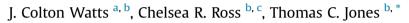
Animal Behaviour 101 (2015) 43-49

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Diel and life-history characteristics of personality: consistency versus flexibility in relation to ecological change



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ARTICLE INFO

Article history: Received 9 September 2014 Initial acceptance 20 October 2014 Final acceptance 1 December 2014 Available online 19 January 2015 MS. number: A14-00725R

Keywords: aggression Anelosimus studiosus behavioural flexibility behavioural types comb-footed spider diel rhythm life history personality Despite the potential benefits of modifying behaviour according to changing ecological conditions, many populations comprise individuals that differ consistently in behaviour across situations, contexts and points in time (i.e. individuals show personality). If personalities are adaptive, the balance between consistency and flexibility of behavioural traits should reflect the ability of individuals to detect and respond to changing conditions in an appropriate and timely manner and, thus, depend upon the pace and predictability of changing conditions. We investigated the balance between individual consistency and flexibility in the subsocial spider *Anelosimus studiosus* by assaying boldness across the diel cycle and correlating these data with patterns of prey and threat abundance in the natural habitat. We found significant diel flexibility in boldness correlating with drastic and predictable changes in prey availability. Moreover, the strength of within-individuals. We also found evidence that mean boldness level and among-individual variation in boldness are correlated with reproductive status. These data emphasize the interplay between behavioural consistency and flexibility and suggest that temporal characteristics of ecological conditions may be vital in assessing the strength, stability and adaptive value of animal personalities.

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Understanding the evolution of phenotypic flexibility (sensu Piersma & Drendt, 2003) is a central theme in evolutionary ecology. However, studies of the evolution of behavioural flexibility are relatively few, probably because behaviour is a reactive phenotype and, thus, is often misconceived as inherently flexible (Duckworth, 2010). To the contrary, a growing body of literature suggests that behavioural flexibility is widely limited (reviewed in Sih, Bell, & Johnson, 2004). Across diverse taxa, at least some populations are composed of individuals that maintain rank-order relationships in behavioural traits across time, situations and ecological contexts (i.e. individuals possess personalities or behavioural syndromes) such that no individual produces the full range of phenotypic values present in the population (Johnson & Sih, 2007; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). However, such rank-order correlations do not mandate that individuals' phenotypes are fixed, as individuals may still modify their

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behaviour according to situation or context (Briffa, Rundle, & Fryer, 2008; Johnson & Sih, 2007; Sih, Kats, & Maurer, 2003). Consequently, individuals in such populations show intermediate levels of behavioural flexibility, achieving 'approximately appropriate' behavioural phenotypes across contexts and situations (Briffa et al., 2008). Briffa et al. (2008) noted that both generous and limited flexibility in behavioural phenotypes may be adaptive strategies, and, in general, the observed degree of flexibility should reflect a balance between the costs and benefits of reacting to changing conditions.

The benefit of behavioural flexibility is intuitive: individuals that modify their behaviour in accordance with environmental changes can avoid fitness costs of phenotype—environment mismatch. However, there are many potential costs and limitations that may detract from the benefit of modifying behaviour. For example, some authors suggest there may be costs associated with producing and maintaining sensory and regulatory mechanisms needed to detect and respond to environmental change (DeWitt, Sih, & Wilson, 1998). Evidence for such 'maintenance costs' is limited and difficult to obtain (Auld, Agrawal, & Relyea, 2010), but, even if maintenance costs are negligible, the benefits of flexibility may depend

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http://dx.doi.org/10.1016/j.anbehav.2014.12.020

heavily on other factors such as the reliability of environmental cues (Langerhans & DeWitt, 2002; Moran, 1992; Tufto, 2000) and time lags in the induction of behavioural change (Padilla & Adolph, 1996). For example, an individual with a fixed phenotype may outperform an individual with a flexible phenotype if the environmental cues that induce phenotypes are unreliable (i.e. poor indicators of the selective environment) and, therefore, increase the probability that the flexible strategy will result in phenotype--environment mismatch (Langerhans & DeWitt, 2002; Moran, 1992; Tufto, 2000). Moreover, even if environmental cues are perfectly reliable, any time delay between the detection of a cue and the induction of a phenotypic shift could increase phenotype-environment mismatch and detract from the adaptive value of flexibility, particularly if the environment changes rapidly (Padilla & Adolph, 1996). Thus, we might expect individuals to show low levels of behavioural flexibility across contexts or situations that change frequently or unpredictably in nature because cue-based induction of phenotypes would often result in phenotype--environment mismatch. Put another way, phenotypic flexibility might be most likely to evolve in association with environmental changes that occur gradually (relative to the pace of phenotypic change; Padilla & Adolph, 1996) and correspond to reliable direct or indirect cues.

These criteria are perhaps best met by cyclic environmental changes such as those that occur over the course of a year or a day. Flexibility may be more likely to confer a fitness benefit in cyclic environments if conditions change gradually relative to plausible rates of behavioural modification and correspond to reliable indirect cues (e.g. photoperiod and luminosity). Moreover, cvclic environmental changes can be drastic enough to produce oscillations in the relative strengths of conflicting selection pressures, thereby favouring different phenotypes at different points in the cycle. Accordingly, there are countless descriptions of behavioural rhythms corresponding to environmental cycles. For example, changes in foraging behaviour in the white-throated round-eared bat, Lophostoma silvicolum, correspond to changing prey availability across the lunar cycle (Lang, Kalko, Romer, Bockholdt, & Dechmann, 2006). Similarly, male Gryllus texensis crickets modify their mate attraction behaviour to be more conspicuous during periods of the day when potential mates are abundant and less conspicuous when parasitoid flies are abundant (Bertram, Orozco, & Bellani, 2004). Although behavioural variation in accordance with environmental cycles has been the focus of much behavioural ecology research, we know of no studies that have investigated the balance between consistency and flexibility of individual behaviour with respect to predictable changes in relevant ecological conditions.

In this study, we test for diel and life-history flexibility of behaviour in the subsocial spider Anelosimus studiosus (Araneae: Theridiidae). These spiders show a social behaviour polymorphism that correlates with a suite of behavioural traits that affect performance in various contexts (Pruitt, Riechert, & Jones, 2008). Individuals that show more tolerance of conspecifics also show more reticence to attack prey, more wariness of predators, less activity and less superfluous killing (Pruitt et al., 2008). The optimal behavioural type (i.e. personality type) in one context or situation may not be optimal in another (Arnqvist & Henriksson, 1997; Duckworth, 2006; Johnson & Sih, 2007; Riechert, Singer, & Jones, 2001); therefore, selection may act to optimize (i.e. 'average') behavioural types across contexts and situations or may favour the evolution of context- or situation-dependent behaviour. Because diel and life-history changes in ecological constraints may be relatively infrequent and predictable, we hypothesize that individuals benefit from modifying their behavioural type across times of day and life-history stages. Specifically, we predicted that the average level of boldness in A. studiosus changes over the diel cycle and reflects predictable patterns of prey availability and threat species abundance in the natural habitat. Moreover, we expected the degree of behavioural flexibility observed over the diel cycle to be high relative to the degree of behavioural consistency. We further predicted that brooding females (guarding eggcases) would be bolder than nonbrooding females, reflecting the need to provision altricial offspring and presumably protect them from potential eggcase predators and parasites. We also examined whether brooding females retain diel rhythms of boldness and consistent among-individual differences in behaviour (i.e. behavioral types or personalities) while guarding eggcases.

METHODS

Study Species

Anelosimus studiosus (Araneae: Theridiidae) is a small combfooted spider that ranges from Argentina to New England (Agnarsson, 2006). In eastern North America, these spiders are abundant along waterways where they construct semi-permanent sheet-webs in the lower vegetation of trees and shrubs (Jones, Riechert, Darlymple, & Parker, 2007). Anelosimus studiosus shows extended maternal care (Brach, 1977), which enhances both juvenile survival and the mother's future reproductive success (Jones & Parker, 2002). Consequently, female A. studiosus are likely to be especially invested in the success of their primary broods.

To investigate diel and life-history flexibility in boldness, we collected brooding (N = 20) and nonbrooding (N = 16) adult female A. studiosus from single-female webs along Fort Patrick Henry Lake in eastern Tennessee, U.S.A. (36°29'N, 82°29'W), during early June 2012. We maintained females individually in 59 ml plastic deli containers at 23 °C on a 12:12 h light:dark cycle for a minimum of 10 days prior to the first trials. During this period we misted individuals' webs with water and provided a mixture of termite workers, Drosophila, and crickets twice weekly. Brooding females were allowed to retain their eggcases until a few hours before the first round of trials, which began at 1500 hours (5 h prior to the onset of darkness), and remained separated from their eggcases for the duration of the study. Trials for nonbrooding females began the following day at 1100 hours. All activities were conducted in compliance with all relevant guidelines for the care and use of invertebrate study species. We did not observe any adverse effects resulting from the use of a predator stimulus during or after trials. After completing the experiments described here, brooding females were reunited with their eggcases and the subjects were used for additional experiments and maintained in the laboratory until they died a natural death.

Laboratory Methods

We assayed antipredator behaviour to determine whether boldness varies with time of day or reproductive status in *A. studiosus*. Boldness is correlated with a variety of behavioural traits in this species, including voracity towards prey and agonistic interactions with conspecifics (Pruitt et al., 2008); therefore, changes in boldness may correspond to changes in correlated behavioural traits that affect performance in other contexts. Moreover, less bold individuals typically respond to predator stimuli by feigning death and show longer latencies to resume activity following the antipredator response (Pruitt et al., 2008). Thus, increased predator avoidance (i.e. decreased boldness) may decrease foraging success, as ensnared prey can escape the nonsticky web quickly if not captured by the spider (Joyner, Ross, Watts, & Jones, 2014). To simulate the approach of an airborne predator, we coaxed individuals from their containers into a clean glass dish Download English Version:

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