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A Brief Report: Capture Order is Repeatable in Chickadees

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Black-capped (*Poecile atricapillus*) and mountain chickadees (*Poecile gambeli*) have been used as a model to examine cognitive functions including perception, episodic-like memory, and spatial learning and orientation. Recently, these species have been used in two studies to examine the relationship between learning and novel environment exploration and novel environment exploration and dominance. In the current study we explored whether these two species show consistency in behavior over time. In same species/same sex groups, male and female black-capped and mountain chickadees were released into a room and then captured by an experimenter with the procedure repeated one week later. Males, but not females in both species show consistency in capture order over both sessions. We discuss implications of this finding in the context of possible sampling biases.

Behavioral syndromes (also known as animal personality) are correlations between two seemingly unrelated behaviors or characteristics within the same context or between similar behaviors in different contexts (Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). For example, animals which behave more boldly when approaching a novel object may also behave more aggressively towards conspecifics (Sih & Bell, 2008). As our appreciation for the taxonomic diversity of such correlations grow, so too does our understanding of the sheer breadth of characteristics that may be involved in a behavioral syndrome (Gosling, 2001).

The life history approach has been instrumental in providing theoretical clarity in our understanding of this wide array of interrelationships between ostensibly different aspects of an individual's behavior (Bell, 2007). In this view of animal personality, individuals differ in their overall behavioral profile in a way that is consistent with differing life history strategies (Stamps, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007; Wolf, van Doorn, & Weissing, 2008). Some

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individuals may focus on current reproduction and thus behave in a more risk-prone manner, whereas others focus on the future and hence behave in a more risk-averse manner (Wolf et al., 2007). Variation in the personality of animals within a species may be maintained if personality types confer an advantage when they are rarer in the population (i.e., negative-frequency dependent selection: Wilson, Clark, Coleman, & Dearstyne, 1994; Wolf et al., 2007) or occur in different local habitats (i.e., habitat dependent selection: Réale, Reader, Sol, McDougall, & Dingemanse, 2007).

The fitness consequences of different behavioral strategies have obvious ecological and evolutionary implications (for reviews see Dingemanse & Réale, 2005; Smith & Blumstein, 2008). When framed in this way, it is easy to see how behavioral syndromes may encompass many aspects of an animal's biology, including but not limited to behavior, physiology, neural organization and cognition (Gosling, 2001; Sih & Bell, 2008).

Individual differences in learning ability represent one such candidate aspect of behavioral syndromes that has received relatively limited attention to date (Sih & Bell, 2008) but may significantly increase our understanding of behavior profiles once it is more fully integrated into the literature. Recently, two studies have used chickadees as a model to examine the relationship between personality trait(s) and learning speed (Guillette, Reddon, Hurd, & Sturdy, 2009) or dominance status (Fox, LaDadge, Roth, & Pravosudov, 2009).

The personality-based research conducted by our laboratory group was motivated in part by the intra-specific variation observed in black-capped and mountain chickadees learning of an acoustic operant discrimination. Our initial goal was to examine learning speed (the number of trials needed to learn an acoustic GO/NOGO discrimination) as a personality trait and see if learning speed varied consistently along other known personality traits (i.e., novel environment exploration: Guillette et al., 2009). Our results revealed that a positive relationship exists between learning speed and exploration in male and female wild-caught black capped chickadees. Individuals that learn an acoustic operant discrimination task quickly are more likely to explore a novel environment. Related research from the Pravosudov laboratory group (Fox et al., 2009) has demonstrated that low-exploring male mountain chickadees were more likely to become dominant in pairwise encounters with high-exploring males.

While both previous studies with chickadees (Fox et al., 2009; Guillette et al., 2009) show important correlations among different behaviors, both studies also lack the demonstration of repeatability in behavior, which is considered to be a crucial feature in studying behavioral syndromes (Stamps & Groothuis, 2009). Here, we search for evidence of repeatability of a behavioral measure, capture order, in wild-caught black-capped and mountain chickadees. If capture order is consistent over a short inter-trial period in chickadees, it may be correlated with other stable personality characteristics that can potentially influence an individual's fitness.

There is evidence from several studies that support this notion. For collared flycatchers (*Ficedula albicollis*), exploration of a familiar environment altered with a novel object and risk taking were related to capture probability while intraspecific aggression was not. Specifically, birds that were more exploratory and risk taking had a higher probability of being captured (Garamszegi, Eens, & Török, 2009). In a capture-recapture study with Japanese quail (*Corurnix japonica*) the individual capture rank of birds was consistent for three capture trials over the first six weeks post hatch (Mills & Faure, 2000). Moreover, quail from lines selected for short duration of tonic immobility and high levels of social reinstatement behavior were captured before quail selected for high duration of tonic immobility and low levels of social reinstatement. There is further evidence from studies with mammals; in North American red squirrels (*Tamiasciurus hudsonicus*) exploration in a novel environment was related to an individual's risk taking behavior, as measured by the number and location of captures. Individuals who were more active in a novel environment took more risks were less likely to survive the winter (Boon, Réale, & Boutin, 2008). These three examples demonstrate that the relative order in which animals are captured, or the number of times they are captured across space (location) and time (days), are likely related to other suites of correlated behaviors that affect an individual's fitness. Therefore, the goal of the current experiment is to test for repeatability in capture order in both male and female black-capped and mountain chickadees.

In same sex/same species groups we released male and female black-capped and mountain chickadees into a room, and then capture them with a large net. This same procedure is repeated one week later to test for repeatability in capture order. This examination will allow for direct evolutionary comparison of a behavioral trait between sister species and set the stage for later studies examining personality traits and their expression within and among species.

Method

Subjects

Fifty-three chickadees of at least 1 year of age (determined by the shape and coloring of outer tail retrices; see Pyle, 1997) were used in this study. Thirty-one black-capped chickadees (17 male, 14 female) originating from Kananaskis Valley (Alberta, Canada, 51° 02'N, 115° 03'W) and Edmonton, Alberta Canada (53° 06'N, 113° 04'W) and 22 mountain chickadees (12 male, 10 female) originating from Kananaskis Valley were captured in the winter of 2004 using potter traps baited with sunflower seeds. The sex of each bird was determined either by visual inspection of the gonads via laparotomy or using DNA analysis (see Griffiths, Double, Orr, & Dawson, 1998).

Each species was housed separately at the University of Alberta in individual Jupiter Parakeet cages (0.3 × 0.4 × 0.4 m; Rolf C. Hagen, Inc., Montreal, Canada). Housing conditions allowed for auditory and visual contact, but not physical contact with conspecifics. Birds had food (Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, Missouri), water (vitamin supplemented on alternate days; Hagen, Rolf C. Hagen, Inc., Montreal, Canada), grit, and cuttle bone *ad libitum.* Birds were given three to five sunflower seeds daily. Birds also received one mealworm three times a week and a mixture of eggs and greens twice a week. Birds were maintained on a light-dark cycle that mimicked the natural cycle for Edmonton, Alberta.

Capture procedure

During each release and capture session, groups of 5 or 6 individuals of the same species and sex were released from their colony room cages into an experimental room (4.4 × 3.2 × 2.7 m).

Three researchers were present in the room. One researcher was blind to the purpose of the experiment and instructed to catch all the birds as quickly as possible using a large, padded net. This researcher caught the birds in all trials. The second researcher took the birds out of the net and returned them to their cages, and the third researcher recorded the identification numbers and order captured. After all birds were captured they were returned to their colony rooms. One week later, this procedure was repeated with the same groups of individuals. All trials were conducted in October 2004.

Statistical analysis

We used Spearman correlations to assess 'repeatability' for two reasons; first, our dependant measure is a rank order. Second, it provides a more useful index of 'differential consistency' (or repeatability) compared to the intraclass correlation when 'mean level consistency' (normative consistency) is low (Stamps & Groothuis, 2009). Mean level consistency is used to estimate whether the mean value of the behavior changes over time (between test and retest). In the current study, the two trials occurred a week apart, and the mean level of the behavioral scores was normalized due to our use of rank order data. We calculated four Spearman's rank order correlations, one for each sex within species, using SPSS v18.

Results

In both male black-capped and male mountain chickadees, capture order remained consistent over the two capture sessions (mountain chickadees, Spearman $r_{12} = 0.771$, $p = 0.002$; black-capped chickadees, Spearman $r_{17} = 0.464$, $p = 0.030$). Female mountain chickadees showed a non-significant trend towards capture order repeatability (Spearman $r_{10} = 0.450$, $p = 0.096$) however female black-capped chickadees exhibited no such trend (Spearman $r_{14} = 0.068$, $p = 0.409$, see Figure 1).

To test for sex-differences in repeatability of capture order, the correlations between first capture order and second capture order for each group (male mountain, female mountain, male black-capped, female black-capped, all male, all female chickadees) were transformed to z scores using Fishers r to z transform. These transformed r values were then compared using a z-test (Hays, 1994). The repeatability in capture order was not significantly different between male and female mountain chickadees ($z = 1.07$, $p = 0.28$), male and females black-capped chickadees ($z = 1.08$, $p = 0.28$) or all male and all female chickadees ($z = 1.08$, $p = 0.12$, all tests two-tailed).

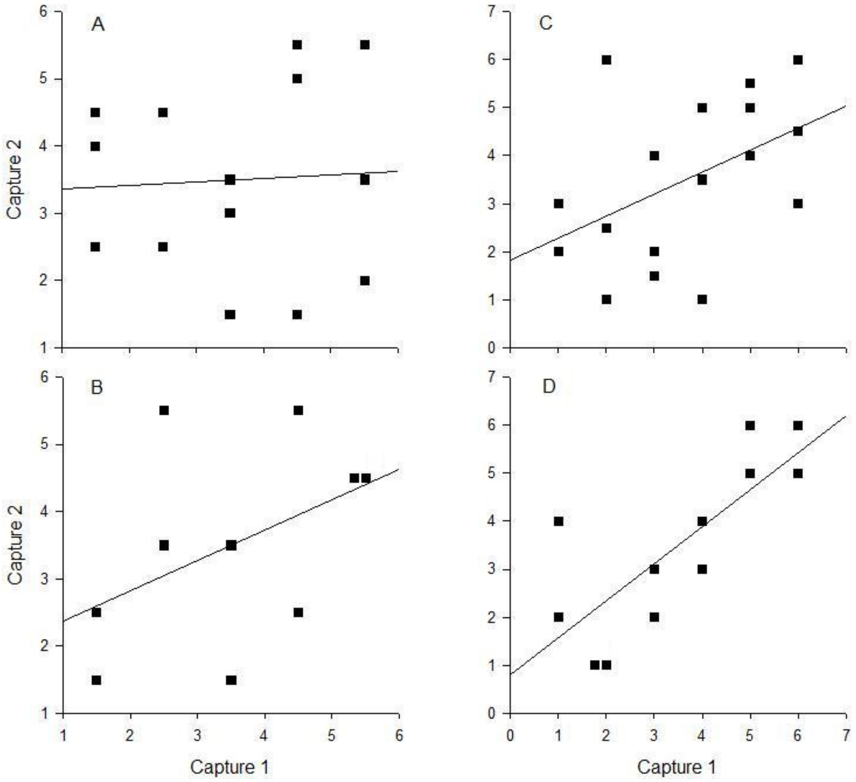

Figure 1. The order that individuals were captured for A) female black-capped chickadees, B) female mountain chickadees, C) male black-capped chickadees, D) and male mountain chickadees . Capture 1 (X-axis) is the first capture and capture 2 (Y-axis) is the second capture 7 days later. All panels are fit with a linear regression.

Discussion

Here we are the first to show the repeatability of a behavioral trait in black-capped and mountain chickadees, two closely-related species that have recently been used to study animal personality traits. The order in which free flying chickadees were captured in an experimental room by a human was consistent over two sessions for males in both species (black-capped and mountain chickadees) but not for females. Recent personality work with these species has revealed that both male and female black-capped chickadees that learn an acoustic discrimination task faster also readily explore a novel environment more than birds that are slower at learning the acoustic discrimination (Guillette et al., 2009). Further, low-exploring male mountain chickadees are dominant in pairwise encounters with high-exploring males (Fox et al., 2009). Our current findings suggest that both males and females should be used in studies exploring animal personality, as consistency appears to vary according to sex, at least for some behaviors. Our results also agree with previous research showing that capture order is repeatable

(Mills & Faure, 2000). Future studies using chickadees should examine if capture order is related to other personality traits (e.g., exploration) since there is evidence in other species (e.g., birds: Garamszeg et al., 2009; Mills & Faure, 2000; mammals: Boon et al., 2008) that this relation exists, and may influence fitness.

Our finding, that consistency in behavior over time is different for male and female chickadees for at least one behavioral measure, is in line with a recent study in another passerine bird, the zebra finch (*Taeniopygia guttata*: Schuett, Tregenza, & Dall, 2010). Schuett and colleagues looked for potential sex differences in exploration between males and females in both social and non-social settings. They found that in males, exploratory behavior remained more consistent over time, and across social/non-social contexts, compared to females. The difference in repeatability of behavior between male and female zebra finches was attributed to the fact that males tend to lead females during most of the year (Zann, 1996). We do not have this type of behavioral data in chickadees as wild-caught chickadees are typically housed in separate cages and do not breed in the laboratory as readily as zebra finches. For at least some behaviors (i.e., parental care) a meta-analysis conducted by Shuett et al. (2010) shows that male behavior is more consistent, and suggests that this differential consistency between sexes could have arose, and be maintained by sexual selection (Schuett et al., 2010). Whether or not this is the case for the behavior in the current study (repeatability in capture order) remains unclear. However, it is at least plausible that capture order in chickadees is linked to some other personality trait that is more directly related to sexual selection. Another meta-analysis of differences in repeatability between males and females was inconclusive. On the one hand, it was found that male behavior was generally more repeatable. On the other hand, the reverse was true when studies about mate preference were excluded from the analysis (Bell, Hankison, & Laskowski, 2009).

We believe that the ease of capture, ranging from being first caught to last caught in the current experiment may be related to the boldness/shyness continuum and/or risk taking (Wilson, 1998). There is evidence to support this notion from several diverse species including fish (Wilson, Coleman, Clark, & Biederman, 1993), mammals (Réale, Gallant, Leblanc, & Festa-Bianchet, 2000) and birds (Garamszegi et al., 2009). These results substantiate our assertion that trappability may be a component of behavioral syndrome, and therefore suggest that measuring capture-recapture order in a laboratory setting is indeed measuring important differences between individuals.

In light of the current finding of repeatability in capture order, it is worth discussing the potential of sampling biases in the capture of wild animals for use in laboratory studies. The current results would suggest that for our study population of black-capped and mountain chickadees, we are perhaps capturing a more homogenous, behaviorally, population of males, compared to females. That is, if capture order is random for females, then it is likely that the females that we are trapping from the wild have behavior types that are more representative of the natural range of behaviors displayed in wild populations. If this logic holds, then the opposite is true for male chickadees, we are consistently catching males with behaviors that are skewed towards one end of some behavioral continuum. Alternately, lack of repeatability in capture order for both black-capped and mountain chickadee females can also be explained if only the boldest individuals from the wild population were trapped. If only one part of the natural behavioral continuum is represented in our lab sample, this group might not show consistency in behavior because they are all from the same "place" in the distribution of wild behavior. Whatever the case, our results suggest that researchers should be mindful of individual differences in personality traits among their subjects, wild-caught or otherwise (see Biro & Dingemanse, 2009 for a review). Further, we suggest that researchers should be mindful of individual differences and not only "control" for unwanted variability in their subject pool. Rather, they should consider the additional, interesting and useful research questions that can be assessed as part of an existing research program by being mindful to such variation.

Here we have demonstrated that capture order is a repeatable behavioral measure for male black-capped and mountain chickadees, but not for females of the same species. We cannot speculate why such differences would arise. This is the first study, to our knowledge, to show repeatability in behavior of black-capped and mountain chickadees, two species that have recently been used in studies of animal personality. We suggest that these two species should be used as a model for investigating learning as a component of a behavioral syndrome for several reasons. First, different cognitive elements, such as perceptual, spatial, and neuronal are well studied in these species (e.g., Batty, Bloomfield, Spetch & Sturdy, 2009; Charrier, Lee, Bloomfield, & Sturdy, 2005; Hoshooley, & Sherry, 2004). Secondly, these species are closely related and live in both areas of sympatry and allopatry. This allows for investigating the evolutionary and learned differences in species typical behavior.

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