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Behavioural syndromes and trappability in free-living collared flycatchers, *Ficedula albicollis*

László Zsolt Garamszegi [a,*], Marcel Eens [a], János Török [b,1]

[a] *Department of Biology, University of Antwerp*
[b] *Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University*

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The concept of behavioural syndromes hypothesizes that consistent behaviours across various situations mediate important life history trade-offs, and predicts correlations among behavioural traits. We studied the consistency of behavioural responses across three ecological situations (exploration of an environment altered with a novel object, aggression towards conspecifics, risk taking) in male collared flycatchers. We developed behavioural tests that could be applied in the birds' natural habitat, thus not requiring the capture of animals. Across individuals, we found positive covariation between exploration, aggression and risk taking, but the magnitude of these relationships varied. Variation in behaviour was also related to capture probability. Exploratory and risk-taking individuals were more likely to enter a trap than individuals with averse characteristics. Moreover, with the trapped birds, there was an association between the time needed for successful capture and exploration, and we found stronger correlations between behaviours in comparison with effects calculated from the whole sample of individuals. These patterns were independent of territory quality, male age, condition and breeding experience. Consequently, behavioural responses to different ecosocial challenges are determined by individual-specific characteristics that are manifested in correlative behaviours. Hence, behavioural types may be potential subjects for reproductive and life history adaptations. Our results have important implications for field studies of animals, because they suggest that capturing protocols may not randomly sample the observed population.

Behavioural syndrome (sometimes referred to as personality, temperament or coping style in the human and ecological literature, terms that we avoid using here to circumvent confusing terminologies) is defined as the consistency of behavioural responses that individuals display in different situations (Sih et al. 2004a, b). Correlated behaviours respond to selection pressures simultaneously, which may determine how animals generally cope with challenges in their physical and social environment. Recently, the phenomenon has been recognized as ecologically and evolutionarily relevant in many animals, because consistent individual variation in a suite of behavioural traits may drive important life history trade-offs (e.g. Hedrick 2000; Bell 2005; Sinn & Moltschaniwskyj 2005; Duckworth 2006; Bell & Sih 2007; Duckworth & Badyaev 2007; Wolf et al. 2007; Smith & Blumstein 2008). For example, one response may be advantageous in a given context, while its correlated response in another context may involve costs (e.g. aggressive individuals may achieve high social dominance on the one hand, but may be subject to frequent predation on the other; Sih et al. 2004a, b). Behavioural types, at least in some species, have been linked to mating and/or reproductive success and/or survival via integrated component traits such as dispersal, parental quality and/or dominance, and may thus have consequences for fitness (Réale et al. 2007).

Birds are important models in this line of research, because extensive field data on their behavioural ecology are available These data can be fruitfully amalgamated with the concepts of behavioural syndromes (Groothuis & Carere 2005). In fact, the most comprehensive study of the adaptive significance of correlated behaviours comes from studies on a single species, the great tit, *Parus major* (Drent 2006). Initial investigations demonstrated that subject animals cope with novel objects and environments in an individual-specific manner. Such individual variation remained consistent across experimental situations, and predicted the degree of aggression (Verbeek et al. 1996). Subsequently, artificial selection experiments in combination with field studies separated different variance components for behavioural types, and showed that these are significantly heritable and genetically correlated (Dingemanse et al. 2002; Drent et al. 2003; Carere et al. 2005; van Oers et al. 2005). A recent study revealed a relationship between individual

* Correspondence: L. Z. Garamszegi, Department of Biology, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, B-2610 Antwerp, Belgium.
E-mail address: laszlo.garamszegi@ua.ac.be (L.Z. Garamszegi).
[1] J. Török is at the Department of Systematic Zoology and Ecology, Eötvös Loráand University, H-1117 Budapest, Hungary.

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variation in behaviour and genetic polymorphism in a neurotransmitter-associated gene (*Drd4*), which suggests genetic contributions to behavioural types (Fidler et al. 2007). The performance of animals in behavioural tests in captivity predicted their realized fitness in natural conditions, as exploration scores were correlated with foraging success, dominance and dispersal, with consequences for reproductive success and survival (Dingemanse et al. 2003; Dingemanse & de Goede 2004; Both et al. 2005).

Although the success of these studies had a remarkable influence on our understanding of the evolutionary role of behavioural syndromes in birds, the focus on a single wild model species limits generalizations. Great tits occupy a given ecological niche, show particular behaviours and face species-specific evolutionary constraints that shape their life history decisions. Hence, selection factors in association with correlated behaviours may be relevant under the conditions that the species experiences in its environment. On the other hand, the adaptive significance of behavioural syndromes found in great tits is not necessarily applicable to other species. There is tremendous interspecific variation in how avian species explore novel objects (Mettke-Hofmann et al. 2002), react to human approach (Blumstein 2006; Møller et al. 2008) and show feeding innovations (Lefebvre et al. 1997; Sol et al. 2002), which may all represent behavioural type axes, and also appear to relate to interspecific differences in several ecological factors. Moreover, species may differ not only in average behavioural responses but also in their frequency distributions which are suited to the given environment (Dingemanse 2003). This increases the importance of studying behavioural syndromes in the wild on other model species with a different ecology.

The collared flycatcher is another hole-nesting passerine from the western Palaearctic (Cramp & Perrins 1994), which displays elaborate behavioural patterns. This species has been intensively studied for its life history and sexual selection (e.g. Gustafsson 1989; Pärt et al. 1992; Gustafsson et al. 1995; Qvarnström et al. 2000; Michl et al. 2002; Török et al. 2003; Garamszegi et al. 2004a). Therefore, in addition to the great tit model, the collared flycatcher can also serve as a good subject for studying the evolution of behavioural syndromes in an evolutionary context, because patterns of individual variation in behaviour can be related to well-described reproductive or ecological traits. However, the breeding biology of the flycatchers differs conspicuously from that of the members of the Paridae family (Lundberg & Alatalo 1992; Gosler 1993), and thus roles for behavioural types in mediating trade-offs will not necessarily be the same. For example, flycatchers are migratory and are confronted with an unpredictable environment upon arrival at the breeding grounds, which may have consequences for exploration (Mettke-Hofmann et al. 2005a, b; Mettke-Hofmann 2007). Moreover, differences in diet can also shape species-specific behavioural types that help to gather information about the environment (Mettke-Hofmann et al. 2002). Such adaptations may shift the optimal value of different behaviours and their correlates, which can have consequences for the role of individual variation. In a previous study, we found that individuals may show consistent behavioural responses over time, as the degree of aggression was significantly repeatable at the within-individual level (Garamszegi et al. 2006).

Our main goal in this study was to test for the existence of consistent individual behavioural performance across ecological situations in accordance with the definition of behavioural syndromes (Sih et al. 2004a, b). In our long-term study of several behavioural traits, such as song (e.g. Garamszegi et al. 2004a), copulation (Michl et al. 2002) and risk taking (Michl et al. 2000), we were faced, on several occasions in the field, with the fact that there are strong individual differences between birds. To initiate the integration of behavioural types within ecological and evolutionary studies in this model species, we established a simple protocol to characterize individual variation in behaviours without the need for capturing animals (see details below). Our approach permitted us to measure behavioural responses to ecologically relevant situations in natural conditions while causing minimal disturbance. Importantly, our experimental scheme did not require the successful trapping of individuals, showing that our sample was not inflated by heterogeneity in trappability. First, we tested for a consistency in individual behavioural performance in three situations: exploration of a breeding environment altered with a novel object, territorial aggression and risk taking when a human approached. We predicted that these traits would covary positively across individuals, if consistent individual variation persists across different behavioural traits according to the behavioural syndrome concept (Sih et al. 2004a, b). Second, we tested the prediction that behavioural types have consequences for trappability, as less explorative animals may show consistent trap-averse behaviour and may be more difficult to capture. This link has been prevalent in the literature (e.g. Wilson et al. 1993; Mills & Faure 2000; Réale et al. 2000; Malmkvist & Hansen 2001), but basically remains an untested assumption because of the difficulty of comparing captured and noncaptured individuals. However, as we attempted to capture individuals after testing, we were able to assign trappability to all tested individuals and to explore the relationships between different behavioural traits and capture probability.

METHODS

General Methods

The collared flycatcher is a small migratory, hole-nesting passerine that is socially monogamous with facultative polygyny (Cramp & Perrins 1994). After arriving at the breeding sites, males immediately occupy nestboxes or natural cavities, and establish territories where they start singing and displaying. Females choose among them, build nests alone and lay and incubate six or seven eggs. Both sexes provide parental care at the nestling stage. After fledging, birds start to prepare for migration, and leave for the sub-Saharan wintering site in early autumn. We established breeding plots at Pilis Field Station near Budapest (47°43′N, 19°01′E), Hungary in 1981 for the long-term study of the species (see Török & Tóth 1988). Fieldwork for the current study was carried out during 2007, when we recorded the behaviour of unpaired males as described below. We chose males for our purposes because they show typical nest presentation behaviour, and their elaborate courtship and territorial behaviour can be well characterized in different situations (see below). In addition, during their display period we were able to design protocols that enabled the measurement of traits without requiring the capture of individuals. This was necessary for both practical and ethical reasons. In a pilot study, we found that individuals become very stressed in captivity, thus making it difficult to assess behavioural types in cage or aviary conditions by using the protocols that have been developed for the great tit.

Behavioural Traits

In accordance with Réale et al. (2007), we established experimental test conditions in which we characterized three behavioural traits in three ecological situations, with consequences for three different trade-offs. The three ecological circumstances were altered habitat, social challenge and the presence of a potential predator, in which we measured exploration, aggressiveness and risk taking, respectively, as elements of correlated behaviours.