equation modelling to test hypotheses about the degree of connectedness of different behaviours (Dochtermann & Jenkins *in preparation*). More generally, there is potential for extending statistical methods such as repeatability analysis (Asendorpf 1990), mixed models and repeated measures ANOVA to apply to behavioural syndromes.

Regardless of which form of analysis is used, lack of variance or statistical power should be ruled out as an explanation for the failure to detect a behavioural syndrome. Provided that the investigator is confident that the lack of a relationship is 'real', the absence of a correlation should not be taken as bad news, because we have little theory to explain when behaviours are domain specific or domain general (Coleman & Wilson 1998). That is, negative results will play an important role in refining what is now the 'wild west' of syndrome possibilities (e.g. Rodel *et al.* 2006). Similarly, even if behavioural syndromes are not stable over long periods of time or if they are state dependent (Dall *et al.* 2004), short-term carryovers across contexts could still be ecologically important. For example, territorial aggressiveness might carry over to cause inappropriate aggression towards offspring, but this carryover might only be present during the reproductive season, or during short-term elevations in testosterone titres (Wingfield *et al.* 1990).

Eventually, the behavioural syndromes approach might cause deep reflection about what should be the appropriate null model for studying behaviour: should our *a priori* hypothesis be that behaviours in different contexts are independent of one another or that everything is connected? We might find it useful to draw from studies on developmental biology and phenotypic integration (Pigliucci & Preston 2004), which aim to understand how parts of organisms can be both specialized and interconnected. At the very least, behavioural syndromes urge us to reconsider our assumption of statistical independence of multiple measures on the same individuals and to correct our analyses accordingly (e.g. corrections for multiple tests).

Clearly, we are at a point when we need more data on the stability (Bell & Stamps 2004) and distribution of behavioural syndromes across various domains of behaviour and at various levels of biological organization (e.g. species, Mettke-Hofmann *et al.* 2002; populations, Hedrick & Riechert 1989; Bell 2005). More urgently,

there is need for theory to explain the factors contributing to the maintenance of consistent individual differences in behaviour. Fortunately, there are several promising modelling approaches that are already in the behavioural ecologists' theoretical toolbox, such as game theory (Giraldeau *et al.* 1994; Dall *et al.* 2004) and plasticity theory (Scheiner 1993; McElreath & Strimling 2006). Certainly, the future of studies on behavioural syndromes will require an active interplay between testable theory and inspiring empirical studies.

The ideas presented in this paper are derived from symposia on behavioural syndromes at the 2006 ISBE meeting in Tours, France and the 2006 Animal Behaviour Meeting in Snowbird, Utah. The author wishes to thank Niels Dingemanse for coining the term 'candidate behaviour', Denis Reale, Max Wolf, Andy Sih, Chad Johnson, Ned Dochterman, Dan Blumstein, Alex Kacelnik and three anonymous reviewers for their valuable suggestions.

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