



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-individual flexibility in boldness was comparable to the strength of rank-order consistency among 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 & Drent, 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

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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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, cyclic 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. behavioural types or personalities) while guarding eggcases.

METHODS

Study Species

Anelosimus studiosus (Araneae: Theridiidae) is a small comb-footed 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 non-sticky 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

(15 × 6 cm) and gave each spider 30 s to acclimate before delivering a puff of air from approximately 10 cm away (Riechert & Hedrick, 1990, 1993). Although the stimulus strength may have varied among applications, this is a well-established method for eliciting antipredator responses in spiders (Keiser, Jones, Modlmeier, & Pruitt, 2014; Pruitt et al., 2008; Riechert et al., 2001; Riechert & Hedrick, 1990, 1993; Watts, Herrig, Allen, & Jones, 2014). Also, there appears to be no habituation to the air puff stimulus (Jones et al., 2011). Individuals that responded to the simulated predator attack did so by raising the first pair of legs (threat posture) or feigning death (thanatosis), while some individuals showed no visible response to the stimulus ('noncommittal'). To reduce the likelihood that noncommittal responses resulted from ineffective stimulus application, we applied the stimulus to each individual three times or until an 'active' response (threat posture or thanatosis) was elicited. Individuals that did not show an active response within three stimulus applications were scored as noncommittal. We repeated this protocol every 4 h for both test groups. Brooding females were assayed on 5 consecutive days, whereas nonbrooding females were assayed for only 4 consecutive days. All observations in the dark were conducted using red light, which is poorly perceived by most spiders (Foelix, 2011). We ranked individual responses in terms of increasing boldness based on the system developed by Pruitt et al. (2008); in our modified scoring system, individuals were scored as bold (1) or shy (-1) based on the active response (threat posture or thanatosis, respectively), or, if no active response was expressed, as noncommittal (0).

Field Methods

During 20–22 June and 19–21 August 2012 we quantified diel variation in the abundance of potential prey and threat species in the natural habitat of *A. studiosus*. We suspended 20 yellow sticky traps (15 × 10 cm) from the lower branches of trees overhanging the water along Boone Lake in eastern Tennessee. Traps were placed at heights typical of *A. studiosus* webs (~1.5 m above water surface) on two opposing shores of the lake. We photographed the traps every 3 h for 2 days, starting at 1500 hours. After 2 days of observation, we collected the traps and used the photographs to determine the time interval during which each insect was captured. We then identified each insect as prey or threat. We considered any non-wasp insects 2–10 mm in total length as potential prey, because smaller prey items may go unnoticed in *A. studiosus* webs and prey items greater than 10 mm in length (e.g. large moths) may be too large to be captured by singleton females (Jones & Parker, 2000). Large wasps and smaller parasitoid wasps were considered potential threat species. The date, time of capture, type (prey or threat) and trap number were recorded for all insects identifiable as prey or threat. Items that could not be identified as either potential prey or a potential threat were excluded from all analyses. Note, however, that we did not assess diel activity patterns of other spider species, some of which are known to prey upon *A. studiosus* (Perkins, Riechert, & Jones, 2007).

Statistical Analysis

We constructed a repeated measures ordinal logistic regression model in SPSS (version 21, IBM Corp., Armonk, NY, U.S.A.) to test for effects of reproductive status (brooding/nonbrooding), time of day and reproductive status*time of day interaction on boldness score. Because the logistic regression model indicated differences in boldness scores between reproductive status groups, we estimated the adjusted repeatability (i.e. across all times of day) of boldness scores for each reproductive status group separately by constructing

linear mixed models (LMMs) predicting boldness score as a function of time of day and test subject (individual), which were modelled as fixed and random effects, respectively (Nakagawa & Schielzeth, 2010). The LMMs were fitted using the GLM procedure in SPSS to obtain ANOVA tables from which repeatability estimates and corresponding standard errors were calculated for each group following Lessells and Boag (1987) and Nakagawa and Schielzeth (2010). We then constructed an 83% confidence interval for each repeatability estimate to allow a comparison of repeatability between reproductive status groups approximating a 5% type I error probability (Deb, Bhattacharya, & Balakrishnan, 2012; Modlmeier, Forrester, & Pruitt, 2014; Payton, Greenstone, & Schenker, 2003). Following Briffa et al. (2008), we assessed the relative strengths of flexibility and consistency of individual behaviour over the diel cycle by comparing effect size estimates for tests of concordance (Kendall's coefficient of concordance) and difference (repeated measures ANOVA).

We determined whether prey abundance varied between the two points of the growing season sampled by creating a GLM testing the effect of time of season (hereafter 'early season' and 'late season') on the log-transformed number of prey caught on each sticky trap during the 2-day sampling period. To determine whether prey species abundance varied over the diel cycle, we tested the observed distribution of prey captured on sticky traps across times of day against a uniform distribution using chi-square tests. Because the GLM indicated a significant difference in prey abundance between points in the growing season (GLM: $F_{1,38} = 9.558$, $P = 0.004$), analyses of diel patterns of prey abundance were conducted separately for the early and late season. We conducted a preliminary assessment of the predictability of prey abundance patterns within and across days by creating temporal autocorrelation plots of prey abundance over the 48 h sampling period for each point in the season. We further assessed the predictability of diel patterns of prey abundance across days at each point in the season by comparing the number of insects captured during each 3 h interval of the first sampling day with the number captured during the same interval of the second sampling day using paired-samples *t* tests. We used the chi-square protocol described for prey abundance data to test for diel patterns in the abundance of threat species (predatory and parasitic wasps) in the early season, but no threat species were detected in the late season. Because we trapped very few threat species, we did not attempt to assess the predictability of their patterns of abundance.

RESULTS

Diel and Life-history Flexibility in Boldness

Our data showed clear diel rhythmicity of antipredator behaviour in *A. studiosus* (Fig. 1). Females showed significant diel variation in mean boldness score (GEE: $Wald = 98.415$, $P < 0.001$; Fig. 1a) and, for both groups, the expression of thanatosis behaviour increased in the early morning and peaked during the daytime (Fig. 1b), whereas the expression of threat behaviour increased during the afternoon and peaked just prior the onset of darkness (Fig. 1c). However, nonbrooding *A. studiosus* showed more pronounced behavioural patterns (GEE: reproductive status*time of day: $Wald$ test: $W = 11.286$, $P = 0.046$; Fig. 1). Unlike brooding females, nonbrooding females became primarily shy prior to lights on and remained shy throughout the majority of the daytime, transitioning to a bold state just prior to lights off (Fig. 1c). Brooding females appeared to lack an overt transition between behavioural states and generally showed more bold behaviour than nonbrooding females over the diel cycle (GEE: $Wald$ test: $W = 9.536$, $P = 0.002$; Fig. 1). Although the boldness score of both reproductive

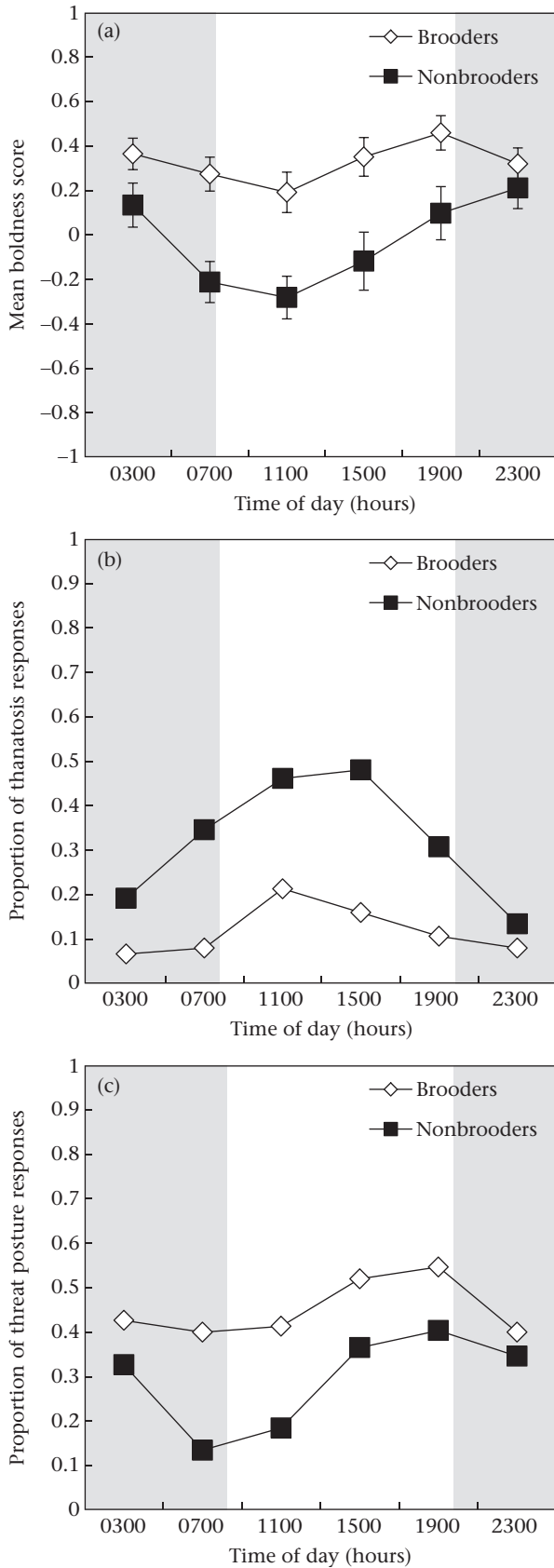


Figure 1. Diel patterns of boldness in *A. studiosus* as inferred from antipredator responses. Shown are (a) the mean boldness score \pm SE of brooding and nonbrooding females over the diel cycle, (b) diel changes in the proportion of females in each group showing thanatosis antipredator responses, and (c) diel changes in the proportion of females in each group showing threat posture antipredator responses.

status groups was significantly repeatable (95% CI: brooding females: 0.00588, 0.20901; nonbrooding females: 0.10381, 0.53618), brooding females were less repeatable in their boldness scores than nonbrooding females, although the distance between confidence intervals was extremely small (83% CI: brooding females: 0.03912, 0.17577; nonbrooding females: 0.17581, 0.46419; Fig. 2a). The reduction in repeatability associated with eggcase guarding appeared to be driven by reduced among-individual variation in boldness, while within-individual variation appeared similar between reproductive statuses (Fig. 2b). Individual boldness scores varied significantly across trials for both groups (repeated measures ANOVA: brooding: $F_{23,253} = 2.79$, $P < 0.001$; nonbrooding: $F_{29,377} = 2.78$, $P < 0.001$); however, the rank order of boldness scores among individuals was significantly concordant across trials (Kendall's coefficient of concordance: brooding: $W_{14} = 0.203$, $P < 0.001$; nonbrooding: $W_{12} = 0.202$, $P < 0.001$). For both brooding and nonbrooding females, the strength of behavioural consistency (as estimated by Kendall's W) over the diel cycle was nearly or exactly matched by the strength of behavioural flexibility (as estimated by η^2 , Briffa et al., 2008; Table 1).

Diel Patterns and Predictability of Prey and Threat Abundance

In addition to detecting seasonal effects (GLM: $F_{1,38} = 9.558$, $P = 0.004$), we found significant diel variation in flying insect abundance during both early and late stages of the growing season (early season: $\chi^2_6 = 152.71$, $P < 0.0001$; late season: $\chi^2_6 = 138.12$, $P < 0.0001$; Fig. 3a). While prey items were trapped at all times of day, prey abundance was lowest during the early hours of the morning in both the early and late season (Fig. 3a). In both cases, prey abundance increased over the course of the afternoon and

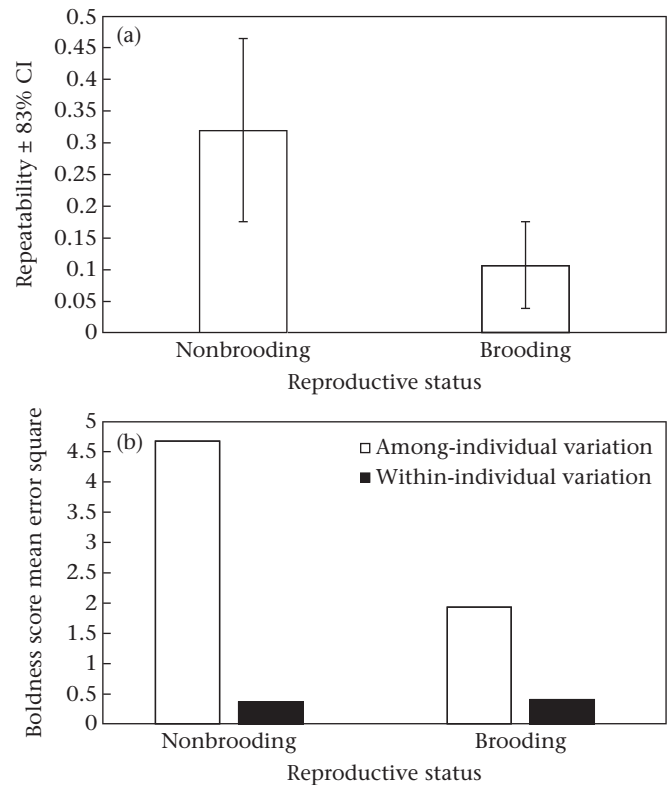


Figure 2. Repeatability of boldness scores for brooding and nonbrooding female *A. studiosus* across all trials. Shown are (a) repeatability estimates \pm 83% CIs for each group and (b) variance components contributing to the repeatability estimate for each group.

Table 1

Comparison of effect sizes for tests of among-individual rank-order consistency (Kendall's coefficient of concordance) and within-individual differences (repeated measures ANOVA) of boldness scores across trials (i.e. times of day and trial days)

Reproductive status	Statistic		Probability		Effect size estimate	
	Kendall's (χ^2)	ANOVA (F)	Kendall's (P)	ANOVA (P)	Kendall's (W)	ANOVA (η^2)
Brooding	82.427	2.78	<0.0001	<0.0001	0.203	0.176
Nonbrooding	55.757	2.79	<0.0001	<0.0001	0.202	0.202

peaked early in the night (Fig. 3a). The number of insects captured in each 3 h interval on the first sampling day did not differ significantly from the number captured during the same 3 h interval on the following sampling day for either point in the season (Wilcoxon signed-ranks test: early season: $T = 14.5$, $N = 8$, $P = 0.624$; late season: $T = 8.5$, $N = 8$, $P = 0.352$). Moreover, the temporal autocorrelation plots suggest that prey abundance in the field was cyclic, as prey abundance tended to show weak or moderate positive autocorrelation for small (i.e. 3–6 h) and large (i.e. 21–24 h) time lags but weak to moderate negative autocorrelation for intermediate time lags (i.e. 9–18 h) (Fig. 3b). However, we sampled too few days to confidently assess the statistical significance of these correlations.

Although no potential threat species were trapped in the late season, we trapped several *Zatypota crassipes* (Hymenoptera: Ichneumonidae), a known ectoparasitoid of *A. studiosus* (Deyrup, Kraus, & Eisner, 2004), in the early season ($N = 28$). The abundance of *Z. crassipes* showed a diel pattern similar to that seen in prey insects, with numbers being lowest in the early morning and

increasing over the day to a maximum in the early night ($\chi^2_6 = 152.55$, $P < 0.0001$; see Supplementary Material).

DISCUSSION

We found evidence that *A. studiosus* shows strong diel flexibility in behaviour despite possessing well-described behavioural correlations across ecological contexts and points in time (Pruitt et al., 2008). This suggests that *A. studiosus* possesses intermediate levels of behavioural flexibility as has been described for other taxa in which populations may comprise individuals that differ consistently in their behaviour (Briffa et al., 2008; Johnson & Sih, 2007). As predicted, we found that *A. studiosus* possesses a high degree of behavioural flexibility relative to behavioural consistency across the diel cycle. In fact, the time of day explained nearly as much of the variation in boldness score as did rank-order consistency among individuals. These data emphasize that high repeatability in behaviour (i.e. personality or behavioural types) does not require a lack of potentially adaptive behavioural flexibility (Briffa et al., 2008; Johnson & Sih, 2007). Moreover, the diel rhythm of boldness observed in *A. studiosus* supports the prediction that variation in behaviour should reflect gradual, predictable changes in relevant ecological conditions such as the probability of encountering potential prey or threat species. When assayed under controlled conditions, female *A. studiosus* were more bold in the evening and early night when prey were most abundant in the natural habitat. These observations are consistent with previous work describing positive correlations between boldness towards predators and aggression towards prey in several *Anelosimus* species (Pruitt, Oufiero, Aviles, & Riechert, 2012). Moreover, boldness may correlate with foraging success through within-context trade-offs (e.g. time-budget constraints), as the likelihood of feigning death and the subsequent latency to resume activity may influence the likelihood of prey escaping the web before being captured by the spider. Thus, behavioural correlations among or within contexts may drive selection for diel flexibility in boldness corresponding to changing prey availability. However, this interpretation is confounded by similar patterns of abundance of a threat species, *Zatypota crassipes* (Hymenoptera: Ichneumonidae), which is known to parasitize *A. studiosus* spiders (Deyrup et al., 2004). Although bolder *A. studiosus* suffer greater predation risk as a result of escalation during encounters with predators (Pruitt & Riechert, 2011), we know of no data describing the effect of escalatory behaviour on parasitism risk. Escalation could decrease the risk of parasitism; alternatively, the drastic increase in prey availability may outweigh the relatively low probability of being parasitized during periods of peak abundance. A rigorous assessment of the adaptive value of the diel rhythm of boldness in *A. studiosus* will require quantifying the effects of boldness on the risk of predation and parasitism in addition to determining the rate at which relatively few parasitoids can parasitize many spiders.

Notably, for some study systems where there are trade-offs associated with boldness, associations between boldness and predator/prey abundance are opposite that described here (e.g. Hedrick & Riechert, 1989; Riechert & Hedrick, 1990; Sih et al.,

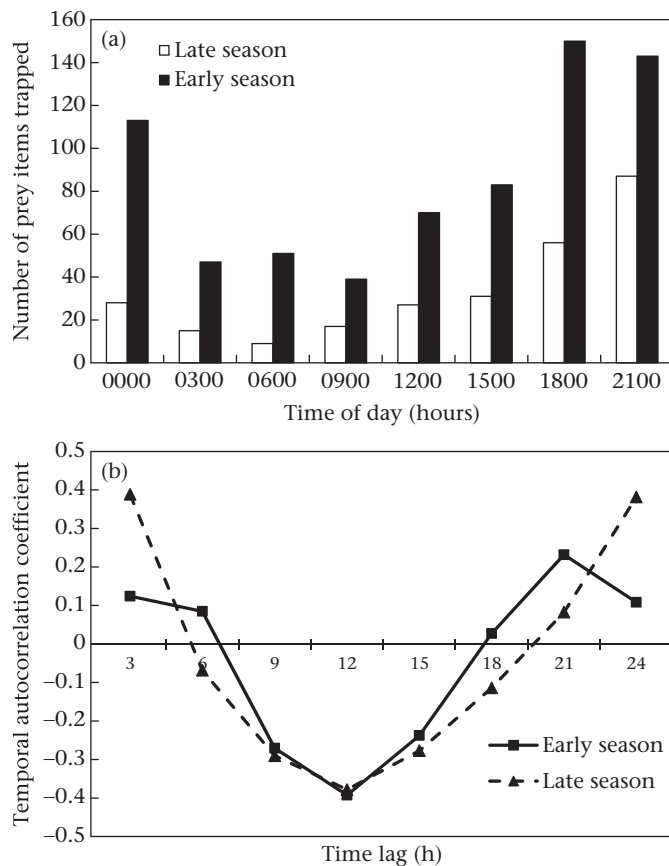


Figure 3. Diel patterns of flying insect abundance in the natural habitat of *A. studiosus* during the early and late stages of the growing season. Shown are (a) the total number of potential prey items captured by time of day over the 2-day sampling period and (b) autocorrelation coefficients of potential prey abundance for time lags of 3–24 h.

2003). This seemingly contradictory pattern probably arises because our comparison is temporal, not spatial. While spatial variation in predation risk and foraging success may affect time budgets such that boldness is favoured in prey-limited or low-risk habitats (e.g. Hedrick & Riechert, 1989; Riechert & Hedrick, 1990), predictable temporal variation in risk and reward within a habitat may drive the allocation of risky (bold) behaviours to periods when rewards are greatest relative to risk (Lima & Bednekoff, 1999). Consequently, habitats that differ considerably in optimal boldness levels may favour qualitatively similar patterns of behavioural flexibility if temporal patterns of risk and reward are similar between them.

We also found evidence that mean boldness level differs significantly between reproductive statuses in *A. studiosus*. Brooding females were generally bolder than nonbrooding females and did not show diel transitions between shy and bold states as observed in nonbrooding females. Moreover, brooding females showed weaker personalities than nonbrooding females, owing to reduced among-individual variation in boldness scores. Although we did not assay brooding females prior to the production of egg-cases, our comparison suggests that female *A. studiosus* may show considerable life-history flexibility in the strength and nature of behavioural types. The convergence of females to an increased level of boldness in the egg-guarding context could correspond to a need to protect eggcases from potential threats or to prepare for greater prey capture and antipredator demands when provisioning and protecting altricial offspring. Female presence is known to enhance growth (Jones & Parker, 2000, 2002) and reduce predation of juveniles in the web (Jones & Parker, 2002; Perkins et al., 2007), and isolated females of the bold, asocial behavioural type appear to have greater brooding success than isolated shy, social females in the natural habitat (Jones, Pruitt, & Riechert, 2010). Alternatively, changes in boldness across reproductive statuses may reflect physiological changes accompanying egg production or eggcase construction. It may also be that bolder (and less temporally variable) females produce eggcases more quickly or successfully, which would suggest that personality traits in *A. studiosus* may be associated with life-history trade-offs (Wolf, van Doorn, Leimar, & Weissing, 2007).

Although widely recognized as an ecologically and evolutionarily important component of behaviour (reviewed in Sih, Cote, Evans, Fogarty, & Pruitt, 2012), little is known about how animal personality evolves and persists despite the potential benefits of modifying behaviour according to situation or context. Recent theoretical and empirical studies have developed various adaptive and nonadaptive hypotheses to explain the maintenance of among-individual variation and within-individual consistency in behaviour, including positive feedbacks between internal state and behaviour, frequency-dependent selection and developmental constraints (reviewed in Dall, Houston, & McNamara, 2004; Dingemanse & Wolf, 2010; Duckworth, 2010). If the behavioural consistency component of personality is adaptive, the temporal characteristics of changes in environmental conditions and internal state should affect the balance between individual consistency and flexibility (Moran, 1992; Padilla & Adolph, 1996; Tufto, 2000). Accordingly, we predicted that individuals should show considerable behavioural flexibility (relative to consistency) across ecological conditions that change predictably and gradually in nature. Although we obtained evidence for our prediction, we have yet to determine whether the balance between flexibility and consistency of behavioural traits varies among sites that differ in the temporal characteristics of changing conditions. However, the effects of cue reliability and environmental stochasticity on the benefits of plasticity are well described (DeWitt et al., 1998; Langerhans & DeWitt, 2002; Moran, 1992; Padilla & Adolph, 1996; Reed, Waples,

Schindler, Hard, & Kinnison, 2010; Tufto, 2000), and we expect the relative strengths of flexibility and consistency in behavioural traits to reflect the predictability of environmental change in this study system and many others. Despite the potential importance of temporal characteristics of the environment in shaping the evolution of behavioural consistency, such characteristics remain largely ignored in studies of animal personality. Gabriel and Black (2010) found evidence that repeatability of bold and exploratory behaviours in Steller's jays, *Cyanocitta stelleri*, depends upon the temporal scale at which consistency is measured, but we know of no studies that have interpreted the strength of personality traits explicitly with respect to the frequency and predictability with which contexts or situations change in nature. If behavioural consistency is favoured where conditions change frequently and unpredictably, then relatively high levels of consistency may be expected under at least some experimental designs. This possibility should be of greatest concern when trait consistency is used to draw inferences about constraints on behavioural evolution, as consistency through time or across contexts and situations may not necessarily indicate intrinsic (e.g. developmental) constraints on the evolution of context-specific behaviour. Thus, studies of animal personality should incorporate natural patterns of relevant ecological changes to develop a priori expectations of optimal levels of behavioural flexibility. Such expectations would enable rigorous explorations of intrinsic constraints on the evolution of behavioural flexibility and ultimately aid in elucidating the evolutionary basis of animal personality.

Acknowledgments

We thank Jonathan N. Pruitt for comments that greatly improved the quality of the manuscript, Edith Seier for invaluable statistical advice, Darrell Moore and Michele Joyner for insightful discussions regarding these data, and the East Tennessee State University Department of Biological Sciences for logistical support. We also thank the editor and two anonymous referees for valuable feedback. This research was supported by the National Science Foundation, Division of Mathematical Sciences award No. 1128954.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2014.12.020>.

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