Associations of anthropogenic activity and disturbance with fitness metrics of eastern bluebirds (*Sialia sialis*)

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ABSTRACT

To predict the long-term consequences of increasing human activity and environmental disturbance on natural populations, it is imperative to understand how human activity relates to fitness variation in wild populations. Here, we report associations of avian fitness metrics with multivariate indices of human activity and bird behavioral responses in eastern bluebirds (*Sialia sialis*). We quantified patterns of human activity, adult bird behavioral time budgets, and four avian fitness metrics (brood growth, brood condition, brood survivorship and nest box productivity) at 52 nest boxes placed along a human disturbance gradient. We found that distance of human activity relates nonlinearly to chick survival and productivity. Nests were more productive at intermediate levels of human activity. The number of box-visits completed by parent bluebirds was positively related to box productivity. We also found a significant negative relationship of intense and variable human activity with adult bird self-maintenance behaviors. These results suggest that adult bluebirds generally buffer their developing broods from human activity in the environment, sacrificing self-maintenance behaviors before compromising the growth and survival of their brood. If adult birds are absorbing the costs of anthropogenic disturbance in lieu of their young, there could be negative sub-lethal consequences of increasing human activity for future breeding attempts. The nonlinear relationships we found between human activity and avian fitness indicate that eastern bluebirds are somewhat pre-adapted to intermediate levels of human disturbance. As local populations have gone through a recent population bottleneck and experienced intense selection for breeding in man-made cavities in the past 40–50 years, we speculate that local populations may have adapted rapidly to human altered habitats. Hence, we advocate a more inclusive evolutionary ecology approach to understanding responses of natural populations to human disturbance.

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1. Introduction

Anthropogenic activity comprises a collection of human-created disturbance events that can have long- and short-term impacts on wildlife by inducing changes in behavior, physiology, and reproduction (Burger and Gochfeld, 1991; Dahlgren and Korschgen, 1992; Frid and Dill, 2002; Gill et al., 1996; Knight and Cole, 1995a,b). Increases in anthropogenic activity are generally thought to decrease the persistence of local populations by compromising habitat suitability (Francl and Schnell, 2002; Soderstrom et al., 2001), restraining feeding and breeding opportunities, and increasing regional extinctions of wildlife species (Case et al., 1992; Fernandez-Juricic et al., 2004; Jackson et al., 2001; Sauvajot et al., 1998; Thompson and Jones, 1999).

The acceleration of human impacts on wild populations (Jackson et al., 2001; Steidl and Anthony, 2000; Vitousek,

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1994; Vitousek et al., 1997a; Vitousek et al., 1997b) has led to a recent surge in studies on the disturbance effects of anthropogenic activity, especially on avian populations (Francl and Schnell, 2002; Furness et al., 1993). To date, most of these disturbance studies have investigated one of three questions. First, do varying human activity regimes affect population abundance and/or diversity (Blair, 1996; Clergeau et al., 2001; Magura et al., 2004; Norris et al., 2003; Riffell et al., 1996; Sauvajot et al., 1998; Waltert et al., 2004)? Unfortunately, population measures such as abundance and diversity may only reflect temporary shifts in land use by individuals who have recently dispersed from source habitats (Hanski, 1999; Pulliam, 1988; Terman, 1997), or are merely passing through. For this reason, many studies have attempted to address the limitations of population censuses by asking a second question: Do varying anthropogenic activity regimes affect adult behaviors (Bechet et al., 2004; Fernandez-Juricic et al., 2005; Henry et al., 2004; Pease et al., 2005; Rees et al., 2005; Stolen, 2003)? This research has explored the impacts of direct human disturbance on both the short- (Bautista et al., 2004; Finney et al., 2005; Gill et al., 1996; Swarthout and Steidl, 2003) and long-term (Blumstein, 2006; Fernandez-Juricic et al., 2001b; Fernandez-Juricic et al., 2004; Ikuta and Blumstein, 2003; Lafferty, 2001; Rees et al., 2005; Stolen, 2003) behavioral ecology of wildlife.

Increasingly, behavioral research has attempted to link adult activities to reproductive success (Blackmer et al., 2004; Bolduc and Guillemette, 2003; Burger, 1995; Carney and Sydeman, 1999; Finney et al., 2005; Flemming et al., 1988; Johnson et al., 1996; Ruhlen et al., 2003; Verhulst et al., 2001; Yarmoloy et al., 1988) by asking a third question: Does adult behavioral response to anthropogenic activity alter nesting success rates? Not surprisingly, species differ greatly in both their behavioral and reproductive responses to human disturbance, as well as the relationships between these two variables (Beale and Monaghan, 2004b; Finney et al., 2005; Giese, 1996). Additionally, many studies utilize a binary metric, where success is measured as producing any young or none at all (Beale and Monaghan, 2005; Blackmer et al., 2004; Bolduc and Guillemette, 2003; Finney et al., 2005; Giese, 1996). This limited method may cause researchers to miss important fitness variation between highly disturbed and less disturbed populations.

Here, we related metrics of adult and brood fitness and breeding adult behavior to variation in local human activity regimes in populations of eastern bluebirds (*Sialia sialis*) inhabiting an anthropogenic disturbance gradient in southeastern Virginia, during the 2004 and 2005 breeding seasons. We quantified three metrics of brood fitness: growth rate (wing chord length for a given age), body condition (body mass for a given wing chord), and survivorship of chicks in the nest (the proportion of eggs that hatched and survived to fledge from the nest). We measured one important metric of adult fitness: the number of chicks fledged from each brood. We also constructed detailed time budgets of adult behavior. In concert with assessing fitness metrics and behavior, we conducted extensive observations of local human activity regimes (including all variations of pedestrian and vehicular traffic) to generate multivariate metrics of spatial and temporal aspects of direct human disturbance.

We approached this research with three hypotheses: (1) closer, more frequent, and less predictable human activity would generate greater behavioral responses from adult birds (Beale and Monaghan, 2004b; Burger, 1995; Burger and Gochfeld, 1991; Fernandez-Juricic et al., 2001a,b; Lafferty, 2001; Stolen, 2003); (2) birds experiencing these direct human disturbance characteristics would increase vigilance and nest-defense activities at the cost of brood care behaviors; and (3) as a result of reduced parental care, broods in more disturbed environments (i.e. those with greater human activity) would suffer a decrease in growth rate, body condition, and fledging success rate.

Our study extends human activity and direct disturbance research by asking whether there are measurable sub-lethal effects of disturbance that may affect future survival and fitness. Additionally, we provide one of the first examinations of how both spatial and temporal variability (i.e. indices of predictability) of human activity are associated with behavior and fitness metrics. Importantly, our research also explores whether eastern bluebird populations are currently experiencing selection pressures on behavioral strategies as a result of anthropogenic disturbance. This evolutionary ecological approach is long overdue in the human disturbance literature (Ashley et al., 2003; Beale and Monaghan., 2004a; Ruth et al., 2003) and represents a first step toward helping us understand whether bird populations can adapt to human activity while simultaneously indicating longer-term consequences of direct anthropogenic disturbance for wild bird populations.

2. Methods

2.1. Species and study area

We performed this study on field populations of eastern bluebirds during the entire 2004 breeding season and the first clutches of the 2005 breeding season (due to personnel constraints). We studied the birds in association with a large network of wooden nest boxes that were located across 18 sites that were 11.87 ± 6.95 (SD) km from a point in York County, Virginia (37°17′24″ latitude, 76°42′25″ longitude). All boxes were a similar design of wooden nest box mounted on a 1.5 m metal pole with a predator guard (70 cm cylindrical baffles fixed to the mounting pole).

Eastern bluebirds are a common secondary cavity nesting passerine in the eastern portion of the United States. Their bright coloring and sexual dichromatism make them easy to locate and sex during field observations. There is also a recorded history of bluebird conservation status across the country. Destruction of their habitat (open, grassy, semi-wooded locations) nearly led to their demise in many regions of the United States by the middle of the 20th century (Gowaty and Plissner, 1998). The establishment of bluebird trails (aggregations of nest boxes) across the country has restored eastern bluebird population numbers and introduced the species to many human-modified breeding locations, such as golf courses, cemeteries, and recreational parks (Belser, 1981; Gowaty and Plissner, 1998; Pinkowski, 1977, 1979).

Presumably as a result of their dependency on these nest box trails, eastern bluebirds will attempt to breed in boxes as long as they have access to suitable feeding habitat

(semi-wooded and short grass fields). Hence, by locating nest boxes along the wooded edges of grass fields in sites of varying human activity, we could sample breeding eastern bluebirds across an anthropogenic disturbance gradient. Both the amount and type of human activity (including traffic from pedestrians, domestic animals, bicycles, vehicles, golf carts, motorized equipment, and other human-propelled objects) varied within and among sites. Sites included recreational lands, golf courses, our university campus, cemeteries, and protected research lands. Some boxes were located where they would receive hourly disturbance from pedestrians and vehicular traffic (e.g., golf courses, recreational facilities, campuses) and others were placed at sites that have been unaltered for over 100 years and very rarely receive direct disturbance from humans (national parks, protected research land). Most boxes had been in place for over two years before the study, when they were originally erected by members of our lab. In addition, previous analyses indicate that box age has little effect on box productivity, breeding demographics, or our brood growth and condition indices (LeClerc et al., 2005). As we purposely placed boxes along a gradient of anthropogenic activity, we describe our approach as semi-experimental. Another advantage of using artificial boxes is that our boxes are constructed with predator guards to reduce nest predation. This helped us isolate effects of anthropogenic activity on metrics of adult and brood fitness, but may also over-estimate total fledging success.

2.2. Breeding demographics, morphometrics, and banding

For the demographic, morphometric, and banding part of the study we gathered data from 373 nest boxes in 2004 and 367 in 2005. We visited each of these nest boxes weekly throughout the nest building phase of the breeding season to determine nesting status. Once eggs were laid, we visited the box every 3–4 days in order to determine hatch date and clutch size. To estimate clutch initiation date we subtracted 14 days of incubation from the hatch date and subtracted one additional day for each egg laid (Gowaty and Plissner, 1998). On many occasions we visited nests during the 4–5 days of (daily) egg laying. Overall we could accurately estimate clutch initiation date to a one day time window.

Once chicks hatched, we continued visiting the nest approximately every 3–4 days to weigh and measure each chick and estimate chick age to one day precision according to general growth morphology and appearance, including skin color and feather emergence (LeClerc et al., 2005). These visits also let us assess how many chicks fledged from each nest. We recorded body mass and wing chord of each chick at least two times (mode = 3) during the first 15 days of the 18 day nestling period. We measured body mass with an electronic balance to 0.1 g precision. We measured unflattened wing chord (from the distal end of the radius to the distal end of either the phalange or the longest primary feather, whichever represented the longest distance) with dial calipers to 0.1 mm precision. We accounted for chick age in all measures of growth through residual analyses (see below). Once chicks were at least 10 days old, we banded them with United States Fish and Wildlife Service bands and unique combinations of three plastic colored leg bands to aid future identification.

2.3. Nest box observations: adult time budgets

We performed behavioral observations of adult birds at 52 focal nests (35 in 2004 and 17 in 2005) twice during the nestling period. These boxes were a subset of those studied for demographics and morphology. To reduce the potentially confounding effects of time of day and day of week on human activity and behavior metrics, we distributed observations as evenly as possible (considering unexpected weather and access permission) between morning and afternoon times as well as weekend and weekday times.

To reduce effects of chick age, each box was observed once in the first week and once in the second week of nestling growth. We conducted observations between 07:00 and 18:00 in 90 min sessions. CRK conducted all initial observations and subsequently trained two field assistants in observation technique so that all data were collected in the same manner. In locations that were extremely busy, observers worked in pairs to ensure accuracy.

Pilot tests using flush distance as a metric of human activity indicated that adult eastern bluebirds were not noticeably disturbed by a researcher until the observer approached to within 25 m of the nest box (N = 14 approaches to non-focal boxes, mean flush distance = 10.5 m, SD = 10.9). Therefore, observers performed all observations from a distance of at least 30–50 m from the nest.

Once the observers had situated themselves (sitting with binoculars) 30–50 m from the box, the stopwatch was not started until the parents began to engage in "new" behaviors (different from the activities they were engaging in when the observer arrived). We included this procedure to increase the probability that parents were engaging in natural behaviors not directly affected by the observer. We used binoculars to determine behavioral activity of both parents at 2 min intervals throughout the 90 min observation period (i.e., 46 total observations for each parent (Dickinson and Weathers, 1999)). We recorded behaviors conducted within 50 m of the nest box, as many of our boxes are approximately 100 m apart, and previous reports (Gowaty and Plissner, 1998) indicate that most feeding and territorial behavior occurs within 50 m of the nest.

Specifically, every 2 min we noted parental bird behavior according to the following categories: locomoting (flying or hopping unrelated to another activity, such as hunting), perching (sitting upright on a perch when that activity was not related to hunting or singing), preening (adjusting their plumage with their bills or feet), being at the nest (either being inside the box or temporarily perching on the box with food items in their bill before entering the box to feed young), defending (pursuing, fighting with, or displaying at an intruder or potential predator), hunting (perched in an attentive, watchful posture or actively pursuing/manipulating prey), and vocalizing (calling or singing). In the event that two behaviors occurred simultaneously, such as vocalizing while sitting, we recorded the more energetically active of the two (in this case, vocalizing). We generated these behavioral categories from published time budgets of eastern bluebirds (Belser, 1981) and other bird species studied within a direct human disturbance/activity context (Steidl and Anthony, 2000; Swarthout and Steidl, 2003).

2.4. Nest box observations: human activity regimes

During each 90-min behavioral observation we simultaneously collected local human activity data for each of our focal 52 nest box territories. Specifically, we continuously recorded all human activity that occurred within a 50 m radius of the nest box according to the following metrics: time of event (with respect to the 90 min observation period), duration of disturbance (to 1 s precision using a stopwatch), and distance from the nest box (to 1 m precision, estimated during the observations and paced out afterwards for verification). We classified each human activity event into specific categories according to their source of disturbance (e.g. foot traffic versus automobile) but we will present those data in a separate series of analyses. The source of human-derived disturbance has a surprisingly small influence on fitness responses of eastern bluebirds (C.R. Kight and J.P. Swaddle, manuscript in preparation). In the current study, we pooled all human activity data independent of its source.

From the pooled human activity data we calculated metrics of mean duration (seconds), variance in duration (seconds), mean distance from the box (meters), variance in distance from the box (meters), minimum distance from the box (meters), and total amount of time a box was disturbed during the 90 min observation (seconds). We also calculated the number of different sources of human activity recorded during each observation period (i.e. the richness of disturbance sources).

2.5. Statistical analyses

We generated indices of chick growth and body condition by storing residuals of regressions of wing chord on age and body mass on wing chord, respectively, using cubic regressions. Hence, our metric of brood growth was an age-standardized measurement of wing chord, and our metric of brood condition was a size-standardized measure of body mass. This process accounted for among-brood variation in age of chicks when measurements were taken.

We applied separate principle components analyses (PCA) to both the adult bird behavioral time budget and human activity datasets to generate multivariate metrics (principle components, PC's) of bird behavior and human activity separately. We used Pearson product moment correlations to investigate the relationships between bird behavioral PC's, human activity PC's, and avian fitness metrics. We used quadratic curve estimation regressions to investigate the presence of nonlinear relationships between these same variables. We performed all statistical analyses using SPSS v13 (Chicago, Illinois) employing two-tailed tests of probability. As appropriate, original variables were natural log transformed to meet the assumptions of normality for parametric tests.

3. Results

3.1. Brood performance metrics: growth, condition, survivorship, and nest productivity

We employed cubic regressions of wing chord on age across all data samples from all chicks on every day they were measured in both 2004 ($F_{3,1880} = 8497$, $P < 0.00001$, $r^2 = 0.931$; wing chord $= -0.0265 \times age^3 + 0.7278 \times age^2 - 1.1832 \times age + 8.4524$) and 2005 ($F_{3,926} = 3973$, $P < 0.00001$, $r^2 = 0.923$; wing chord $= -0.0237 \times age^3 + 0.6899 \times age^2 - 1.6146 \times age + 9.078$). We then averaged residual values of wing chord standardized for age from these two regressions across chicks within a brood to generate a single brood growth rate metric for each nest in 2004 and 2005 separately. Hence, we use the term brood growth to refer to the average wing chord of chicks within a brood standardized for their age.

We performed similar cubic regressions of chick body mass on wing chord to generate residuals of chick mass given their size (i.e., an index of body condition), in both 2004 ($F_{3,1876} = 6545$, $P < 0.00001$, $r^2 = 0.913$; body mass $= 0.001 \times$ wing chord$^3 - 0.0247 \times$ wing chord$^2 - 1.515 \times$ wing chord $- 4.01$) and 2005 ($F_{3,926} = 5997$, $P < 0.00001$, $r^2 = 0.951$; body mass $= 0.0001 \times$ wing chord$^3 - 0.0204 \times$ wing chord$^2 + 1.397 \times$ wing chord $- 3.732$). Again, we averaged these condition residuals across chicks within a brood to render a single measure of brood condition for each nest. Hence, we use the term brood condition to refer to average body mass of chicks in a brood standardized for the wing chord.

We performed two separate multiple regression analyses using either the growth index or the condition index as the dependent variable and number of researcher visits (a measure of experimenter disturbance), clutch initiation date (in days through each season), brood size, and number of boxes at the site (as an estimate of site area, which can affect individual and population productivity (Hanski, 1999)), as the predictor variables. We used the residuals from both these regressions in subsequent analyses so that we took into account the (non-significant) effects that researcher disturbance, clutch initiation date, brood size, and breeding site size had on our measures of brood growth rate ($F_{4,46} = 1.148$, $P = 0.346$, $r^2 = 0.091$) and brood condition ($F_{4,46} = 1.335$, $P = 0.271$, $r^2 = 0.104$).

As we inspected every nest approximately every 3–4 days, we did not miss any broods or misestimate clutch size, brood size, or number of fledglings produced. Hence we used raw numbers of fledglings and eggs in our calculations of brood survivorship (fledglings produced per egg laid) and box productivity (total number of fledglings produced per box).

To generate our final measures of brood survivorship and box productivity, we performed two separate multiple regression analyses with survivorship and productivity as dependent variables and number of researcher visits, clutch initiation date, and the number of boxes at the breeding site as independent variables (brood survivorship: $F_{3,47} = 1.340$, $P = 0.273$, $r^2 = 0.079$; and productivity: $F_{3,47} = 0.790$, $P = 0.506$, $r^2 = 0.048$). As before, we stored residuals from these regressions for use in further analyses.

3.2. Relationships between human activity and avian fitness metrics

We performed a PCA of the original human activity variables, which generated two significant components (intense-variable disturbance and distant disturbance) that explained 74.3% of the original variance in this dataset (Table 1). Disturbance PC1 (intense-variable disturbance) loaded positively for all values except minimum and average proximity of the human activity.

Table 1 – Summary of loading factors for the two significant PCs generated from the human activity data PCA

Human activity variable	Component (% of total variance)	
	PC1 (61.1%)	PC2 (13.2%)
Total time disturbed	0.938	0.196
Richness of disturbance	0.851	0.146
Variance in duration	0.838	0.232
Average duration	0.816	0.012
Total number of events	0.736	0.310
Variance in distance	0.686	0.170
Minimum distance	−0.669	0.600
Average distance	−0.646	0.677

In other words, disturbance PC1 increased as the intensity and variability (in temporal, spatial, and richness dimensions; see Table 1) increased. Disturbance PC2 (*distant disturbance*) loaded positively with both minimum and average proximity of human activity. In other words, disturbance PC2 increased as human activity was generally farther away from the nest box. It is noteworthy that temporal and spatial variance were important components of the among-box variation in disturbance.

We correlated each of the human disturbance PC's against our metrics of avian fitness. We also explored nonlinear relationships of disturbance PC's with avian fitness metrics by quadratic regressions. Disturbance PC2 (*distant disturbance*) was nonlinearly related to both brood survivorship ($F_{2,47} = 7.712$, $P = 0.001$, $r^2 = 0.247$; Fig. 1) and box productivity ($F_{2,47} = 7.254$, $P = 0.002$, $r^2 = 0.236$; Fig. 2), where intermediate-
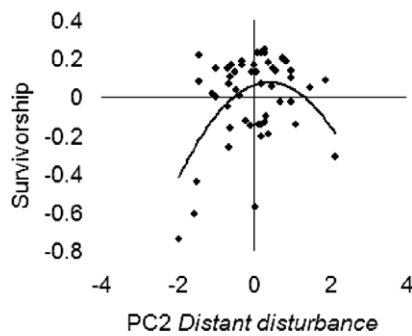

Fig. 1 – Nonlinear relationship between human disturbance PC2 *distant disturbance* and brood survivorship.
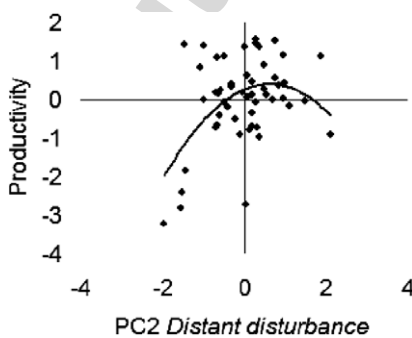

Fig. 2 – Nonlinear relationship between human disturbance PC2 *distant disturbance* and box productivity.

distance human activity was associated with greatest survivorship and productivity. No other (linear or nonlinear) comparisons of disturbance PC's with avian fitness metrics were significant ($0.009 < r_{51} < 0.147$, $P > 0.303$, in all cases).

3.3. Relationships between adult bird behavior and avian fitness metrics

Similar to our analyses of human activity data, we reduced dimensionality in our bird behavioral dataset through PCA. PCA of original adult bird behavior metrics yielded four significant components which explained 61.2% of the total variance in bird behavioral data (Table 2). Specifically, adult behavior PC1 (*self-maintenance-perching*) predominantly loaded positively with perching and preening, but negatively with time spent out of territory/sight. Adult behavior PC1 appears to reflect time the bluebirds spent resting and preening, while perching conspicuously within the territory. Adult behavior PC2 (*box-visits*) loads positively for visits to the nest (both total number of visits and fraction of time budget spent visiting), which usually happened during chick incubation and feeding. Adult behavior PC3 (*quiet*) loaded negatively for vocalizations, which indicated that adults were reducing their songs/calls in some situations. Adult behavior PC4 (*incubating–defending*) loaded positively for length of visits to the nest box and defensive behaviors. Most brood feeding visits were relatively short, so we interpreted these longer visits as incubation behavior during early growth or inclement conditions. A one-way analysis of variance using time of day as the independent variable and each of the bird behavior PCs as dependent variables indicates that adult behaviors remained consistent throughout the day and were not an artifact of when behavior observations were conducted ($0.001 < F_{1,98} < 2.217$, all $P > 0.140$).

Correlations of adult behavior PCs and avian fitness yielded two significant patterns. Both brood survivorship ($r_{51} = 0.364$, $P = 0.009$; Fig. 3) and box productivity ($r_{51} = 0.357$, $P = 0.010$; Fig. 4) were positively related to adult behavior PC2 (*box-visits*). There was also a non-significant negative trend between brood condition and behavior PC1 (*self-mainte-nance-perching*) ($r_{51} = −0.329$, $P = 0.091$; Fig. 5). While it is not surprising to find that increased rate of box-visits is

Table 2 – Summary of loading factors for the four significant PCs generated from the adult bluebird behavior PCA

| Behavioral variable	Component (% of total variance)			
	PC1 (21.6%)	PC2 (16.1%)	PC3 (12.8%)	PC4 (11.1%)
Out of territory/sight	−0.869	−0.241	0.069	−0.247
Perching	0.798	−0.013	0.292	0.104
Preening	0.627	−0.199	0.008	−0.347
Hunting	0.449	0.245	0.230	−0.218
Vocalizing	0.375	−0.035	−0.742	0.031
In the box (proportion)	−0.114	0.820	−0.174	0.383
Defending	0.101	−0.233	−0.233	0.600
Total # visits to box	−0.087	0.809	0.028	−0.166
Locomoting	0.052	0.221	0.426	−0.107
Average length box visit	−0.033	−0.156	0.564	0.565
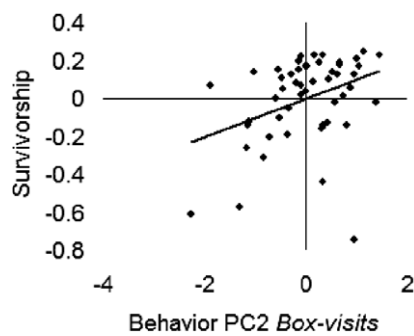
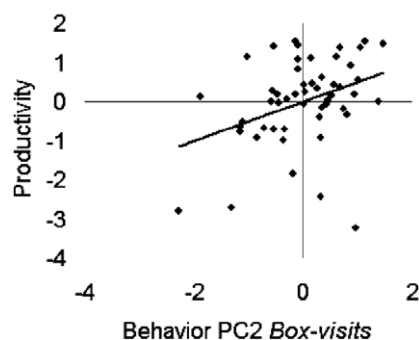Fig. 3 – Positive linear relationship between bird behavior PC2 *box-visits* and brood survivorship.

Fig. 4 – Positive linear relationship between bird behavior PC2 *box-visits* and box productivity.
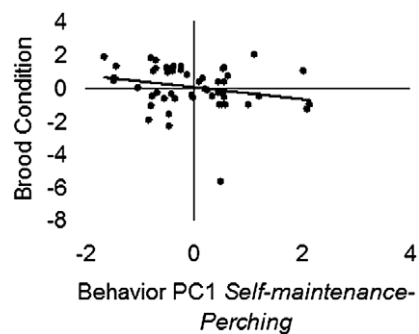

Fig. 5 – Non-significant linear trend between bird behavior PC1 *self-maintenance-perching* and brood condition.

associated with increased chances of fledging young, it is interesting that adult bluebirds may experience a weak trade-off between time spent caring for themselves and the condition of their brood.

3.4. Relationships between human activity and adult bird behavior

We explored relationships between adult bird behavioral and human activity PC's through correlation analyses. Adult bird behavior PC1 (*self-maintenance-perching*) was negatively related to human disturbance PC1 (*intense-variable disturbance*) ($r_{52} = -0.395$, $P = 0.004$; Fig. 6). This relationship suggests that adult bluebirds reduce self-maintenance behaviors when dis-
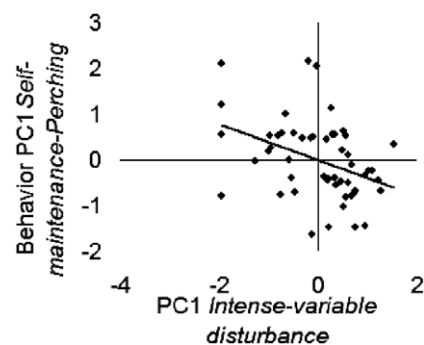

Fig. 6 – Negative relationship between bird behavior PC1 *self-maintenance-perching* and human disturbance PC1 *intense-variable disturbance*.

turbance by human activity becomes both intense and unpredictable. No other correlations between human activity and bird behavior PC's were significant ($-0.165 < r_{52} < 0.163$, all $P > 0.239$).

4. Discussion

We studied how a gradient of human activity was associated with variation in adult bluebird behavior and metrics of avian fitness. Overall, our results suggest that adult eastern bluebirds buffer their developing chicks from the effects of anthropogenic activity. Specifically, we were able to accept our first hypothesis, that closer, more frequent, and less predictable disturbance elicited changes in adult bird behavior. However, the change in behavior was not what we predicted in our second hypothesis. Rather than increasing vigilance and nest-defense behaviors, adult eastern bluebirds reduced self-maintenance activities in the face of increasing human activity (Fig. 6). This pattern of behavioral response has been documented previously in highly sensitive predatory birds such as Mexican spotted owls (*Strix occidentalis*) (Swarthout and Steidl, 2003) and bald eagles (*Haliaeetus leucocephalus*) (Steidl and Anthony, 2000) but not, to our knowledge, in any passerine species.

A reduction in self-maintenance activities of adult birds is also (although somewhat weakly) associated with an increase in the size-standardized mass of their broods (i.e. our measure of brood condition). Hence, adult birds appear to favor sacrifice of their own self-maintenance rather than subjecting their growing brood to any detrimental effects of increased human activity in the environment. Our data suggest that adult eastern bluebirds can largely buffer their chicks from human activity.

Correspondingly, we also reject our third hypothesis, as broods in environments of greatest human activity and disturbance did not suffer noticeably in terms of their growth, body condition, or survival. Somewhat surprisingly, we observed that both brood survivorship and box productivity were maximized at intermediate levels of human activity (Figs. 1 and 2) (Fernandez-Juricic et al., 2003).

We speculate that the behavioral consequence (i.e. reduced self-maintenance) of more intense and variable human activity could create longer-term fitness consequences

for adult bluebirds. For instance, they may not be able to maintain fully functional plumage (Williams and Swaddle, 2003; Zampiga et al., 2004), and/or their relative lack of attention to self-maintenance could lead to greater risk of starvation or reduced breeding performance and survival (e.g. Hunt et al., 2004; King and Workman, 1986). If we extrapolate these behavioral changes to the end of the breeding season when many bluebirds experience molt-breeding overlap (C.R. Kight and J.P. Swaddle, unpublished data), adults occupying increasingly disturbed areas may have less energy to devote to producing high-quality plumage, which in turn could have implications for future mate choice and male–male competitive ability (Siefferman and Hill, 2003, 2005a,b). We are currently investigating these possibilities in our populations.

We were somewhat surprised that few of our bird behavioral PCs related to our avian fitness metrics. Of the behaviors that did relate, the patterns are intuitive. As parents visited the nest box more, the probability of chick survivorship increased, resulting in more chicks fledging from those nests (Figs. 3 and 4). Hence, along our disturbance gradient, there is a positive selection pressure for increased box visits by parents.

Our multivariate indices of human activity had some unexpected relationships with metrics of avian fitness. In general, brood growth and condition were not related to human activity in the environment, perhaps further suggesting the buffering capacity of adult bluebirds. However, there was an interesting nonlinear, ∩-shaped relationship between distant disturbance and brood survivorship and box productivity. This pattern suggests that eastern bluebirds are pre-adapted to intermediate levels of direct human disturbance/activity. Given the fairly recent population decline and recovery that eastern bluebirds have experienced in our area (Gowaty and Plissner, 1998), the nonlinear relationship of fitness with human activity suggests that these birds may have undergone recent evolutionary change to adapt to human-altered environments. As many life history and complex behavioral traits express significant additive genetic variance (MacColl and Hatchwell, 2003; Stirling et al., 2002), it is not unreasonable to speculate that bluebirds could have adapted to such environments in 40–50 years as the selection pressure to breed in man-made nest boxes was (and still is) fairly intense in most of the eastern US. Further, with such a relatively recent shift in nesting ecology and current expansion of nest box trails (Gowaty and Plissner, 1998; Zimmerman, 2007), we may even expect eastern bluebirds to still be responding, evolutionarily, to increased human activity around their nesting sites. Typical natural eastern bluebird habitat consists of previously excavated cavities in large, dead pine trees in low density tree stands and forest edges (Gowaty and Plissner, 1998), but most nest trails in our area are placed in areas closer to human development and in more open fields (C.R. Kight and J.P. Swaddle, unpublished data). In further field seasons we will be looking for longitudinal signs of behavioral adaptation to human activity and increasing fitness of bluebirds in the more disturbed areas.

If, as our current data imply, eastern bluebirds have adapted to anthropogenic disturbance over this relatively short time span, it is likely that other passerines can show similar evolutionary responses (e.g. Bearhop et al., 2005). This intriguing possibility highlights the importance of evolutionary ecology to conservation efforts (Marzluff et al., 2001; Marzluff and Ewing, 2001). Alternatively, the apparent selection pressure we observed may be a result of attracting an unrepresentative sample of adult bluebirds to our artificial cavities. Specifically, we may have studied adults that were more inclined than the rest of the population to utilize and successfully breed in artificial cavities. However, mark-and-recapture/resighting studies (C.R. Kight and J.P. Swaddle, unpublished data) lead us to believe that the majority of each local population is nesting in our boxes, so we do not feel this is the case. We rarely observe non-banded birds in our sites during the breeding season.

Based on our analyses, we suggest that managers of local eastern bluebird trails strategically place boxes in areas with moderate levels of predictable traffic that does not come within approximately 10 m of the box. In our study, this type of disturbance regime was associated with increased brood survivorship. Placing boxes in areas that have defined pathways and fences may be better than erecting boxes in locations adjacent to open recreational fields where people can be unpredictable distances from the nest box (Ikuta and Blumstein, 2003).

In general, we advocate that researchers take a longer-term, evolutionary view of behavioral responses to anthropogenic disturbance. At the very least, we encourage efforts to track individuals over more than one breeding attempt, as subtle, but important, fitness effects can be overlooked if we always restrict our studies to a single breeding season. Additionally, we suggest that future disturbance studies explicitly examine indices of the spatial and temporal predictability of disturbance. In our review of the literature, we could not find any previous research that explicitly investigated these characteristics, yet these measures described human activity in our sites just as well as more traditional quantifications, such as proximity and duration. Predictability may well have the greatest impact on the fitness and viability of populations, the "critical factor" in conservation work (Beale and Monaghan., 2004a; Gill et al., 1996; Goss-Custard et al., 2006; Lafferty, 2001). Thus, incorporating analyses of these variables could have practical management applications in deciding on traffic control measures and/or local land development issues.

Intriguingly, our preliminary data indicate that eastern bluebirds are somewhat pre-adapted for disturbed habitats of intermediate human activity. It will be revealing to investigate whether other species that occupy nest boxes along the same human activity gradient (e.g., house wrens (Troglodytes aedon), Carolina wrens (Thyrothorus ludovicianus), and Carolina chickadees (Poecile carolinensis)) exhibit similar patterns in fitness and behavior. If this is the case, we can start to build the case for significant evolutionary responses in avian populations over a fairly brief period of time.

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