

# Repeatable nest defense behavior in a wild population of Eastern bluebirds (*Sialia sialis*) as evidence of personality

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**Abstract** Consistent individual differences in behavior, or personality, have been demonstrated in a variety of species other than humans, including mammals, birds, and invertebrates. Behavioral consistency has been shown to affect dispersal, foraging, exploration, and antipredator responses, which may have an impact on parental and offspring survival. Despite increasing research in behavioral consistency, the repeatability of nest defense behavior has rarely been assessed in wild bird populations. Furthermore, previous studies investigating nest defense behavior have utilized laboratory studies or mounted predators to elicit defensive behavior. It is important to assess personality in wild populations to fully understand the fitness consequences of behavioral consistency across natural contexts and to utilize live predators or competitors for accurate assessment of defensive behavior. We used an ecologically relevant, live, invasive, nest site competitor, the house sparrow (*Passer domesticus*), to elicit nest defense behavior in a wild population of Eastern bluebirds (*Sialia sialis*) to determine if nest defense behavior is repeatable within and between years for males and females (males: 2009,  $N=17$ ; 2010,  $N=18$ ; both years,  $N=9$ . Females: 2009,  $N=22$ ; 2010,  $N=15$ ; both years,  $N=11$ ). We also determined if individual behavior changes as a function of season, parental age, brood size, or the number of house sparrows around the nest site. We found that females demonstrated repeatable behavior both within and between years. Male nest defense behavior was only repeatable in 1 year and was influenced by season in the other year. Parental age, brood size, and the number of house sparrows around the nest site did not affect nest

defense behavior. We conclude that Eastern bluebirds demonstrate consistent nest defense behavior, or personality, although males are more plastic than females.

**Keywords** Personality · Nest defense · Repeatability · Simulated territorial intrusion

## Introduction

Differences in the same behavior among individuals within a population were thought to be uniquely human until studies of multiple species revealed that individuals differ consistently in behavioral responses (Wilson 1998; Gosling and John 1999). Furthermore, these behavioral differences vary not only among populations, but within them as well (Bell 2005; Dingemanse et al. 2007). Consistent individual differences in behavior within populations have been demonstrated in a variety of taxa, including invertebrates (e.g., Mather and Anderson 1993; Sinn et al. 2008), fish (e.g., Budaev 1999; Wilson and Godin 2009; Stein and Bell 2011), mammals (e.g., Forkman et al. 1995; Réale et al. 2000), and birds (e.g., Dingemanse et al. 2003; Hollander et al. 2008). Although these individual differences are well documented, they are referred to by a variety of terms that are not completely synonymous: such as coping styles, temperaments, predispositions, profiles, axes, neophobia, constructs, and personalities (Gosling 2001; Sih et al. 2004a; Groothuis and Carere 2005; Réale et al. 2007). More specifically, individuals within the same population exhibit a personality if their behavior is consistent across time and in different contexts (Réale et al. 2007). For purposes of this paper, we will refer to birds in our population that exhibited consistent individual differences as evidence of a personality because we analyzed temporal consistency of nest defense behavior.

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Many studies have documented that consistent individual differences in behavior and correlated suites of behaviors (behavioral syndromes; Sih et al. 2004a; Sih and Bell 2008; Stamps and Groothuis 2010) have fitness consequences (Dingemanse et al. 2004; reviewed in Dingemanse and Réale 2005) and have conservation and management implications (reviewed in McDougall et al. 2006). In wild populations, consistent individual differences may influence dispersal (Cote 2007; Duckworth and Badyaev 2007), exploration (Dingemanse et al. 2002), foraging (Cole et al. 2011), and antipredator responses (Sih et al. 2003; Smith and Blumstein 2010). Research investigating consistent individual differences in aggressive behavior in birds has revealed survival and evolutionary effects, as well. Birds exhibiting more aggressive behavior have accelerated range expansion in both Townsend's warblers (*Dendroica townsendi*; Owen-Ashley and Butler 2004) and Western bluebirds (*Sialia mexicana*; Duckworth and Badyaev 2007). Similarly, aggressive nest defenders recruited more offspring in female Ural owls (*Strix uralensis*) compared to less fierce individuals (Kontinen et al. 2009).

The intensity of nest defense exhibited by parents is widely variable among individuals and may be driven by several nonmutually exclusive factors (reviewed in Trivers 1972; Montgomerie and Weatherhead 1988), such as nest stage (Andersson et al. 1980; Greig-Smith 1980; Regelman and Curio 1983; Wiklund 1990; Sproat and Ritchison 1993), parental sex (Knight and Temple 1988; Brunton 1990; Winkler 1992; Sproat and Ritchison 1993), brood size (Greig-Smith 1980; Regelman and Curio 1983), and time within the breeding season (Regelman and Curio 1983; Tolonen and Korpimäki 1995; Redmond et al. 2009). Predation is one of the most important factors affecting nestling survival (Ricklefs 1969), but engaging in nest defense is a risky behavior that may result in injury or even death of the parents with no guarantee of nestling survivorship. The efficacy of nest defense in passerine birds is unclear; some studies have documented a positive relationship between parental nest defense and nestling survival (Greig-Smith 1980; Blancher and Robertson 1982; Weatherhead 1990), whereas others have not detected a relationship between parental nest defense and nestling survival (McLean et al. 1986; Hatch 1997; Redmond et al. 2009).

We studied a wild population of Eastern bluebirds (*Sialia sialis*) to determine if individuals exhibited repeatable levels of nest defense intensity both within and between years as evidence of personality. We used a live, invasive, nest site competitor, the house sparrow (*Passer domesticus*), to elicit nest defense behavior from Eastern bluebirds. Bluebirds exhibit biparental care, have multiple broods per season, and both sexes defend the nest against predators (Gowaty and Plissner 1998). Thus, it is feasible to measure the consistency of nest defense behavior in both sexes both

within and across seasons. The use of live male house sparrows to elicit nest defense behavior represents a realistic ecological interaction between these two species. Although both species readily nest in and defend constructed nest boxes (Pogue and Schnell 1994), house sparrows can displace bluebirds from a nesting site (Estabrook 1907; Zeleny 1976) and may destroy eggs and kill both adults and nestlings to compete for nest box space (Gowaty 1984; Burtka, personal observation).

Despite previous research demonstrating the benefits of both consistent individual behavior and aggressive behavior in populations, little research has documented the repeatability of nest defense behavior in individuals over time (but see Hatch 1997; Duckworth 2006; Redmond et al. 2009; Betini and Norris 2012). Perhaps due to the numerous ecological and life history traits that have been demonstrated to underlie variation among individuals in nest defense behavior, few studies have addressed the consistency of nest defense. It is important to study the consistency of parental behavior in wild populations as consistent individual differences have fitness consequences (Dingemanse and Réale 2005) and consistent behavior can potentially limit plasticity and, therefore, restrict the range of optimal behavior available to individuals (Bell 2007). Furthermore, identifying behavioral consistency in wild populations may contribute to identifying other correlated behaviors that evolve concurrently with nest defense behavior (Bell 2007).

Consistency of nest defense behavior within years would indicate that nest defense is a stable trait in the short term. Alternatively, if nest defense is not consistent within years, then individuals exhibit plastic nest defense behavior and variation in defense may be driven primarily by environmental factors (Hakkarainen and Korpimäki 1994) or an internal physiological state, such as circulating hormone levels (Ramenofsky 1984; Wingfield et al. 1987). Consistent defense behavior between years would indicate that nest defense behavior is relatively static and may have evolutionary implications if one extreme is favored over another, especially if nest defense behavior is linked to other behaviors that influence parental and nestling survival in a behavioral syndrome.

We also investigated the effects of a number of environmental factors, including: time in the season, parental age, brood size, the number of house sparrows near the nest site, and house sparrow intruder behavior on nest defense behavior. With the exception of house sparrow abundance and behavior, other studies have documented that these factors positively or negatively influence nest defense behavior (reviewed in Montgomerie and Weatherhead 1988) and may, therefore, affect the repeatability of nest defense. We collected data on house sparrow abundance because previous experience with a competitor may influence nest defense behavior (Knight and Temple 1986a) and our nest box

trails were established in areas with differential exposure to house sparrows.

## Methods

### Model organism

Eastern bluebirds are socially monogamous altricial passerines. Adults are sexually dimorphic with males exhibiting bright blue plumage and a deep chestnut breast, whereas females are duller (Gowaty and Plissner 1998, Grindstaff et al. 2012), which allows for easy field identification. They typically nest in open habitats and are obligate secondary cavity nesters (Gowaty and Plissner 1998). Because cavities are a limited resource (Newton 1994), Eastern bluebirds frequently compete with house sparrows, European starlings (*Sturnus vulgaris*) and tree swallows (*Tachycineta bicolor*) for access to nest sites (Meek and Robertson 1994; Gowaty and Plissner 1998). We utilized house sparrows for this study as they are the most frequent competitor in the population and cannot be excluded from nest boxes by altering the entrance hole diameter (Pogue and Schnell 1994).

Eastern bluebirds have clutch sizes that range from three to seven eggs (Gowaty and Plissner 1998) with pairs in this study population producing up to three broods per season. Bluebirds lay one egg per day following incubation by the female for approximately 14 days after the penultimate or ultimate egg is laid (Gowaty and Plissner 1998). Eggs hatch fairly synchronously, usually within 1 day (Gowaty and Plissner 1998), and nestlings leave the nest approximately 17–18 days post-hatch (Pinkowski 1975; Gowaty and Plissner 1998). Both parents participate in nestling care and engage in nest defense behavior (Gowaty and Plissner 1998).

### Study site

The study was conducted on bluebird nest box trails located in and around Stillwater, OK, USA (36°06′ 56.57″N and 97°03′35.15″W). Eastern bluebird nest boxes ( $N=144$ ) were mounted at ~1.5 m above the ground on t-posts or wooden fence posts bordering fenced rangeland, agricultural land, or open areas. Boxes (~14×11.5×24 cm) were located at least 50 m away from one another and were setup before the start of the 2009 breeding season.

### Nest box monitoring

Nest boxes were monitored between March and September in 2009 and 2010. All nest boxes were monitored twice weekly for signs of nesting. Once a completed nest was discovered, boxes were checked daily for the first egg.

When no additional eggs appeared after monitoring on the twice weekly schedule, clutches were considered complete and nests were checked daily starting 10 days after the ultimate egg was laid to determine hatch day (nestling day 0). After hatching, nestlings were banded with a US Geological Survey (USGS) aluminum band on day 11 and nests were monitored daily after day 14 to determine fledging date. The number of nestlings surviving to fledging was recorded for each nest.

Most adults were captured using a modified prop trap (Robinson et al. 2004; Friedman et al. 2008) between nestling days 4 and 9. Some females were captured before hatching by trapping them in the nest box during late incubation. Females were not trapped earlier than 4–6 days pre-hatch in order to prevent abandonment. All adults were banded with a USGS aluminum leg band and a unique combination of three color bands for identification. Adults captured in 2010 were aged using molt limits (Shizuka and Dickinson 2005) and the shape of the tenth primary feather (Pitts 1985) and classified as second year (SY) or after second year (ASY) birds.

### House sparrow abundance estimates

We estimated house sparrow abundance around active Eastern bluebird nest sites by performing stationary point counts with the nest box as the center ( $N=148$ ). Point counts were conducted for 10 min and all house sparrows heard or seen through binoculars were counted. Counts were performed between 06:30 and 10:00 hours Central Standard Time (CST) for 3 days between the day the second egg was laid and the predicted sixth egg date. We attempted to count sparrows on consecutive days but did not conduct point counts if it was raining, foggy, or high winds prevented complete observation (Ralph et al. 1995). The number of house sparrows detected was averaged over 3 days and then grouped into two categories: (0) low, with an average of zero to four sparrows ( $N=114$ ) and (1) high, with an average of >4 sparrows ( $N=34$ ), based on the observed distribution of house sparrow abundances. Sparrow numbers ranged from 0 to 16 with an average of 2.21 sparrows detected at each site.

### Nest defense behavior

To quantify nest defense intensity, we conducted simulated territorial intrusions with a live male house sparrow between nestling days 7–9 to control for behavioral variation caused by nestling age and to prevent abandonment by human disturbance. House sparrows were captured in a mist net or a repeating sparrow trap from a remote location (>1.5 km from the focal nest box). Sparrows were placed in a galvanized wire cage (23×23×30.5 cm) secured to the top of the

nest box with rope and covered with a cloth. This cage provided sufficient space to allow the sparrow to retreat from the resident bluebirds and avoid physical contact. Observers were concealed behind a blind, vehicle, or natural vegetation located at least 15 m away. The cloth covering the cage was removed via an attached string when both Eastern bluebird parents were within 100 m of the nest box or 20 min had elapsed with the sighting of only one parent. In almost all cases where the trial began with one parent, the second parent joined quickly or was heard within the vicinity. Trials were conducted between 07:00 and 13:00 hours CST. House sparrows were active during trials and resumed normal behavior upon release.

Parental nest defense was quantified as the numbers of hovers and attacks exhibited by each sex for 2 min. Observations were conducted through binoculars and behavior was verbally reiterated on a portable voice recorder. The same two observers, JLB and EC, conducted all behavioral trials to prevent potential observer bias. Individuals were then given a nest defense score of 1–6 with 6 as the most intense using the numbers of hovers and attacks as assignment criteria *sensu* Duckworth (2006; Table 1; Grindstaff et al. 2012). Adults had to defend the nest within 0.5 m of the sparrow cage in order to count as a response. “Hovers” and “flying” included any behavior that involved rapidly flying in a stationary manner within the allotted distance from the cage or swooping and diving without contacting the cage. Birds were considered “attacking” when they landed on the cage and physically pecked at the sparrow. This method of ranking nest defense behavior has been previously validated in Western bluebirds, which exhibit similar defensive behavior (Duckworth 2006).

Adult social pairs were subjected to a simulated territorial intrusion with a novel sparrow at each successive breeding attempt, so each individual was tested between one and four

**Table 1** Criteria used to score adult Eastern bluebird nest defense intensity during simulated territorial intrusion trials (*sensu* Duckworth 2006). The number of times an individual flew or hovered within 0.5 m of the sparrow cage or physically pecked at the sparrow during the 2-min simulated territorial intrusion were counted and tallied to produce the overall score. Individuals were tested between one and four times per season (total trials,  $N=164$ )

Score	Number of times flying/hovering	Attacks	Description
1	0	–	Not aggressive
2	1–5	–	Minimal response, moderately aggressive
3	>5	–	Moderate response, moderately aggressive
4	–	1–5	Moderate response, highly aggressive
5	–	6–9	High response, highly aggressive
6	–	>9	Very high response, very aggressive

times per season (total trials  $N=164$ ). Only birds with two or more measurements within a season were included in the within-year analysis. We measured the repeatability of nest defense behavior for 17 males and 22 females in 2009 and 18 males and 15 females in 2010. To determine between-year repeatability, we only included individuals with intrusion trials conducted in 2010 within a 30-day window of the 2009 trial in order to control for any seasonal effects. Thus, 9 males and 11 females were included in the between-year analysis. Repeatability was calculated separately for each sex both within and between years.

#### Control trials

Nest defense behavior of a subset of Eastern bluebird pairs in both years in response to an empty cage was assessed as a control ( $N=138$ ). The cage was mounted and revealed in the same manner as the simulated territorial intrusion trials to ensure that birds were reacting to the presence of the house sparrow and not the cage itself. Control trials also occurred between nestling days 7 and 9 but never on the same day as a simulated territorial intrusion trial. Control trials were randomized such that pairs were presented with an empty cage prior to or after an intrusion trial with a live sparrow. Behavioral responses to the empty cage were recorded in the same manner as house sparrow trials.

#### House sparrow behavior

In 2010, one observer (BH) observed the behavior of the caged house sparrow to evaluate if house sparrow behavior affected the nest defense response of Eastern bluebirds ( $N=23$ ). A voice recorder was used to verbally reiterate sparrow behavior during the intrusion trial. House sparrows were ranked on a similar scale with the exception that house sparrows were scored on two criteria, avoidance and attacking behavior, and the scores were then averaged to obtain one number (Table 2). Avoidance behavior was categorized as any movement away from an

**Table 2** Criteria used to score house sparrow behavior during simulated intrusion trials to determine the effect of house sparrow behavior on Eastern bluebird nest defense intensity ( $N=23$ ). Sparrows were scored both on the number of avoidances and the number of attacks and those scores were then averaged to obtain one behavioral score. House sparrows that did not respond were assigned a score of 3.5

Score	Avoidances	Attacks	Description
1	>10	–	Very avoidant
2	5–9	–	Moderately avoidant
3	1–4	–	Slightly avoidant
4	–	1–5	Slightly aggressive
5	–	6–11	Moderately aggressive
6	–	>11	Very aggressive



Eastern bluebird defensive maneuver and attacks were considered physically pecking at the bluebirds. An average of these two scores was used in order to incorporate both avoidance and aggressive behavior. House sparrows that did not respond during the simulated territorial intrusion were assigned a score of 3.5, the median between the most passive and the most aggressive behaviors.

### Statistical methods

Statistical analyses were performed using SAS (v. 9.2, SAS Institute Inc. 2002). Data were normally distributed and male and female analyses were conducted separately. We first conducted independent sample *t* tests to determine if clutch size (2009,  $N=127$ ; 2010,  $N=120$ ), brood size (2009,  $N=96$ ; 2010,  $N=96$ ), or nest defense intensity differed between years with all monitored nests included. We randomly selected individuals to appear once in the dataset to avoid pseudoreplication when testing the effect of year on nest defense intensity (males: 2009,  $N=37$ ; 2010,  $N=38$ /females: 2009,  $N=41$ ; 2010,  $N=46$ ). Clutch size ( $t=0.80$ ,  $p=0.42$ ), brood size ( $t=0.25$ ,  $p=0.80$ ), male nest defense behavior ( $t=-0.28$ ,  $df=73$ ,  $p=0.78$ ), and female nest defense behavior ( $t=-1.21$ ,  $df=84$ ,  $p=0.23$ ) did not differ significantly between 2009 and 2010. Therefore, we pooled data from the 2 years in subsequent analyses with the exception of the repeatability analysis.

We also used an independent sample *t* test to determine if adult age influenced nest defense intensity in 2010. Individuals with multiple measurements were randomly selected to appear only once in the dataset (males: SY,  $N=15$ ; ASY,  $N=27$ /females: SY,  $N=14$ ; ASY,  $N=34$ ).

General linear mixed models (GLMM) were used to analyze the effects of brood size, season, and house sparrow abundance on nest defense intensity. For all models, individuals were treated as repeated factors and only individuals with known identities were included. Because the nest defense intensity of some individuals was tested more than once, repeated trials for an individual were numbered sequentially (intrusion trial number). The intrusion trial number was then incorporated as a nested effect within the repeated factor. Methods to approximate the denominator degrees of freedom and covariance models were extensively modeled and selected based on the lowest Akaike information criterion value. We used an unstructured covariance model to incorporate unequally spaced territorial intrusions (Littell et al. 2006) and the Kenward–Rodger method to approximate the denominator degrees of freedom.

For analyses of the effects of brood size on nest defense behavior, the intrusion trial number within the repeated individual factor reflected the total number of trials as a continuous count across both years (unique male,  $N=75$ ; unique female,  $N=86$ ). For example, the maximum number

of trials for individuals tested in both 2009 and 2010 was six. Thus, every individual appeared in the dataset with a nested trial number from one to six dependent on the number of times that individual was tested over the 2-year study. In this model, Julian date was initially included as a covariate and year was included as a fixed effect but both were removed as the contributions were not significant ( $p>0.05$ ). For analyses of seasonal changes in nest defense behavior, all individuals subjected to a simulated territorial intrusion during the 2-year study were included (unique individuals: males 2009,  $N=46$ ; 2010,  $N=42$ ; females 2009,  $N=53$ ; 2010,  $N=52$ ). The intrusion trial number ranged from one to four trials per individual per year as individuals were tested up to four times per season.

For analyses of the effects of house sparrow abundance on nest defense behavior, the abundance category, year, and the interaction between abundance and year were treated as fixed effects and Julian date was included as a covariate. All individuals with nest defense intensity scores and house sparrow abundance data were included in the analysis (unique males,  $N=56$ ; unique females,  $N=61$ ) as repeated factors and the intrusion trial number as a continuous count across years was included as a nested effect (one to four trials). Fixed effects and the interaction factors were removed through backwards stepwise elimination.

GLMMs were also used to determine if house sparrow behavior affected Eastern bluebird nest defense intensity. For this analysis, individual house sparrow identity was used as a repeated effect with the intrusion trial number for that individual as a nested effect. We did not incorporate Julian date as a covariate because trials were only conducted during June and July in 2010 ( $N=23$ ).

Repeatability ( $\tau$ ) of Eastern bluebird nest defense was calculated using the intraclass correlation coefficient (ICC) as described in Lessells and Boag (1987). The ICC is the ratio of among-individual variance to total variance calculated with a one-way analysis of variance (ANOVA). Using this method, it is possible to obtain a negative value, which indicates that the variation among individuals is less than the variation within individuals (Lessells and Boag 1987). The ICC returns a value indicating the strength of repeatability. Values that approach one indicate high repeatability. The *p* value associated with the ANOVA is then used to determine if the repeatability is significantly greater than zero (Lessells and Boag 1987; Nakagawa and Schielzeth 2010). We used ICC instead of Pearson's correlation coefficient because the latter only incorporates two measurements per individual. The ICC was an appropriate statistic to determine the repeatability of the individuals within this population because we had a normally distributed dataset and an unbalanced design with a minimum of two and a maximum of four behavioral scores per individual (Table 3). Results from a meta-analysis of repeatability revealed that increasing the number of times an

**Table 3** The number of trials per individual used for within-year analyses of repeatability. The between-year analysis utilized only two trials per individual, one for each year

Sex/year		Number of trials per individual		
		2	3	4
Male	2009	14	3	0
	2010	17	1	0
Female	2009	17	4	1
	2010	11	4	0

individual was tested decreases the error around the repeatability estimate as opposed to strengthening the estimate (Bell et al. 2009). Standard errors (SE) for repeatability were calculated with the formulae in Becker (1984).

More specifically, nest defense score was treated as a dependent variable and bird identity was the main effect in the ANOVA model. Separate analyses were conducted for each sex within and between years, resulting in a total of six models.

## Results

### Response to simulated territorial intrusion trials

Eastern bluebirds in this study clearly recognized house sparrows as a threat. The majority of bluebirds presented with a sparrow during an intrusion trial responded by actively defending the nest (82.76 % of males and 75.97 % of females defended with an intensity of 2 or higher). Moreover, we witnessed natural encounters in which Eastern bluebirds chased house sparrows away from active nest sites. None of the Eastern bluebirds exhibited nest defense behavior during empty cage control trials. Pairs initially appeared at the nest box when the cage was covered but after revealing the empty cage, neither sex displayed any defensive reaction. Bluebirds resumed normal behavior during the 2-min control trials and some even entered the nest box to provision the nestlings.

### House sparrow behavior

House sparrow avoidance and attack behaviors ranged from a total of 1–26 and 1–28, respectively, resulting in a range of behavioral scores from 2 to 6. House sparrows did not respond in 8 of 23 trials. During two of the house sparrow observation trials, only one Eastern bluebird appeared during the simulated territorial intrusion so we were only able to collect bluebird behavior for one adult in those cases. House sparrow behavior did not affect nest defense behavior of male ( $F_{1,20}=1.07$ ,  $p=0.31$ ) or female ( $F_{1,20}=0.09$ ,  $p=0.77$ ) Eastern bluebirds.

### Age, season, brood size, and house sparrow abundance effects

There was no significant difference in average nest defense score between SY and ASY males ( $t=-0.98$ ,  $df=40$ ,  $p=0.33$ ) or between SY and ASY females ( $t=0.80$ ,  $df=46$ ,  $p=0.80$ ). In 2009, male nest defense behavior exhibited a significant seasonal decline ( $F_{1,64}=3.95$ ,  $p=0.05$ ; Fig. 1a), whereas male aggression was consistent across the season in 2010 ( $F_{1,61}=0.10$ ,  $p=0.75$ ; Fig. 1c). Female nest defense behavior was consistent across the season in both years (2009:  $F_{1,77}=2.60$ ,  $p=0.11$ ; 2010:  $F_{1,69}=0.19$ ,  $p=0.67$ ; Fig. 1b and d).

Brood size ranged from one to six nestlings (mean  $2.82 \pm 1.71$  SE) and was not related to nest defense intensity exhibited by either males ( $F_{1,128}=0.65$ ,  $p=0.42$ ) or females ( $F_{1,149}=0.70$ ,  $p=0.41$ ). Furthermore, Eastern bluebirds breeding in areas with higher numbers of house sparrows ( $>4$ ) did not exhibit more intense nest defense compared to bluebirds living in areas with no or fewer invasive competitors (males:  $F_{1,75}=0.26$ ,  $p=0.61$ ; females:  $F_{1,86}=0.29$ ,  $p=0.59$ ).

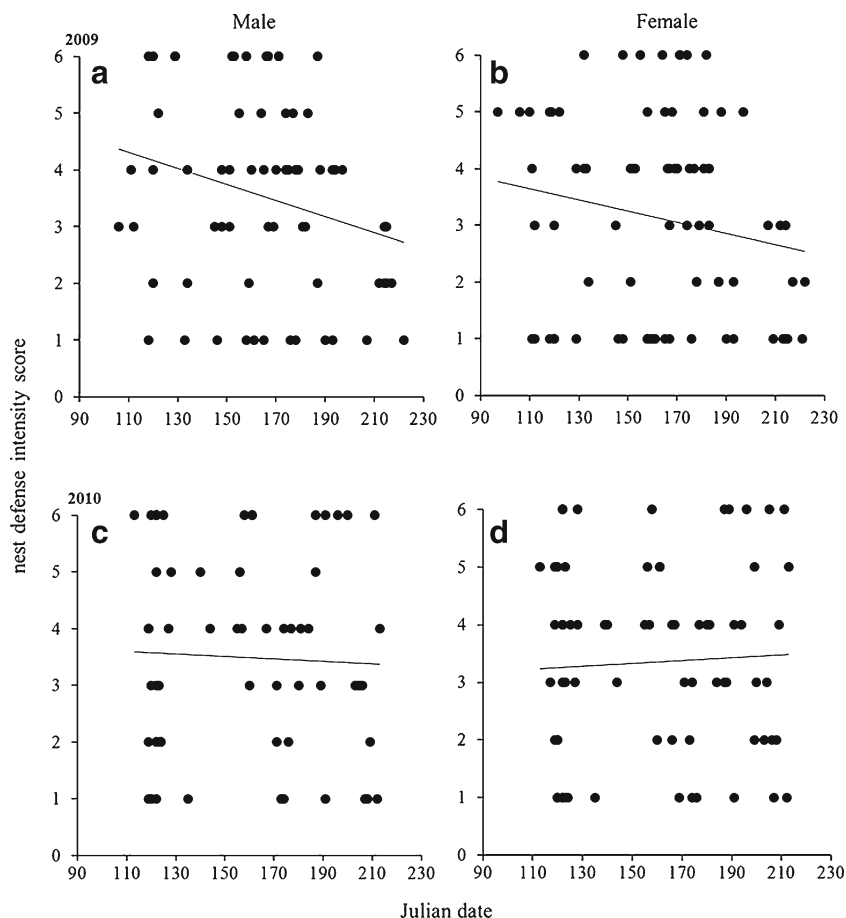
### Repeatability of nest defense behavior

Of the Eastern bluebirds captured in 2009, 17 (26.53 %) females and 16 (32.65 %) males returned to breed in our nest boxes in 2010. In addition, some individuals were excluded from the between-year analyses because we were either unable to perform an intrusion trial or the trial in 2010 was not within the 30-day window of the date on which the simulated territorial intrusion trial was conducted in 2009. Female nest defense behavior was repeatable both within years and across the 2 years. Female behavior within 2009 was moderately repeatable, whereas female behavior was strongly repeatable within 2010 (Table 4). Conversely, male behavior was highly repeatable within 2010 but was not repeatable within 2009 or across years (Table 4). The lack of repeatable male behavior in 2009 was primarily due to low variation among individuals in nest defense behavior, rather than high variability within individuals. In contrast, in all other cases, variation in nest defense behavior among individuals was higher, resulting in significantly repeatable behavior.

## Discussion

In this study, we determined that Eastern bluebird nest defense behavior against an invasive competitor, the house sparrow, is evidence for personality by testing the repeatability of aggression both within and between two consecutive years, as well as identified factors that may influence repeatability of nest defense behavior. In this population of Eastern bluebirds, females exhibited repeatable behavior

**Fig. 1** Male (**a** and **c**) and female (**b** and **d**) nest defense intensity scores in relation to the date of the behavioral trial indicated by Julian date (January 1=1) and compared between 2009 (**a** and **b**) and 2010 (**c** and **d**). All individuals sampled across the 2-year study were included in this analysis (unique individuals: males 2009,  $N=46$ ; 2010,  $N=42$ ; females 2009,  $N=53$ ; 2010,  $N=52$ ). Only males in 2009 (**a**) exhibited a significant decline in nest defense behavior over the season ( $F_{1,64}=3.95$ ,  $p=0.05$ )



both within and between years, which suggests that females are relatively consistent in their behavior irrespective of the external or internal environment. Males, however, did not follow the same pattern as females. Males exhibited repeatable nest defense behavior within 2010, but not within 2009 or between years. In 2009, male behavior was more variable within individuals as opposed to among individuals. However, it is important to note that the lack of male repeatability between years may have been influenced by a small sample size ( $N=9$ ). Overall, males may exhibit greater behavioral flexibility than females and may be more sensitive to environmental changes and adjust their behavior accordingly. Because we detected repeatable behavior in both sexes, it is likely that this population of Eastern bluebirds exhibits

consistent differences in nest defense behavior, although males have greater behavioral plasticity than females.

Personality has been interpreted as limiting plasticity and a potentially maladaptive behavior that may negatively influence parent and offspring survival (Dall et al. 2004). However, recent research utilizing a behavioral reaction norm approach to study how an individual's average behavior changes along an environmental gradient (Dingemanse et al. 2010) has revealed that personality and plasticity are more integrated than previously thought. For example, Westneat et al. (2011) studied reaction norms of provisioning behavior in house sparrows and uncovered complex patterns of among- (personality) and within-individual (plasticity) variation by measuring individual provisioning

**Table 4** Mean squares, repeatability ( $\tau$ ), and SE for within- and between-year analyses of nest defense behavior in male and female Eastern bluebirds

Category	$N$	$MS_A$	$MS_W$	$\tau$	SE	$F$	$p$
2009 Male	17	2.412	2.891	-0.083	0.077	0.83	0.64
2009 Female	22	4.560	2.009	0.359	0.17	2.27	0.02
2010 Male	18	6.191	0.719	0.787	0.090	8.61	<0.001
2010 Female	15	3.707	0.649	0.676	0.134	5.71	<0.001
Male between years	9	5.139	2.222	0.396	0.298	2.31	0.12
Female between years	11	5.409	1.364	0.597	0.203	3.97	0.02

over a suite of environmental conditions ( $I \times E$ ; Nussey et al. 2007). Although individual house sparrows exhibited consistent differences in provisioning behavior (personality), nestling age and partner visit rate also affected among- and within-individual variation, respectively. In the present study, we minimized the influence of the environment by controlling for traits such as nestling age; however, repeated individual assessments of nest defense intensity with nestlings of different ages would allow effective utilization of the behavioral reaction norm approach.

Male and female bluebirds in our population exhibited different levels of behavioral consistency. These differences in consistency between the sexes might have been influenced by interactions between male and female social mates (Royle et al. 2010; Schuett et al. 2011). Differing levels of parental investment within pairs may stimulate one partner to compensate for a lack of care or to cooperate if the partner is reliable (Dall 2004; Royale et al. 2010), which can have fitness consequences. For example, pairs of zebra finches (*Taeniopygia guttata*) with similar personalities (Schuett et al. 2011) and great tit (*Parus major*) pairs with similar extreme levels of exploratory behavior (Both et al. 2005) raised offspring that were in better condition.

Aggressive behavior has been demonstrated to be repeatable in other species (e.g., Kralj-Fišer et al. 2007; Redmond et al. 2009; reviewed in Bell et al. 2009). A meta-analysis revealed that male behavior is more consistent than female behavior in most vertebrates, but when mate preference behavior was removed from the dataset, female behavior was more repeatable (Bell et al. 2009). However, avian studies of parental provisioning behavior frequently uncover higher repeatability of male behavior than female behavior (Freeman-Gallant and Rothstein 1999; Schwagmeyer and Mock 2003; Nakagawa et al. 2007; but see Hatch 1997; Betini and Norris 2012). Our results report exactly the opposite trend, with females demonstrating less behavioral flexibility than males. A few previous avian studies have examined the repeatability of nest defense behavior. Redmond et al. (2009) established that Eastern kingbird (*Tyrannus tyrannus*) males have repeatable nest defense behavior against a mounted crow and male Western bluebirds also demonstrated repeatable nest defense behavior against a live tree swallow (Duckworth 2006). In support of our results, Hatch (1997) discovered that female song sparrows (*Melospiza melodia*) demonstrate repeatable defense behavior against a mounted junco but not against a mounted crow and Betini and Norris (2012) found that female tree swallows exhibited repeatable defensive behavior against a human intruder. These studies lend support for the hypothesis that nest defense behavior is consistent in Eastern bluebirds, but sex differences in response to an intruder may be a result of parental investment, environmental sensitivity, or internal state.

Furthermore, these results suggest that Eastern bluebirds engage in defensive behavior regardless of the behavior of a

house sparrow intruder. These results provide additional, indirect support for evidence of personality in this Eastern bluebird population. If sparrow behavior affected Eastern bluebird nest defense behavior, we would expect behavior to be nonrepeatable as bluebird pairs were not presented with the same sparrow in subsequent trials.

#### Variation in nest defense behavior

We were unable to control for natural interactions between Eastern bluebirds and house sparrows so used age group as a proxy for experience level. We assumed SY birds would have had fewer previous interactions with house sparrows as they were in their first year acquiring a territory and breeding. However, nest defense intensity did not differ significantly between age classes. Many passerine studies have also failed to find an effect of age on nest defense intensity (Winkler 1992; Hatch 1997; Hollander et al. 2008). Conversely, other research suggests that the level of experience with a predator may influence nest defense intensity as individuals learn about the predator's abilities. For example, Knight and Temple (1986a) suggested that repeated exposure to an observer or predator caused increased nest defense behavior in American robins (*Turdus migratorius*) and red-winged blackbirds (*Agelaius phoeniceus*) due to loss of fear (the positive reinforcement hypothesis). However, this hypothesis has mixed support (e.g., Westneat 1989; Rytönen and Soppela 1995). In our study, bluebirds were tested no more than four times over a 6-month period. Thus, it is unlikely that birds habituated to the simulated territorial intrusion. Adults did not exhibit more aggressive tendencies through repeated exposure, which we would expect to see if these results supported the positive reinforcement hypothesis. Thus experience level likely did not influence nest defense intensity as indicated by the fact that there were no significant differences in the behavioral responses of either sex for SY and ASY Eastern bluebirds.

Previous studies examining the relationship between nest defense intensity and brood size have found inconsistent results. In brood size manipulation studies, parents with experimentally enlarged broods exhibited elevated nest defense intensity in relation to parents with experimentally reduced broods (e.g., Knight and Temple 1986b, but see Winkler 1992). In the present, nonmanipulative study, we did not find a relationship between brood size and parental behavior.

It is clear from our results that the local abundance of house sparrows is not related to consistent individual differences in nest defense behavior in Eastern bluebirds. We expected that birds living in areas with more house sparrows would have increased nest defense intensity due to repeated encounters with competitors in support of the “positive reinforcement” hypothesis (Knight and Temple 1986a).



For example, Čapek et al. (2010) found that Eurasian reed warblers (*Acrocephalus scirpaceus*) exposed to multiple intrusions of a mounted common cuckoo (*Ciculus canorus*) increased nest defense from the first to the second presentation, although encounters after the second trial revealed no increase in aggressive behavior. In support of this hypothesis, Fokidis et al. (2011) reported that Abert's towhees (*Melospiza aberti*) behaved more aggressively when defending territories with a greater population density of conspecifics in urban, but not desert, areas. Although we did not measure the frequency of natural encounters and can only assume that bluebirds living in areas where we detected more house sparrows had an increased encounter rate, it is possible that natural disputes do not differ between areas with varying abundances of house sparrows. However, instances where we observed Eastern bluebirds naturally defending active nests or in which bluebirds were evicted from established nest boxes only occurred in areas where we frequently encountered house sparrows during point counts. Thus, it is likely that Eastern bluebirds living in areas where we detected many house sparrows during point counts encountered more natural competition with sparrows compared to birds living in areas with none or few sparrows.

Male nest defense behavior declined significantly across the breeding season in 1 year of the study. However, these results should be interpreted cautiously as many non-independent tests were utilized in this study and the result was only marginally significant. Although this pattern was only detected in 1 year, there are three potential hypotheses that may explain why males exhibited a seasonal decline in behavior. First, nest defense has previously been hypothesized to decline seasonally due to a decline in reproductive success during the breeding season (Perrins 1970; Weatherhead 1989). It is possible that early brood nestlings in the first year of the study were more valuable than those later in the season; however, this hypothesis would predict that the same pattern should have occurred in the second year of the study, which is not what we found. We would also expect to see a difference between the average defensive responses of males in the 2 years. Furthermore, if brood value were driving behavior, we would expect to see a similar pattern in female aggressive response towards a house sparrow intruder. Therefore, it is unlikely that differences in brood value drove the seasonal decline observed in nest defense behavior for males in 2009. It is important to note that a majority of other studies have found a seasonal increase in nest defense associated with declining re-nesting potential as the season progresses (Barash 1975; Montgomerie and Weatherhead 1988; Rytönen et al. 1989; Hollander et al. 2008; but see Greig-Smith 1980).

The second hypothesis regarding the seasonal decline in male nest defense behavior is derived from parental investment theory. Both male and female Eastern bluebirds engage in extrapair copulations (Gowaty and Plissner 1998).

The consequent asymmetry in the certainty of relatedness between parent and offspring for males and females may underlie differences in investment in parental care (Trivers 1972). This may explain why female nest defense behavior was repeatable, whereas male nest defense behavior was not. Eastern bluebird females have low rates of conspecific brood parasitism (Gowaty and Karlin 1984) and are more likely to be related to young in the nest than their male social mate. Thus, females should invest more in nest success than males to increase fitness. Conversely, males may achieve greater gains in reproductive success by pursuing extrapair copulations rather than through nest defense and parental care.

The third hypothesis involves hormonal control of behavior. Many studies have suggested that consistent individual differences may be influenced by variation in circulating hormone levels (reviewed in Koolhaas et al. 1999; Sih et al. 2004b; Cockrem 2007). Specifically, elevated levels of testosterone have been associated with increased aggressive behavior (reviewed in Wingfield et al. 1987). Other behaviors, such as foraging and movement, were also increased in dark-eyed juncos (*Junco hyemalis*) with experimentally elevated levels of testosterone (Lynn et al. 2000). However, testosterone level was negatively associated with speed of exploration in great tits (van Oers et al. 2011), but not house sparrows (Mutzel et al. 2011). Furthermore, avian testosterone levels vary due to season and reproductive stage, with males exhibiting peak testosterone levels during territory establishment followed by declines with subsequent peaks for the second brood in some species (Wingfield 1984; Wingfield et al. 1987). It is possible that seasonal changes in male hormone levels may explain the seasonal decline in behavior, but if this were the only source of variation we would expect to have seen the same pattern in 2010. Without experimental manipulation, we can only speculate on the factors that caused the seasonal decline in male nest defense behavior in 2009, which may have decreased the repeatability of male aggression between years.

## Conclusions and future research

We conclude that Eastern bluebird nest defense behavior is evidence for personality as individuals exhibited repeatable behavior. Males appear to be more plastic in terms of nest defense behavior compared to females. Future research needs to further investigate the cause for static female behavior and the variation in male response by utilizing supplemental feeding studies and quantifying food availability. Simulated territorial intrusions also need to be conducted throughout the nesting stage to further identify the level of consistency of nest defense behavior within the season. Furthermore, research identifying other correlated behaviors that may be linked to consistent nest defense behavior, such

as exploratory behavior or territory acquisition, will provide insight into selective forces acting on aggressive behavior in populations.

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