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EFFECTS OF HUMAN DISTURBANCE ON THE BREEDING SUCCESS OF  
EASTERN BLUEBIRDS (*SIALIA SIALIS*)

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A Thesis

Presented to

The Faculty of the Department of Biology  
The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Science

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by

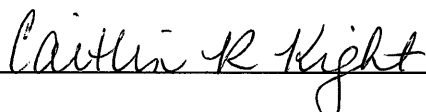
Caitlin Rebecca Kight

2005

APPROVAL SHEET

This thesis is submitted in partial fulfillment of  
the requirements for the degree of

Master of Science



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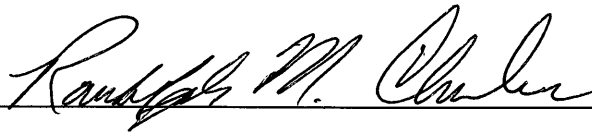
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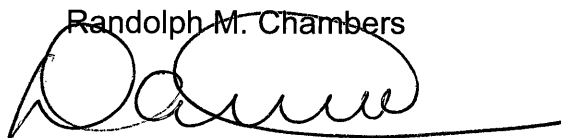
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## TABLE OF CONTENTS

	Page
Acknowledgements	v
List of Tables	vi
List of Figures	vii
Abstract	ix
Chapter 1: Introduction 1—Interactions Between Human Disturbance and Wildlife	2
Chapter 2: Methods	12
2.1 Study Area	12
2.2 Breeding Demography, Morphometrics, and Banding	13
2.3 Nest Box Observations: Time Budgets of Breeding Eastern Bluebirds	14
2.4 Nest Box Observations: Disturbance Regime	16
2.5 Subjective Disturbance Scores	18
2.6 Statistical Analyses	18
Chapter 3: Results of All-Sites Analysis	20
3.1 Fitness Metrics	20
3.2 Generating Disturbance PCs	22
3.2.1 Disturbance Source PCs	22
3.2.2 Disturbance Characteristic PCs	25
3.2.3 Within-Box and Temporal Repeatability of Disturbance	25
3.2.4 Anemometer Data	28
3.3 Generating Behavior PCs	30
3.4 Disturbance and Fitness	33
3.4.1 Correlations of Fitness Metrics and Disturbance Source PCs	33
3.4.2 Correlations of Fitness Metrics and Disturbance Characteristic PCs	33
3.5 Disturbance and Behavior	37
3.5.1 Correlations of Adult Behavior PCs and Disturbance Source PCs	37
3.5.2 Correlations of Adult Behavior PCs and Disturbance Characteristic PCs	40

3.6 Behavior and Fitness: Correlations of Fitness Metrics and Behavior PCs	44
3.7 Correlations of Fitness Metrics and Subjective Disturbance Scores	49
Chapter 4: Introduction II—Comparing Golf Courses and Non-Golf Courses	55
Chapter 5: Results of Comparison of Golf Courses and Non-Golf Courses	61
5.1 Differences in Fitness Metrics and PCs	61
5.2 Differences in Relationships Between Disturbance PCs and Fitness Metrics	61
5.3 Differences in Relationships Between Disturbance and Behavior PCs	61
5.4 Differences in Relationships Between Behavior PCs and Fitness Metrics	66
Chapter 6: Discussion	78
6.1 What are the effects of disturbance on chick fitness metrics?	78
6.2 What are the effects of disturbance on adult time budgets?	79
6.3 Evolutionary Implications	82
6.4 Conservation and Management Implications	85
Appendix I: Table of Loading Factors for Disturbance Source PCA	87
Works Cited	89
Vita	95

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## LIST OF TABLES

Table	Page
3.1 Summary of results for multiple regressions on chick fitness metrics	21
3.2 Disturbance Source PCA extraction values	24
3.3 Disturbance Characteristic PCA extraction values	26
3.4 Loading factors for Disturbance Characteristic PCA	27
3.5 Adult behavior PCA extraction values	31
3.6 Loading factors for adult behavior PCA	32
3.7 Correlations of Disturbance Characteristic PCs and subjective scores	50
5.1 Results of multivariate analysis of variance comparing fitness metrics	62
5.2 Results of multivariate analysis of variance comparing Disturbance Characteristic PCs on and off golf course sites	63
5.3 Results of multivariate analysis of variance comparing adult behavior PCs on and off golf course sites	64

## LIST OF FIGURES

Figure	Page
3.1 Correlation between wind speed and decibel level	29
3.2 Correlation between Trail Vehicle PC and brood growth rate	34
3.3 Correlation between Frequent-Short-Predictable PC and number fledged	35
3.4 Correlation between Foot Traffic PC and Reduced Calling PC	36
3.5 Correlation between Foot Traffic PC and Defense and Foraging PC	38
3.6 Nonlinear relationship between Non-GC Road Traffic PC and In the Box PC	39
3.7 Correlation between Variation in Proximity PC and Box Visits PC	41
3.8 Correlation between Variation in Proximity PC and Reduced Calling PC	42
3.9 Correlation between Close PC and Box Visits PC	43
3.10 Correlation between Self-maintenance and Perching PC and number fledged	45
3.11 Correlation between Self-Maintenance and Perching PC and brood survival	46
3.12 Correlation between Defense and Foraging PC and brood condition	47
3.13 Nonlinear relationship between Defense and Foraging PC and number fledged	48
3.14 Nonlinear relationship between subjective disturbance score and brood survival of Eastern bluebirds	51
3.15 Nonlinear relationship between subjective disturbance score and number fledged for Eastern bluebirds	52
3.16 Correlation between subjective disturbance score and brood growth of Carolina chickadees	53



3.17 Correlation between subjective disturbance score and brood condition of Carolina chickadees	54
5.1 Differences in the relationship between Longer/More Variable Length PC and Defense and Foraging PC at golf course and non-golf course sites	65
5.2 Differences in the relationship between Close PC and Reduced Calling PC at golf course and non-golf course sites	67
5.3 Differences in the relationship between Variation in Proximity PC and Reduced Calling PC at golf course and non-golf course sites	68
5.4 Differences in the relationship between Defense and Foraging PC and brood growth at golf course and non-golf course sites	69
5.5 Differences in the relationship between Defense and Foraging PC and number fledged at golf course and non-golf course sites	70
5.6 Differences in the relationship between Defense and Foraging PC and brood condition at golf course and non-golf course sites	72
5.7 Differences in the relationship between In the Box PC and number fledged at golf course and non-golf course sites	73
5.8 Differences in the relationship between In the Box PC and brood survival at golf course and non-golf course sites	74
5.9 Difference in the relationship between Self-maintenance and Perching PC and number fledged at golf course and non-golf course sites	75
5.10 Differences in the relationship between Self-Maintenance and Perching PC and brood survival at golf course and non-golf course sites	77

## ABSTRACT

Human disturbance is defined as an anthropogenic event having long- or short-term effects on wildlife, both directly and indirectly, externally and internally. Disturbance has been shown to influence avian abundance and diversity, behavioral patterns, and breeding success. Previous studies have illustrated that birds may alter behaviors in response to disturbance yet display no reduction in breeding success, and vice versa. These results suggest that there may be sublethal effects of breeding in disturbed environments which can only be uncovered through longer-term research that incorporates measurements of chick health and adult responses to human disturbance over time. To date, there have been few, if any, comprehensive descriptive studies integrating quantifications of disturbance and behavior with measurements of fitness. Here, we have examined Eastern bluebirds (*Sialia sialis*) breeding in nest boxes across a disturbance gradient. We have quantified disturbance regime and parental time budgets at 52 boxes and have taken measurements of both chick and adult fitness. Behavior and fitness were significantly related to particular aspects of disturbance regimes, notably close, variable events. There also appears to be a trade-off in parental self-maintenance behaviors and fitness and survivorship of their young. These results have both evolutionary and management implications. Breeding in disturbed areas may have cumulative effects that are detectable only over the long-term, indicating that the prevalent one-season approach to breeding studies may be inadequate at detecting important effects of disturbance. Continuing to inhabit and reproduce in disturbed areas may select for the evolution of behaviors that allow or even predispose wildlife to return to disturbed habitat for future breeding attempts. Over time this could have significant effects on both the life histories and viability of birds and other human-disturbed wildlife.

EFFECTS OF HUMAN DISTURBANCE ON THE BREEDING SUCCESS OF  
EASTERN BLUEBIRDS (*SIALIA SIALIS*)

## CHAPTER 1

### INTRODUCTION: INTERACTIONS BETWEEN HUMAN DISTURBANCE AND WILDLIFE

Human disturbance has been defined as an “event, intentionally or unintentionally created by people,” having long- or short-term effects on wildlife (Dahlgren and Korschgen 1992). Such activities may be either direct (exploitation, presence/proximity) or indirect (habitat modification, pollution) (Knight and Cole 1995) and may effect obvious behavioral changes such as alertness or fright; flight, swimming, or running; death or disablement (Dahlgren and Korschgen 1992). Behavioral changes may also entail more subtle physiological and/or reproductive outcomes due to stress. For instance, an increased heart rate or surge in metabolic activity may drain an animal of energy that would be available for other essential behaviors such as feeding (Burger and Gochfeld 1991). Disturbance may also reduce access to appropriate breeding or feeding habitat (Knight and Cole 1995; Gill and et al. 1996).

In a time when urbanization and recreational use of natural environments are increasing, countless species are coming into greater, and more frequent, contact with human-induced disturbance. Recent studies have shown that some species have been surprisingly successful at maintaining natural population levels in artificially-maintained, human-altered areas such as golf courses and farms (Terman 1997; Soderstrom et al. 2001). For instance, studies of the New Zealand dabchick

(*Poliiocephalus rufopectus*) revealed that not only does human disturbance have no effect on the formation of adult breeding pairs and creation of nests, but that numbers of dabchick young are positively correlated with number of nearby human structures (Bright et al. 2004).

Yet, despite such information, research on the effects of human disturbance on wildlife is only in its early stages (Lepczyk et al. 2004). Most prior research has been devoted to exploring the relationship between disturbance and population success in birds, thanks to their economic importance and the ease with which they can be identified by sight and sound (Francl 2002). The availability of annual population counts such as the Christmas Bird Count and Backyard Bird Survey also make possible long-term comparisons of bird population numbers (Francl and Schnell 2002). Bird disturbance research tends to fall into one of three categories: (1) microhabitat effects on abundance/diversity, (2) behavioral studies, and (3) nesting success studies.

#### 1. Abundance/Diversity and Avian Microhabitat

In terms of conservation, the most important cost to measure is breeding success (Gill et al. 1996; Lafferty 2001), especially in species of classified as endangered, or at risk of becoming so (Beale and Monaghan 2004). To gauge breeding success, several studies have calculated abundance (number of individuals within a species) and diversity (number of different species; sometimes also referred to as species richness) (Smith and Smith 2001), especially as seen across a range of disturbance amounts and types. "Urban gradient" is a term used

to describe the “fragmented and patchy nature of urban land use” as driven by human disturbance in the form of structures and land use (Blair 1996). Studies comparing abundances and diversities across disturbance gradients suggest that while avian population numbers may be at natural or even elevated levels in urban areas, the species present are often non-natives or those considered pests (e.g. pigeons (*Columba livia*), house sparrows (*Passer domesticus*), European starlings (*Sturnus vulgaris*)) (Blair 1996). Such species also tend to be “edge” species, or those, such as the brown-headed cowbird (*Moluthrus ater*) that thrive at habitat boundaries. Suburban areas such as golf courses may also maintain their bird communities at unnaturally high densities (Terman 1997), which could lead to an increase in competition for resources and promote the spread of avian illnesses.

The gradient concept has also been applied to succession as a result of logging and farming disturbances. Avian richness and abundance of a forest succession gradient in Iowa were best explained by disturbance regimes, rather than habitat structure or floristics (Norris et al. 2003), and bird-species composition was more highly correlated to human activity than to vegetative structure at Lake Texoma, Oklahoma (Francl and Schnell 2002). However, diversity has been shown to increase as manipulation of farmland decreases, indicating that both human activities *and* their effects on flora are important to bird population numbers (Soderstrom et al. 2001).

Abundance and diversity have also been linked to degree of habitat fragmentation. Human disturbance in habitat fragments may restrain feeding and breeding opportunities, decrease habitat suitability, and increase regional extinctions

of avian species (Fernandez-Juricic 2002). Larger fragments and fragments closer to other suitable habitat appear to promote higher species diversity (Fernandez-Juricic and Jokimaki 2001; Fernandez-Juricic 2004). Landscape-scale approaches to abundance studies have yielded conflicting results. Bird species richness in urban areas was apparently independent of that in adjacent landscapes (Clergeau et al. 2001), whereas farming and grazing practices in the prairie pothole landscape of the U.S. have altered bird community composition in individual pothole communities (May et al. 2002).

## 2. Behavioral Studies

Abundance and diversity studies center on the potentially unreliable technique of counting breeding pairs and/or chicks in areas experiencing different disturbance regimes. Traditionally, a population source is defined as an area which produces an excess of offspring that are available to breed elsewhere, while a sink is an area where local mortality is not offset by local reproductive success (Pulliam 1988). At any given time, local population numbers may temporarily fluctuate due to a number of non-disturbance-related characteristics, such as weather or food availability. Thus, higher disturbed areas that may act as sinks may seem to contain larger abundances and diversities than less disturbed regions that may act as sources. These distance sampling techniques may therefore fail to address the quality of a local habitat and overall health of its population. For these reasons, researchers have shifted their focus towards understanding the impacts of human

disturbance on the behavioral ecology of wildlife and extrapolating these results to the breeding season.

Long-term changes in behavior have been documented with approach tolerance studies, which measure one of the following: flight initiation distance, “the distance birds would allow a human to approach before fleeing” (Ikuta and Blumstein 2003); alert distance, the distance at which an animal begins to exhibit alert behaviors to a human disturbance (Fernandez-Juricic et al. 2001); and flush distance, “the distance at which a species escapes from a visitor” (Fernandez-Juricic et al. 2001). Tolerance distances have been measured in a variety of species, including wading birds (Stolen 2003), gulls (Lafferty 2001), forest-dwelling (“rural”) birds (Fernández-Juricic et al. 2004), and waterfowl (Gill et al. 1996; Rees et al. 2005).

Many researchers have been interested in using tolerance distance studies to demonstrate avian habituation to human disturbance, especially as dose increases (Anderson 1988; Yarmoloy et al. 1988; Ikuta and Blumstein 2003), or as the disturbance gradient ranges from rural to urban (Cooke 1980). However, several other factors may affect the degree to which species respond to disturbance. These include, but are not limited to, body size of the disturbed individual, proximity and abundance of vegetative escape areas (Fernandez-Juricic et al. 2001), and whether a species is resident or migratory (Burger and Gochfeld 1991).

Shorter-term changes in behavior have been monitored to demonstrate the adaptability of avian species to human disturbance. Research on pink-footed geese (*Anser brachyrhynchus*) indicates that, during mid-winter feeding, geese will learn to



avoid grazing areas with higher levels of human disturbance (Gill et al. 1996). Similarly, golden plovers (*Pluvialis apricaria*) are less likely to be found near foot paths cutting through their habitat, especially when the paths are unpaved and human foot traffic is therefore less predictable (Finney et al. 2005). When raptors were observed along roadways during periods of varying traffic density, several species decreased their proximity when traffic was heavier. Although direct human disturbance was not thought to be responsible, it may have indirectly affected the presence of raptors through its impact on prey items near the road's edge (Bautista et al. 2004).

A small but increasing portion of behavioral research has been devoted to behaviors specifically linked to reproductive success. For example, experiments on incubating oystercatchers (*Haematopus ostralegus*) suggest that human disturbance significantly reduces incubation time and that the presence of humans decreases the number of feeding visits to oystercatcher nests (Verhulst et al. 2001). Leach's storm-petrels (*Oceanodroma leucorhoa*) also modify their behavior in response to human disturbance. Petrels with disturbed nests show significantly lower nest-site fidelity in subsequent breeding seasons than those with undisturbed nests (Blackmer et al. 2004). Human disturbance may also reduce breeding success by causing adult birds to abandon or neglect their eggs and/or young (Flemming et al. 1988; Burger 1995; Ruhlen et al. 2003; Finney et al. 2005).

### 3. Nesting Success Studies

Studies of penguins (*Pygoscelis adeliae*) (Giese 1996), kittiwakes (*Rissa tridactyla*), and guillemots (*Uria aalge*) (Beale and Monaghan 2004) document reduced nesting success despite no obvious behavioral changes. This underlines the importance of extending research beyond the behavioral realm to include measures of nesting success. This is especially true since the effects of human disturbance on wildlife are most important to conservation if they alter survival or fecundity, therefore contributing to a population decline (Gill et al. 2001).

Nesting eiders (*Somateria mollissima*) exhibit decreased nesting success when disturbed early in their nesting period as opposed to late. This effect is seen regardless of whether the disturbance occurred at high or low frequencies (Bolduc and Guillemette 2003). These results indicate that even a solitary human disturbance event can be detrimental to breeding birds, perhaps because predators may take the opportunity to prey on unattended eggs.

Human disturbance appears to increase the loss of snowy plover (*Charadrius alexandrinus*) chicks before they can survive independent of their parents (Ruhlen et al. 2003). This may occur as a result of reduced foraging time, overexertion, or an increased exposure to weather and/or predators. The latter in fact, may decrease nesting success even if they are only perceived threats. Anti-predator physiological responses to humans (Beale and Monaghan 2004) have been documented in sea birds, reducing the condition of incubating parents and leading to an increase in nest desertion (Beale and Monaghan 2004; Blackmer et al. 2004). On the opposite end of the spectrum, golden plovers show a clear alarm-call and human-avoidance

response to pedestrians in their habitat, yet no evidence exists of a negative impact to brood survival (Finney et al. 2005).

This apparent paradox—in which behaviors change while breeding success does not, and vice versa—raises two important questions that no research, to our knowledge, has addressed. First, are there previously undocumented, sublethal effects of disturbance on the fitness metrics—growth rate, condition, and survivorship—of chicks raised in disturbed habitats? Second, could the behavioral responses elicited by human disturbance have *future* fitness consequences for currently breeding birds (e.g. by affecting energy used for increased vigilance, flight, or defensive behaviors) (Lafferty 2001; Beale and Monaghan 2004)? To comprehensively understand the relationship between disturbance and long-term population stability, it is necessary to take an evolutionary approach. This involves going beyond productivity by measuring the fitness impact of breeding in disturbed habitats, for both the adults raising young and for the chicks being produced.

Using this unique but appropriate approach, we have developed a project, discussed in Chapters 2 and 3, that will provide data essential for understanding how disturbed populations will grow/decline in the long term. We monitored breeding Eastern bluebirds (*Sialis sialis*) and, opportunistically, Carolina chickadees (*Poecile carolinensis*) across a disturbance gradient in southeastern Virginia during the 2004 and 2005 breeding seasons. We quantified chick fitness (measured as growth rate, body condition, and survivorship), adult fitness (measured as number of chicks fledging from each brood), local disturbance regimes, and bluebird parental behavior (assessed by time budgets of adult activities). We predicted that

disturbance would negatively impact adult behavior by increasing vigilance and defensive behaviors, which in turn would decrease the amount of time available to the adults to care for themselves and their young. We therefore also predicted that disturbance would have a negative impact on the young, by decreasing adult care and potentially also reducing potential resources in the environment.

Eastern bluebirds were an ideal study organism because they are native nesters in our region and willingly occupy nest boxes placed across a disturbance gradient. Their bright coloring and sexual dimorphism make them easy to locate and sex during field observations. Another interesting aspect of bluebirds is the history of their conservation status across the United States. 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 20<sup>th</sup> century. The establishment of bluebird trails (aggregations of nest boxes) across the country has restored bluebird populations to pre-colonization numbers and introduced the species to many human-modified breeding locations, such as golf courses, cemeteries, and recreational parks (Gowaty 1998; Pinkowski 1977; Pinkowski 1979; Belser 1981). We can therefore use bluebirds not only as a general bioindicator, but also to answer the specific question of whether we have placed boxes in locations that are healthy for breeding adults and the young they produce.

In particular, current literature debates the potential negative impacts of golf courses on the breeding success of wildlife. Critics argue that pesticides, human disturbance, and habitat alteration decrease population numbers and reduce breeding success of resident species. In Chapters 4 and 5, we address this

question specifically by comparing the disturbance regimes, chick fitness metrics, and adult time budgets at golf course and non-golf course locations.

Wildlife management practices have traditionally stemmed from information on reproduction, mortality, emigration, and immigration rates (Verhulst et al. 2001). Our study supplements these data with a novel demonstration of the ways in which disturbance alters the life histories of a native bird species and how it affects their productivity. Perhaps more importantly, our study design explores whether Eastern bluebird (and to some extent Carolina chickadee) populations have undergone, or are currently experiencing, selection on behavioral strategies and modified life histories as a result of anthropogenic disturbance. As is discussed in Chapter 6, this evolutionary ecological approach will help us understand whether human disturbance can encourage potentially harmful behaviors and/or behaviors that could predispose an animal to live in an area with a particular disturbance regime.

Such quantifications are invaluable in assessing whether species like the Eastern bluebird are merely attracted to artificial habitats, or whether the birds are actually maintaining viable populations there (Marzluff and Ewing 2001). This information can, in turn, be used to establish management practices specifically tailored to areas of differing disturbance regimes so that we can accommodate both sensitive avian life histories and changing human land use patterns.

## CHAPTER 2

### METHODS

#### 2.1 Study Area

We performed experiments throughout the entire 2004 breeding season (1 April to 30 August 2004) and during the first clutch attempts of the 2005 breeding season (1 April to 8 June 2005). In 2004, our network consisted of 373 boxes across 17 sites located, on average, 11.87 +/- 6.95 (SD) km from a point in York County (37°17' 24" lat, 76°42' 25" long). These locations included golf courses (Kiskiack, Stonehouse, Williamsburg Country Club, and Williamsburg National), parks (Colonial Parkway, Greensprings, James City Recreation Center, Matoaka Woods, Newport News Park, Williamsburg Indoor Sports Complex, York River State Park), campuses (Dillard Complex, Eastern State Hospital, South Henry Street, College of William and Mary), and farms (Carlton Farm, Gospel Spreading Farm). In 2005, we added one site to our network—Chambrel, a retirement community—for a total of 18 sites. Damage to boxes and habitat alteration reduced our network to 367 boxes in 2005. For both years of the study, most boxes had been in place for over 2 years. Before 2004, we added 98 boxes (26.3%) across 8 sites in early spring; before 2005, we added 20 boxes (5.4%) across 4 sites. The disparity of box ages should not have affected our chick fitness measurements, as it has previously been

shown that age of box has no significant effects on box use or on the demographics of birds produced in the boxes (LeClerc et al. in press).

## 2.2 Breeding Demography, Morphometrics, and Banding

Each nest box was visited once weekly throughout the nest-building phase of the breeding season to determine the status of the nest (empty, partial, complete). Once eggs were laid, we visited the box every 3-4 days in order to determine hatch date. Once the chicks hatched, we continued visiting the nest every 3-4 days, on average, to weigh and measure each chick and estimate chick age to 1-day precision according to growth morphology (LeClerc et al. in press). We visited between 6:00 and 22:00, depending on accessibility and permission.

Weight and wing chord measurements of Eastern bluebird nestlings were conducted throughout the two-week nestling period. We also opportunistically caught adults, primarily females, in the nest box and measured them during these visits. We measured weight to 0.1 g accuracy using an electronic scale. We measured unflattened wing chord (from the bottom of the radius to the end of the longest primary feather) to 0.1 mm accuracy using dial calipers. To preserve chick health, we took no measurements when it was raining.

All measured birds were banded with uniquely numbered United States Fish and Wildlife Service bands. The birds were also banded with unique combinations of three plastic color bands to aid identification. Colors used were red, orange, yellow, green, violet, pink, brown, white, and black; color combinations were

randomly allocated to birds. Chicks were color banded at 10+ days of age, once their tarsi were sufficiently large to provide adequate room for the bands.

### 2.3 Nest Box Observations: Time Budgets of Breeding Eastern Bluebirds

We performed behavioral observations at our focal nests twice during the nestling growth phase. To reduce the potentially confounding effects of time of day and day of week on disturbance 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 7:00 and 18:00 in 90 minute sessions. The author conducted all initial observations and subsequently trained two field assistants in observation technique so that all data were collected in the same way. In locations that were extremely busy, two observers worked in pairs to ensure accuracy.

Pilot tests using flush distance as a metric of disturbance indicated that adult Eastern bluebirds were not disturbed by a researcher until the observer approached to within 25 m of the nest box (n=14 approaches to different boxes, mean flush distance = 10.5 m, SD = 10.9). As a precaution, however, observers entered the territory of the focal box as far as possible from the nest and/or the parents and sat 30-50 m from the nest boxes during observation periods. To increase the probability that adults had adjusted to the observer's presence, we started observations only when one of the following conditions was met:



- a. If the bluebird parent was already in the box when the observer arrived, the observation period began when the parent left the box to begin a new activity.
- b. If the bluebird parent was seen in the territory but was not at the box, the observation period began when the parent began a new activity. If the bluebird's former or new activity was obviously related to the presence of the observer, the observer waited up to 5 minutes until the behavior changed.
- c. If no bluebird parents were seen, the observer waited up to 10 minutes for the parent(s) to arrive. If the adults appeared within that time, the observation period began immediately. If 10 minutes elapsed with no adult appearance, and the observer was sure the nest box was active, the observation was begun regardless of the absence of adults.

Using binoculars to determine behavioral activity and sex of each bird, observers noted parental activity at 2-minute intervals throughout the 90-minute observation period (i.e. 46 total activities recorded for each parent). 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 box.

Every 2 minutes, we noted which of the following behaviors was occurring: locomoting (flying or hopping unrelated to another activity, such as hunting), perching (sitting unrelated to hunting or singing), preening, being at the nest (either incubating or feeding the young), defending, hunting, and vocalizing. In the event

that two behaviors occurred simultaneously, such as vocalizing while sitting, we recorded the more active of the two (in this case, vocalizing). The author predetermined and field-tested categories based on published time budgets for Eastern bluebirds (Belser 1981). We used stopwatches and handheld voice recorders in conjunction with handwritten notes to ensure accuracy of timing and notation.

#### 2.4 Nest Box Observations: Disturbance Regime

We also collected disturbance data during each 90-minute behavior observation. As with behaviors, we documented disturbances only when they occurred within a 50-meter radius of the nest box. However, unlike behaviors, we documented *all* disturbances rather than only those occurring at 2-minute intervals. We quantified each disturbance by measuring the following: time of event (with respect to the 90-minute observation period), length (in seconds, using a stopwatch), and distance to nest box (in meters, estimated during the observations and paced afterwards for verification). We classified each disturbance event into the following categories: foot traffic, foot traffic with animals, animal (wild or domestic), automobile, golf cart, bicycle, non-cart and non-car motorized traffic (all-terrain vehicles, lawnmowers), and projectiles (golf balls, falling branches). With the exception of the last two categories, which were created following unanticipated disturbances, all categories were pre-determined and field-tested during the aforementioned pilot observations.

For each box, we compiled two disturbance datasets. The first, which we call “Disturbance Source,” comprised individual types of disturbance (e.g. pedestrian vs. car vs. animal), for which we calculated mean length (in seconds) and distance (in meters), variation in length and distance, minimum distance, and total length of disturbance (e.g. length of first pedestrian disturbance + length of second pedestrian disturbance + ... + length of nth pedestrian disturbance). The second dataset, which we call “Disturbance Characteristic,” looks at the same variables—mean length and distance, variation in length and distance, minimum distance, and total length of disturbance—for *all* disturbance events, regardless of type (e.g. all pedestrian + all vehicular, etc.).

After each disturbance observation, the observer placed a digital sound level meter (Extech Instruments Model 407727; Waltham, MA) on the baffle of the box or at the base of the pole. The observer took recordings for five minutes, with the sound meter set to capture the maximum decibel reading within the recording period. Due to a shortage of sound meters at the beginning of the season, 23 of 104 (22%) decibel readings were not taken until late August, approximately 2 weeks after the end of the breeding season. After reviewing preliminary sound meter data, we hypothesized that decibel levels at nest boxes were related to wind speed in the habitat. During the late August recordings, we therefore simultaneously measured maximum wind speed at the boxes using an anemometer (Nielsen-Kellerman Manufacturing Kestrel 4000; Boothwyn, PA) for five minutes.

## 2.5 Subjective Disturbance Scores

JPS and CRK used a five-point scale to subjectively rank every active bluebird box, including those not observed, of the 2004 and 2005 seasons. This allowed us to increase our sample size to 246 boxes when correlating disturbance and fitness metrics. Because we hypothesized that other species, such as the Carolina chickadee, might show different reactions to disturbance than do Eastern bluebirds, we also scored each active chickadee box of the 2005 season (21 boxes, for a total of 267 boxes between the two species). Evaluations were averaged to obtain one score per box; on the rare occasion that any scores differed by more than one point, evaluators discussed the conflict and compromised prior to averaging

## 2.6 Statistical Analyses

All statistical analyses were performed using SPSS v. 10.5 or SPSS v. 12.0 (SPSS Inc. Chicago, Illinois) employing two-tailed tests of probability. Original variables were suitably transformed to meet the assumptions of normality for parametric tests. We used principle components analysis (PCA) to reduce the number of variables in the Disturbance Source, Disturbance Characteristic, and behavior categories.

We used bivariate correlations to investigate the relationships between behavior principle components, disturbance principle components, and fitness. We used quadratic curve estimation regressions to investigate all nonlinear relationships. For subjective disturbance scores, we used parametric correlations to

compare growth, condition, number of fledglings, and survival rate across disturbance levels.

## CHAPTER 3

### RESULTS OF ALL-SITES ANALYSIS

#### 3.1 Fitness Metrics

Over the course of the study, our 52 focal boxes received 156 hours of observation over 226 visits, and produced 203 nestlings.

We employed cubic regressions of wing chord on age to generate residuals of chick growth for their given age, in both 2004 ( $F_{3,1880}=8497$ ,  $p<0.00001$ ,  $R^2=0.931$ ; wing chord= $-0.0265*\text{age}^3 + 0.7278*\text{age}^2 - 1.1832*\text{age} + 8.4524$ ) and 2005 ( $F_{3,926}=3973$ ,  $p<0.00001$ ,  $R^2=0.923$ ; wing chord= $-0.0237*\text{age}^3 + 0.6899*\text{age}^2 - 1.6146*\text{age} + 9.078$ ). We then averaged all residual values across chicks within a brood to generate a single brood growth rate metric for each brood. We performed similar cubic regression of chick body mass on wing chord to generate residuals of chick mass given their age, in both 2004 ( $F_{3,1876}=6545$ ,  $p<0.00001$ ,  $R^2=0.913$ ; body mass= $0.001*\text{wing chord}^3 - 0.0247*\text{wing chord}^2 - 1.515*\text{wing chord} - 4.01$ ) and 2005 ( $F_{3,926}=5997$ ,  $p<0.00001$ ,  $R^2=0.951$ ; body mass =  $0.0001*\text{wing chord}^3 - 0.0204*\text{wing chord}^2 + 1.397*\text{wing chord} - 3.732$ ). Again we averaged these residuals across chicks within a brood to render a single measure of brood condition.

Using these growth and condition metrics, we applied multiple regression analyses to control for number of researcher visits, clutch initiation date, number of chicks in the brood, and number of boxes at the site. We used the residuals from

	Brood Growth Rate		Brood Condition		Number Fledged		Brood Survival	
	t	P	t	p	t	p	t	p
Clutch Initiation Date	-1.38	0.173	-0.101	0.920	1.12	0.267	-1.383	0.173
Number of Researcher Visits	-0.12	0.905	-0.704	0.485	-1.06	0.295	-0.12	0.905
Number of Boxes in Site	-1.25	0.219	1.22	0.229	0.842	0.404	-1.246	0.219
Number of Birds in Brood	-1.94	0.058	-0.029	0.977	-		-	

Table 3.1: Summary of results for multiple regressions on chick fitness metrics.

these regressions as our measures of brood growth and condition in subsequent analyses (see Table 3.1 for summary of all multiple regression results). Brood survivorship in the nest (number of fledglings/number of eggs in clutch) was calculated as an additional brood fitness metric. It was controlled for number of researcher visits, clutch initiation date, and the number of boxes at each site by storing residuals from a multiple regression analysis. Number of fledglings was used as an indicator of adult fitness and we used residuals in further analysis. These values were controlled via a multiple regression employing the same parameters as for survivorship.

### 3.2 Generating Disturbance PCs

#### 3.2.1 *Disturbance Source PCA*

The Disturbance Source PCA consisted of eight categories of disturbance type (pedestrians, pedestrians with animals, bicycles, cars, golf carts, other motorized disturbances, animals, and projectiles). For each category, we averaged quantification variables (see Chapter 2.4), yielding six measurements per disturbance category: total time disturbed, mean time disturbed, variability in time disturbed, closest proximity, mean proximity, and variability in proximity. All original variables were  $\ln+1$  transformed to better fit assumptions of normality. PCA of Disturbance Source collapsed 47 variables into 10 significant components, accounting for 84.5% of the original variance (variability in time disturbed could not be analyzed for projectiles because all values were null; see Appendix I for the table of loading factors). The first six components, accounting for 68% of the variance,



were easily interpretable. The remaining four had low loading factors for all the original variables and are not discussed any further. Loading factors were grouped by the source of disturbance and did not appear to be separated by metrics within sources (e.g. duration, proximity, predictability) (Table 3.2).

Disturbance Source PC1 loaded negatively for all golf cart values, but positively for length of disturbance of cars and bikes. This indicates disturbance regimes near roads but away from golf courses. For the remainder of this paper, this will be called Non-GC Road Traffic. PC2 loaded positively for 3 pedestrian values, indicating disturbance regimes near hiking trails or footpaths. We have called this Foot Traffic. PC3 loaded positively for proximity of bikes and other motorized vehicles (e.g. lawnmowers, ATVs), but negatively for pedestrians and pedestrians with animals. This was indicative of non-walking trails, and will be referred to as Trail Vehicles. PC4 loaded positively for projectiles, a category almost entirely composed of golf ball disturbances (it also included one falling branch). These disturbances would predominantly be found in the busiest parts of golf courses, particularly along the fairway. This component will be called Projectiles. PC5 loaded positively for wild animal disturbances, indicating the areas with the largest “natural” disturbance regime. For the remainder of the paper, this will be called Animals. Lastly, PC6 loaded positively for golf carts but negatively for pedestrians and other motorized vehicles. We interpreted this as describing areas at a golf course where through traffic was common but lingering was not—for instance, cart paths near woods between holes. This will be referred to as GC Transition.

Component	Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %
1	9.61	20.44	20.4
2	7.00	14.9	35.3
3	5.16	11.0	46.3
4	3.91	8.33	54.6
5	3.64	7.74	62.4
6	3.11	6.61	69.0
7	2.76	5.87	74.9
8	1.82	3.87	78.7
9	1.47	3.12	81.8
10	1.25	2.66	84.5

Table 3.2: Disturbance Source PCA extraction values.

### 3.2.2 *Disturbance Characteristic PCA*

For the Disturbance Characteristic PCA, we averaged all six quantification aspects (see 2.4 and 3.2.1) across categories, regardless of disturbance source. We also included a sum of all disturbance events (also regardless of source), an average of the two decibel readings taken during the box observations, and a measurement of the diversity of disturbance events (calculated as the number of different sources of disturbance). This allowed us to isolate which disturbance traits most significantly affected fitness and behavior. PCA of these nine variables yielded 4 significant components, accounting for 76.5% of all variance (Table 3.3).

PC1 loaded positively for all three temporal measurements (total length, mean length, and variability in length) so we have called this Longer/More Variable Length. PC2 loaded positively for total number of events, but negatively for both mean time and variation in time disturbed. This has been called Frequent-Short-Predictable. PC3 loaded negatively for both minimum proximity and average proximity, so this has been named Close. PC4 loaded positively for, and will be referred to as, variation in proximity (see Table 3.4 for a summary of all loading factors).

### 3.2.3 *Within-Box and Temporal Repeatability of Disturbance*

To account for variance in disturbance within boxes over time, data were only used from nests that received a minimum of two behavior/disturbance observations. Repeated measures analysis revealed that no Disturbance Characteristic PCs were significantly repeatable between observations. However, while PCs 1 ( $F_{96,2}=1.594$ ,

Component	Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %
1	2.63	29.2	29.2
2	1.58	17.5	46.7
3	1.50	16.6	63.3
4	1.19	13.2	76.5

Table 3.3 Disturbance Characteristic PCA extraction values.

	Component			
	1	2	3	4
total number of events	0.375	0.693	0.432	-0.165
diversity of disturbance	0.434	0.413	0.004	0.288
decibel reading	0.186	-0.041	0.441	-0.098
total time disturbed	0.712	0.313	0.458	0.143
mean time disturbed	0.767	-0.596	0.059	0.054
variation in time disturbed	0.729	-0.605	0.150	0.032
minimum proximity	0.548	0.159	-0.598	-0.479
average proximity	0.577	0.273	-0.688	0.076
variation in proximity	0.009	0.059	-0.215	0.898

Table 3.4: Loading factors for Disturbance Characteristic PCA.

$p=0.474$ ) and 4 ( $F_{96,2}=1.446$ ,  $p=0.497$ ) were not repeatable, PCs 2 ( $F_{96,2}=15.356$ ,  $p=0.063$ ) and 3 ( $F_{96,2}=16.597$ ,  $p=0.058$ ) were nearly repeatable.

Time of day did not significantly alter PCs for Disturbance Source ( $F_{1,96}<2.24$ ,  $p>0.137$ ) or Disturbance Characteristic ( $F_{1,94}<1.232$ ,  $p>0.270$ ). Day of week had a significant effect on both Disturbance Source PC1 (non-golf course road traffic) ( $F_{1,96}=8.41$ ,  $p=0.005$ ; all other  $F_{1,96}<2.29$ ,  $p>0.133$ ) and Disturbance Characteristic PC3 ( $F_{1,94}=5.45$ ,  $p=0.022$ ; all other  $F_{1,96}<0.453$ ,  $p>0.503$ ). Year had no significant effects on Disturbance Source (all  $F_{1,96}<1.59$ ,  $p>0.210$ ). Year significantly affected both PC3 (close disturbance) ( $F_{1,94}=8.66$ ,  $p=0.004$ ) and PC4 (disturbance of varying proximity) ( $F_{1,94}=10.176$ ,  $p=0.002$ ; all other  $F_{1,94}<0.278$ ,  $p>0.600$ ).

Despite these differences, we pooled data across both observation and year. We feel this is justifiable because we both expected and planned for variations in disturbance regimes due to temporal changes in human land use patterns.

#### 3.2.4 *Anemometer Data*

Decibel reading was highly correlated to wind speed ( $r=0.629$ ,  $n=22$ ,  $p=0.002$ ) (Fig. 3.1). This metric is perhaps a better indicator of habitat structure than current disturbance regime, though human disturbance may originally have influenced the environment through habitat modification.

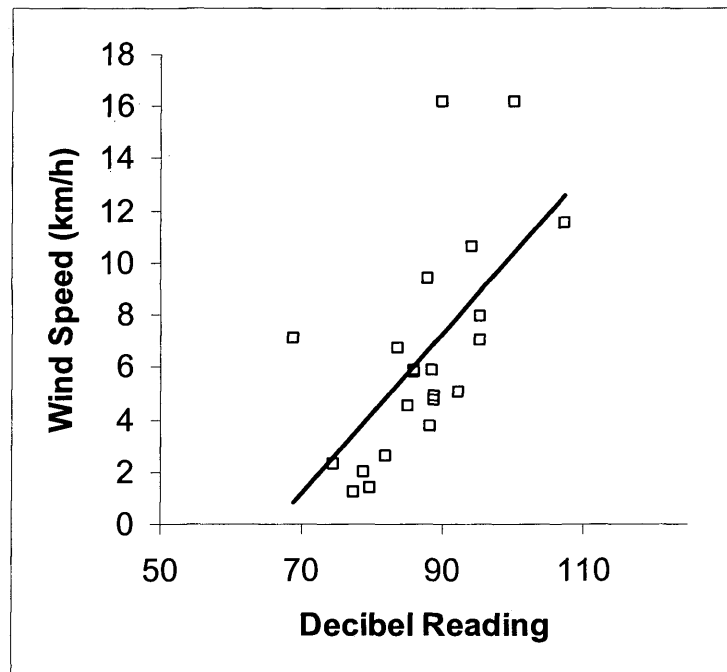


Fig. 3.1: Correlation between wind speed and decibel level.

### 3.3 Generating Behavior PCs

Three adult behaviors, “perching,” “locomoting,” and “total visit number,” were normally distributed and required no transformation. “Out of sight/territory” required square root transformation, and all other variables required  $\ln+1$  transformation to achieve even distribution. PCA of adult behaviors yielded five significant components, accounting for 71.7% of the variance (Table 3.5).

Behavior PC1 (Self-Maintenance and Perching) loaded positively for perching and preening, but negatively for time spent out of territory/sight. This PC appears to reflect time the adults spent resting and preening themselves, while perching conspicuously within the territory. Behavior PC2 (Box Visits) loaded positively for visits to the nest (both total number of visits and fraction of time budget spent visiting). Behavior PC3 (Reduced Calling) loaded negatively for vocalizations. Behavior PC4 (In the Box) loaded positively for length of visits to the nest box. Because most feeding visits were relatively short, this PC likely reflects incubation behavior during early growth or inclement conditions. Behavior PC5 (Defense and Foraging) loaded positively for defense behaviors and active hunting (see Table 3.6 for loading factors).



Component	Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %
1	2.26	22.6	22.6
2	1.52	15.2	37.8
3	1.23	12.3	50.1
4	1.14	11.4	61.5
5	1.03	10.2	71.7

Table 3.5: Adult behavior PCA extraction values.

	Component				
	1	2	3	4	5
Perching	0.848	-0.054	0.122	0.125	-0.176
Locomoting	0.014	0.164	0.471	-0.002	-0.471
In the Box (proportion)	-0.189	0.736	0.205	-0.210	0.255
Total # Visits to Box	-0.178	0.791	-0.076	0.461	-0.051
Out of Territory/Sight	-0.868	-0.312	0.057	-0.303	0.151
Ave. Length Box Visit	-0.029	-0.327	0.422	0.661	0.077
Preening	0.648	-0.128	0.194	-0.358	0.195
Defending	0.091	-0.172	-0.278	0.402	0.601
Vocalizing	0.360	0.145	-0.727	-0.077	-0.142
Hunting	0.402	0.223	0.345	-0.209	0.508

Table 3.6: Loading factors for adult behavior PCA.

### 3.4 Disturbance and Fitness

#### 3.4.1 *Correlations of Fitness Metrics and Disturbance Source PCs*

There were no significant linear relationships between fitness metrics and Disturbance Source PCs ( $-0.206 < r < 0.233$ ,  $n=51$ , all  $p > 0.099$ ). There was a significant U-shaped relationship between Trail Vehicles and growth ( $F_{2,48}=3.41$ ,  $p=0.041$ ) (Fig. 3.2). Brood growth rate is highest where Trail Vehicle disturbance is intermediate, a relationship which may be more indicative of the environment in which this disturbance occurs (i.e. places with better resources) than of a specific interaction between this disturbance and bluebird chicks. The overall lack of significant relationships between all six Disturbance Source PCs and the four chick metrics indicates that the particular source of disturbance (e.g. pedestrian, car, golf cart) is not an important determinant of chick health or fitness.

#### 3.4.2 *Correlations of Fitness Metrics and Disturbance Characteristic PCs.*

Frequent-Short-Predictable disturbance was positively nonlinearly related to number fledged ( $F_{2,45}=4.19$ ,  $p=0.021$ ) (Fig. 3.3). No other disturbance metrics were significantly related to chick fitness ( $-0.223 < r < 0.278$ ,  $n=47$ , all  $p > 0.058$ ).

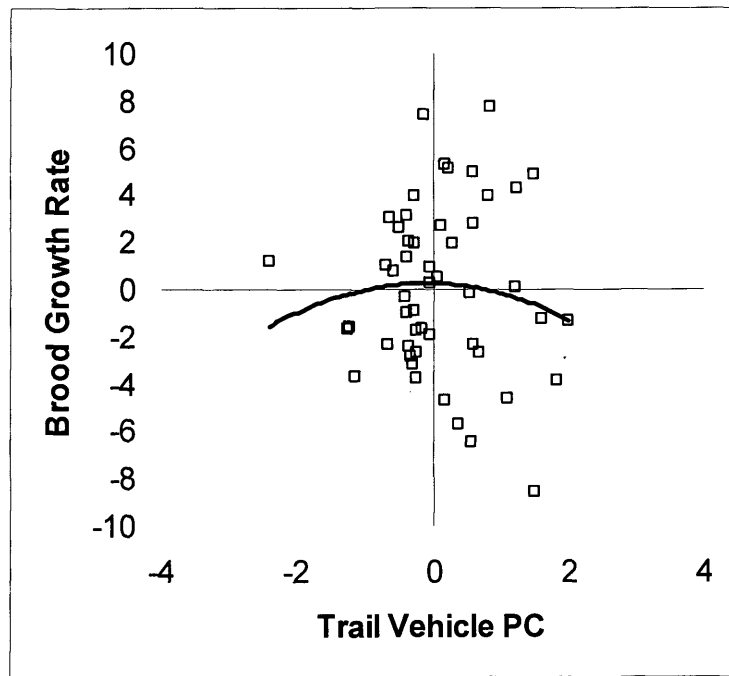


Fig. 3.2: Correlation between Trail Vehicle PC and brood growth rate.

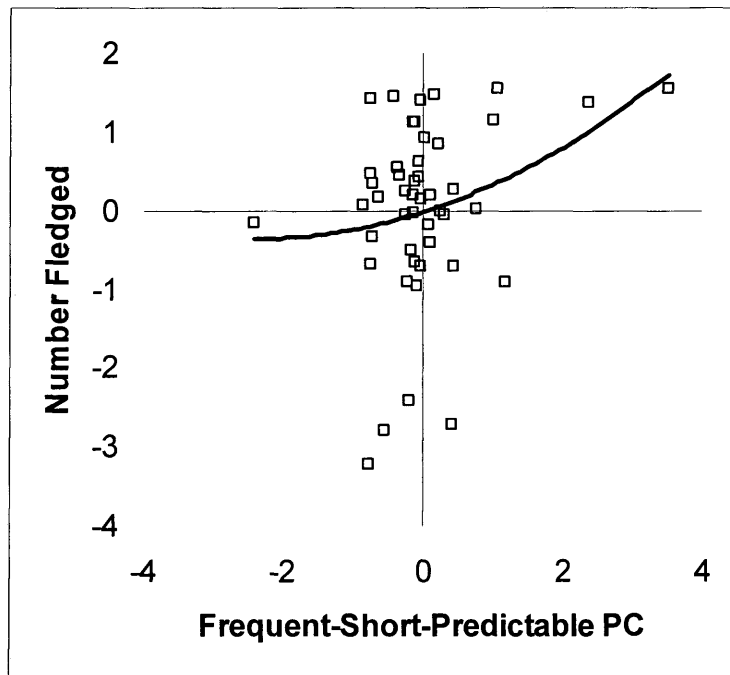


Fig. 3.3: Correlation between Frequent-Short-Predictable PC and number fledged.

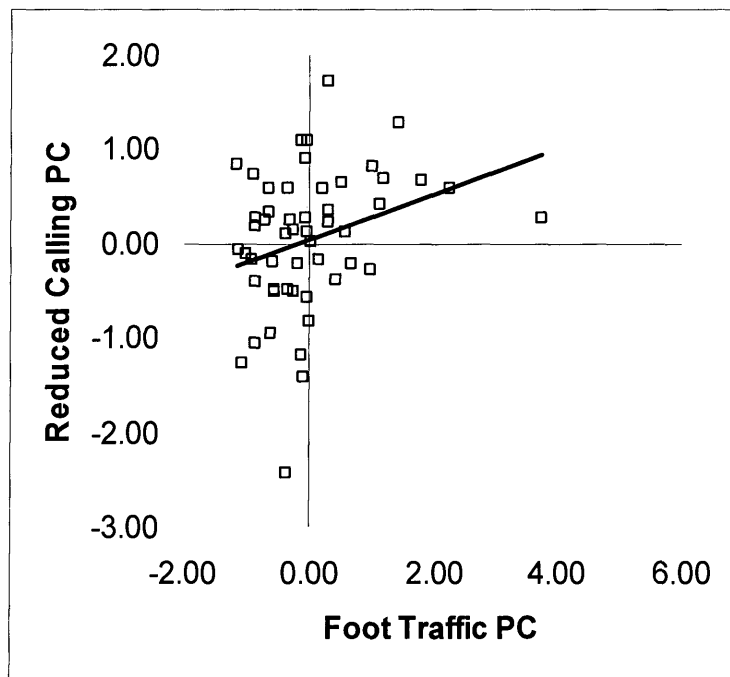


Fig. 3.4: Correlation between Foot Traffic PC and Reduced Calling PC.

### 3.5 Disturbance and Behavior

#### 3.5.1 *Correlations of Adult Behavior PCs and Disturbance Source PCs*

Only one Disturbance Source PC showed a significant linear relationship to adult behavior. Foot Traffic was positively related to Reduced Calling ( $r=0.295$ ,  $n=52$ ,  $p=0.034$ ) (Fig. 3.4) but negatively related to Defense ( $r=-0.373$ ,  $n=52$ ,  $p=0.006$ ; all other correlations  $-0.229 < r < 0.266$ ,  $n=52$ ,  $p > 0.057$ ) (Fig. 3.5). All defensive behaviors observed occurred when wild animals strayed too near bluebird nest boxes. It would therefore appear that Foot Traffic itself, or the type of environments in which it occurs, serves to decrease the likelihood of threatening animal encounters and therefore defensive behaviors elicited from bluebird parents. However, the disturbance apparently alarms the parents enough that they decrease communications with each other or other species, probably to avoid drawing attention to themselves or their nests.

We also detected one significant nonlinear relationship (Fig. 3.6). In the Box vs. Non-GC Road Traffic yielded a U-shaped curve ( $F_{2,49}=4.72$ ,  $p=0.013$ ). This indicates that where traffic is lowest, there is nothing to disturb birds from incubation; where traffic is highest, habituation may occur so that incubation continues as normal. At intermediate levels of disturbance, however, the birds lose incubation time.

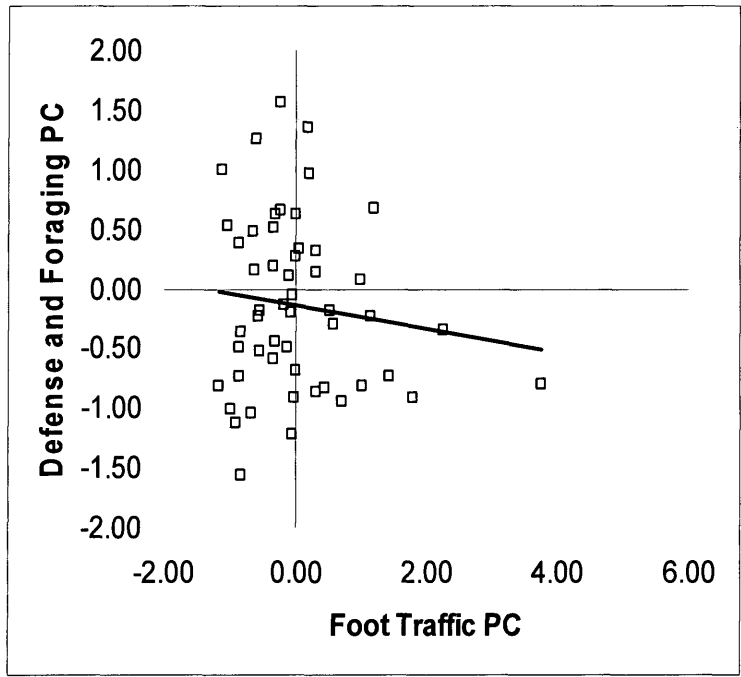


Fig. 3.5: Correlation between Foot Traffic PC and Defense and Foraging PC.



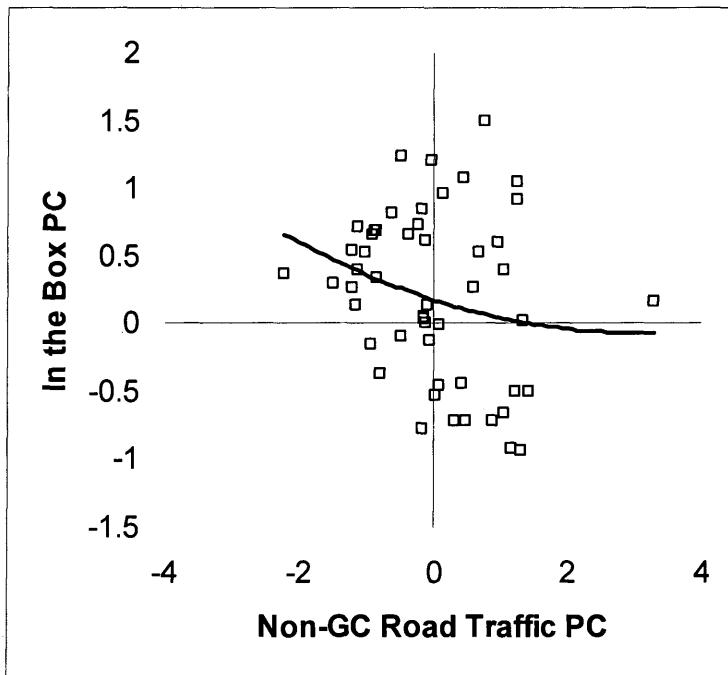


Fig. 3.6: Nonlinear relationship between Non-GC Road Traffic PC and In the Box PC.

### 3.5.2 Correlations of Adult Behavior PCs and Disturbance Characteristic PCs.

The only two disturbance PCs significantly related to adult behaviors both included measures of proximity. Variation in Proximity showed a significant negative linear relationship with Box Visits ( $r=-0.325$ ,  $n=48$ ,  $p=0.024$ ) (Fig. 3.7) and a positive nonlinear relationship to Reduced Calling ( $F_{2,45}=4.19$ ,  $p=0.021$ ) (Fig. 3.8). Box Visits also showed a U-shaped relationship to Close ( $F_{2,45}=3.59$ ,  $p=0.036$ ) (Fig. 3.9). These results indicate that proximity is an important factor in eliciting a response to disturbance from bluebird parents. Variability in proximity alarms parent bluebirds, causing them to both stay away from the nest box and become more vocal; the latter reaction may be either an increase in alarm calls or an increase in communication between the birds (e.g. male to female, adults to chicks). The predominantly positive relationship between Close disturbance and Box Visits behavior, however, highlights that while *variability* of proximity is a deterrent to box visits, *absolute* proximity is not. In fact, adults visit the nest box more when the disturbance regime is closer, likely because they are “checking in” on their young.

No other disturbance metrics were significantly related to adult behavior PCs (all other correlations  $-0.274 < r < 0.241$ ,  $n=48$ ,  $p > 0.059$ ).

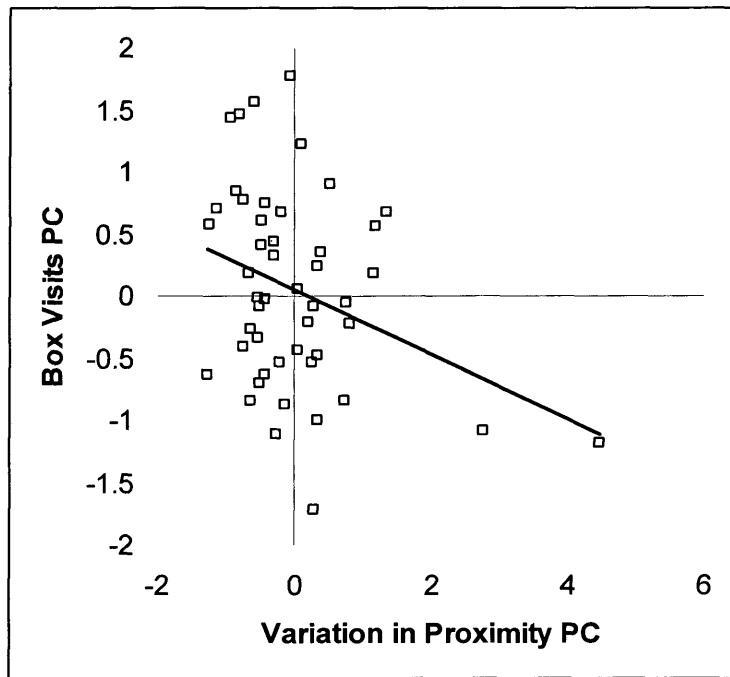


Fig. 3.7: Correlation between Variation in Proximity PC and Box Visits PC.

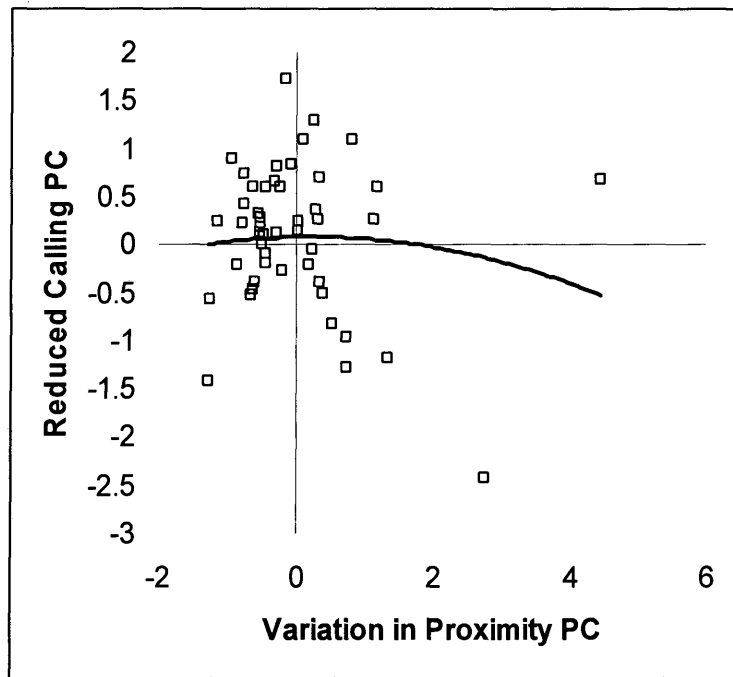


Fig. 3.8: Correlation between Variation in Proximity PC and Reduced Calling PC.

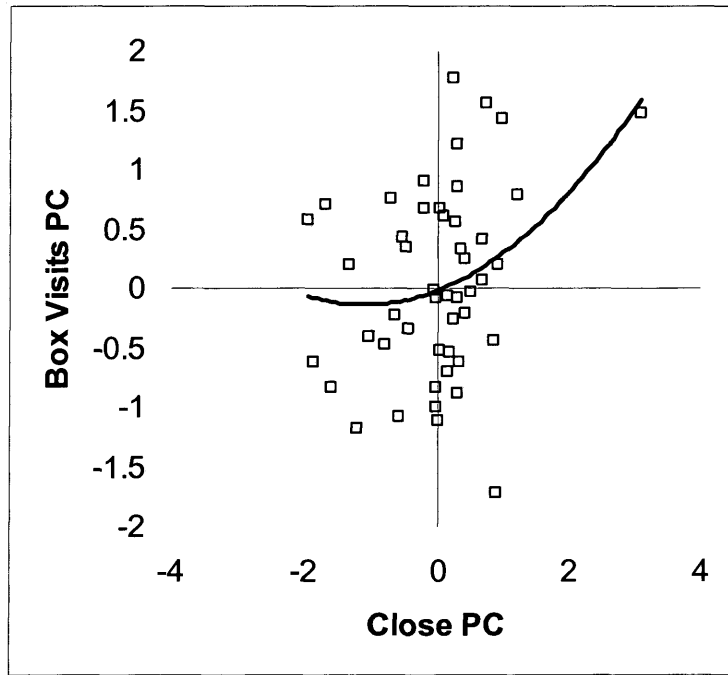


Fig. 3.9: Correlation between Close PC and Box Visits PC.

### 3.6 Behavior and Fitness: Correlations of Fitness Metrics and Behavior PCs

Three significant linear relationships were found between fitness metrics and behavior PCs. Self-Maintenance and Perching was negatively related to both number of fledglings ( $r=-0.378$ ,  $n=51$ ,  $p=0.00$ ) and brood survival ( $r=-0.385$ ,  $n=51$ ,  $p=0.005$ ) (Figures 3.10 and 3.11, respectively). These two relationships imply that there is a compromise in self-maintenance when raising healthy, successful broods. Defense and Foraging was negatively related to brood condition ( $r=-0.306$ ,  $n=51$ ,  $p=0.029$ ) (Fig. 3.12). This indicates that the increased costs of defense, both in terms of physical condition and time, decrease chick condition because parents are less able, or have less time, to devote themselves to chick care.

Defense and Foraging also showed a significant nonlinear relationship with number of fledglings ( $F_{2,47}=11.78$ ,  $p<0.001$ ) (Fig. 3.13). These indicates that at intermediate defense levels, parents can balance their time budgets between defending the nest and taking care of both their young and themselves. When defense decreases, they may be neglecting the chicks such that predation can occur, while when defense increases they may be neglecting their own or their chicks' diets, to the ultimate detriment of the young.

No other significant relationships were found between fitness metrics and behavior PCs ( $-0.238<r<0.242$ ,  $n=51$ , all other  $p>0.075$ ).

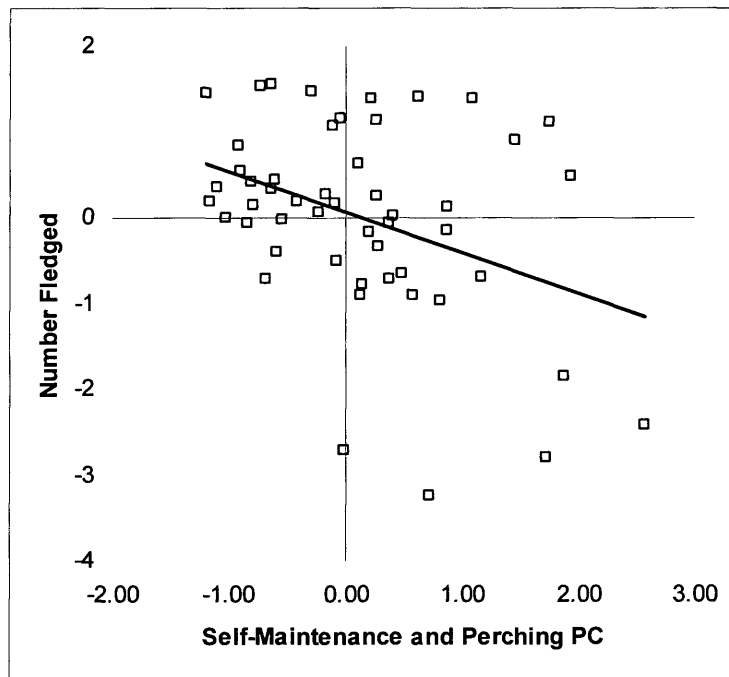


Fig. 3.10: Correlation between Self-Maintenance and Perching PC and number fledged.

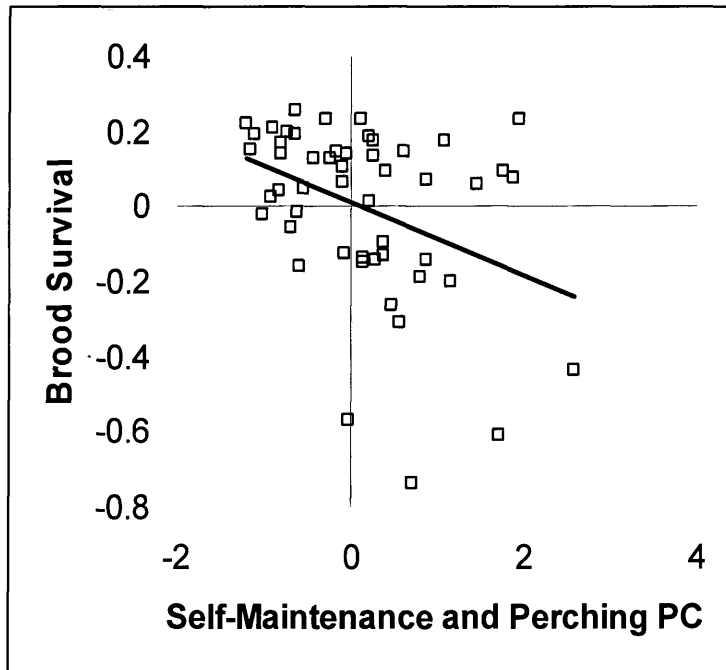


Fig. 3.11: Correlation between Self-Maintenance and Perching PC and brood survival.



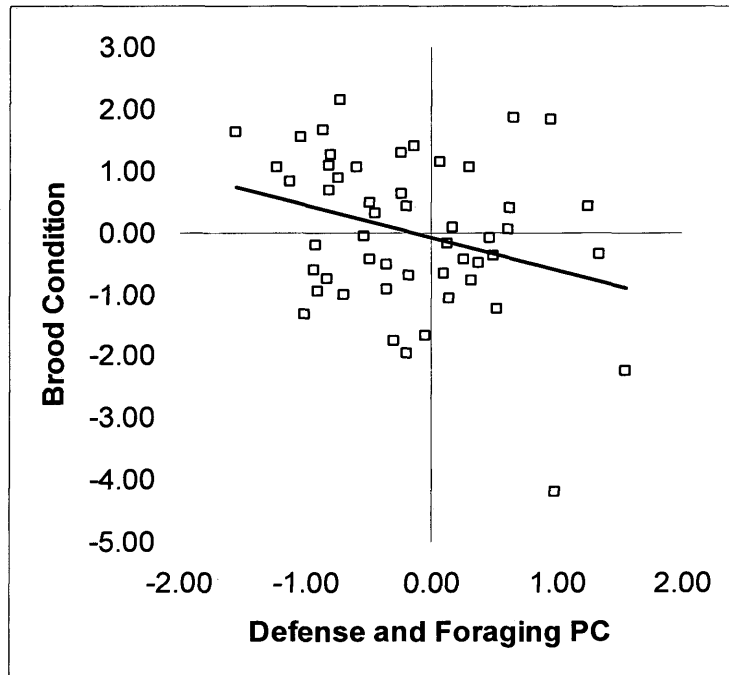


Fig. 3.12: Correlation between Defense and Foraging PC and brood condition.

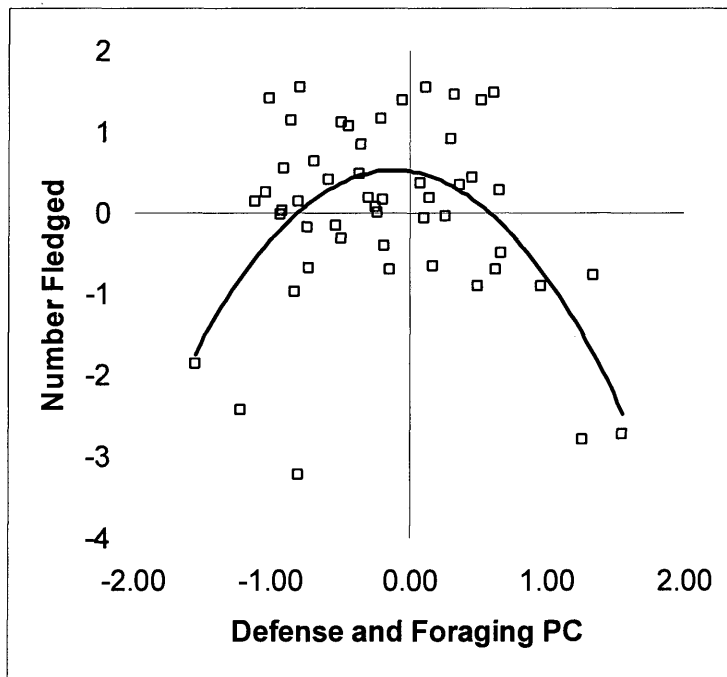


Fig. 3.13: Nonlinear relationship between Defense and Foraging PC and number fledged.

### 3.7 Correlations of Fitness Metrics and Subjective Disturbance Scores

To confirm the relevance and accuracy of our subjective scores, we correlated them to Disturbance Characteristic PCs. The first three PCs were significantly correlated to our scores, indicating that our estimations are useful in this preliminary analysis (Table 3.7)

There were no significant linear relationships between disturbance scores and fitness metrics for Eastern bluebirds ( $-0.042 < r < 0.062$ ,  $n=244$ ,  $p > 0.332$ ). Exploratory regressions were performed to test for nonlinear relationships between rankings and fitness metrics. Survival ( $F_{2,240}=4.44$ ,  $p=0.036$ ) and number fledged ( $F_{2,240}=5.14$ ,  $p=0.007$ ) both showed inverted curves (Figures 3.14 and 3.15, respectively), indicating highest survival and productivity at intermediate levels of disturbance.

Carolina chickadees showed only linear relationships, but for the other two chick fitness metrics: Both growth ( $r=-0.460$ ,  $n=21$ ,  $p=0.036$ ) and condition ( $r=-0.558$ ,  $n=21$ ,  $p=0.009$ ) were negatively linearly related to disturbance scores (Figures 3.16 and 3.17, respectively; all other correlations  $-0.166 < r < -0.086$ ,  $n=21$ ,  $p > 0.473$ ).

These results suggest that while bluebirds may be adapted to intermediate disturbance regimes, other species such as chickadees are more sensitive and therefore may experience negative effects on fitness and survivorship of young.

Disturbance Characteristic PC	Correlation to Subjective Score (n=48)	
	r	p
1	0.366	0.011
2	0.553	<0.001
3	0.317	0.028
4	-0.107	0.471

Table 3.7: Correlations of Disturbance Characteristic PCs and subjective scores.

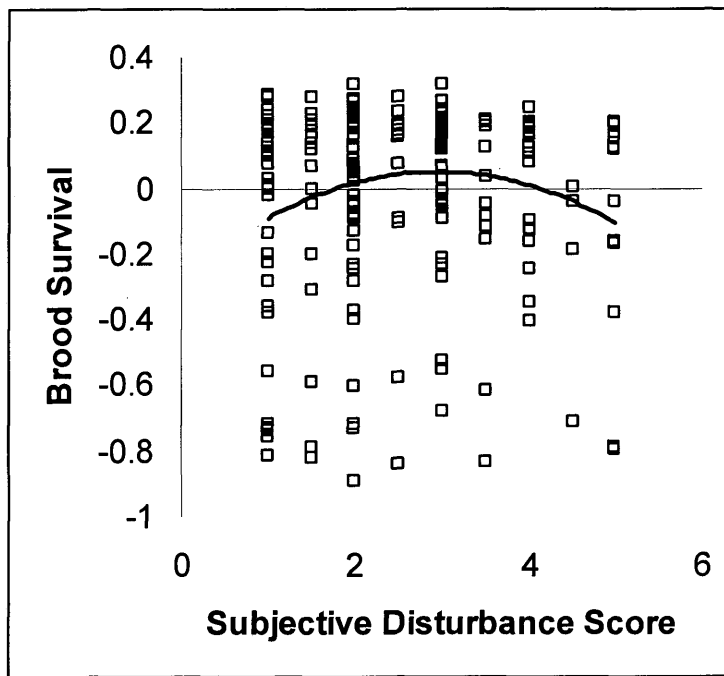


Fig. 3.14: Nonlinear relationship between subjective disturbance score and brood survival of Eastern bluebirds.

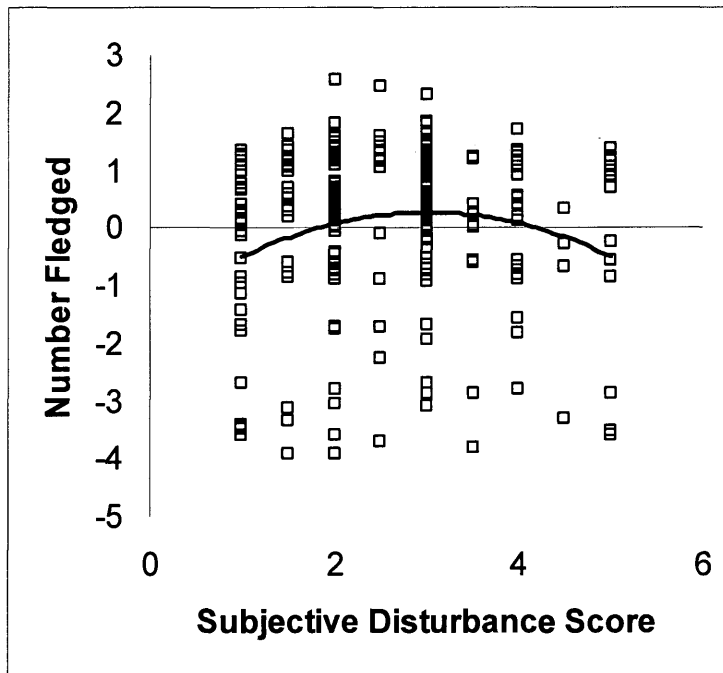


Fig. 3.15: Nonlinear relationship between subjective disturbance score and number fledged for Eastern bluebirds.

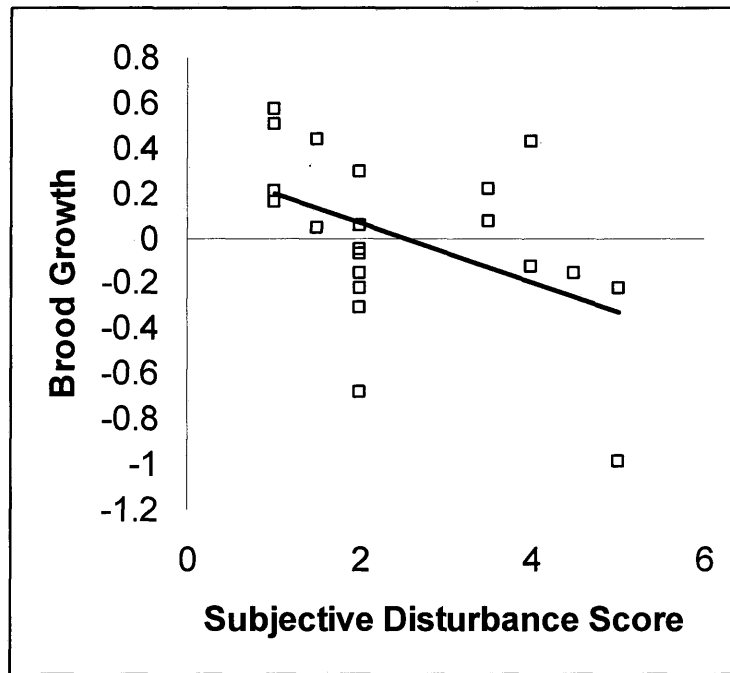


Fig. 3.16: Correlation between subjective disturbance score and brood growth of Carolina chickadees.

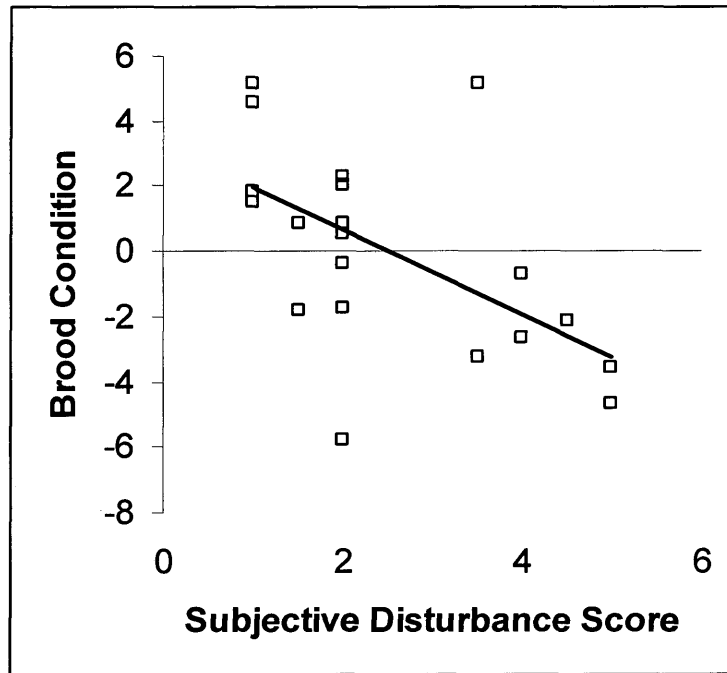


Fig. 3.17: Correlation between subjective disturbance score and brood condition of Carolina chickadees.



## CHAPTER 4

### COMPARING GOLF COURSES AND NON-GOLF COURSES

The origin of golf dates to the 15<sup>th</sup> century when King James introduced the game to the Scottish populace (Platt 1994). In its original form, golf was a game to be played on coastal links, or islands of dunes and marshes, between the land and sea. The days of using such rough and challenging surfaces are long gone: Modern courses are manicured for aesthetic and athletic reasons (Green and Marshall 1987), with the “parkland” design predominating (Brennan 1992). Parkland designs emerged in the 19<sup>th</sup> century, increasing shade and shelter on golf courses by adding trees and bushes both on and around the course (Tanner and Gange 2005). For contemporary golf courses, average area is a comparatively larger (Platt 1994) 56 ha, with about 40% of the space devoted to non-playing areas (Gange and Lindsay 2002). Some experts believe that modern practices of groundskeeping have gone so far as to alter the game itself so that golf fits the landscape, rather than vice versa (Green and Marshall 1987).

There are currently over 31,500 golf courses worldwide (Tanner and Gange 2005), with an estimate of at least one new course being opened daily (Terman 1997). It has been estimated that no other sport occupies and maintains such large areas of the countryside (Gange et al. 2003). While golf course production has seemingly slowed in many Western areas such as the United Kingdom, where there are approximately 10 new golf courses opening annually (Proctor 2002), business is

booming in Eastern countries such as Thailand and Malaysia (Platt 1994). Despite their comparatively small size, these nations are adding approximately one golf course every 10 days and increasing the number of golf players by 20 to 30 percent annually (Platt 1994).

In the United States, the popularity of golf has increased steadily since 1946 (Balogh et al. 1992), with participation increasing from 5 million participants to over 26 million in the past 50 years, and over 570 million rounds of golf played annually (O'Hara and Beckwith 2002). The increase in golf athleticism has produced a rise in golf-related spending: Golfers sink approximately \$21 million per year on games, gear, and club costs (O'Hara and Beckwith 2002).

Despite the attractively lucrative nature of the golfing industry, many red flags have been raised about potential environmental damage caused by the construction and maintenance of courses. Although some golf historians claim that many older, long-established courses are responsible for preserving tracts of land from other types of development (e.g. housing, industry, farming) (Brennan 1992), others complain about the placement of courses in rare, diverse, and ecologically important habitats (Platt 1994). The chemicals used to prepare and maintain golf courses have also been accused of contaminating groundwater and possibly poisoning wildlife (Tietge 1992; Terman 1997). Other complaints have targeted potential habitat loss, water depletion, and increasing urbanization around the course (Gange 2002).

Human dimensions studies indicate a significant difference in the opinions of golfers and non-golfers. Respondents who play golf are significantly more likely to

believe that golf courses are not only *not* harmful, but also *contribute* to conservation of wildlife, whereas respondents who do not play golf are more likely to take a negative stance on courses (Gange and Lindsay 2002).

Scientific research of golf courses have not sufficiently supported either side for a verdict to be made. Several studies have compared the abundance and diversity of wildlife on golf courses to those found in either neighboring patches of more “natural” land, or land similar to the original habitat found before the course was built (Terman 1997; Tanner and Gange 2005). Golf courses appear to compare favorably in terms of wildlife abundances and diversity. However, they support few or no habitat specialists but instead favor habitat generalists or “urban exploiters” such as European starlings, pigeons, and house sparrows, whose unnaturally high abundances may also drive the higher densities seen on courses. Species evenness on golf courses also appears to be reduced, with a greater number of species but fewer individuals than in natural habitats.

It has been noted that continuing urban development will render the “green space” available on golf courses increasingly vital as wildlife habitat (Tietge 1992). One potential role of this green space is as “stepping stones” between larger, natural patches (Gange and Lindsay 2002). If this is possible, courses could be ecologically significant regardless of whether species are breeding there or not. Instead, the areas could act as refuges, particularly for migrants (Gange 2002), and have the added benefit of offering a more dependable supply of food and water, less competition among individuals, and more amenable microclimates (Terman 1997). This is an appealing idea in the age of “contested countryside,” when large scale

commercial golfing tourism threatens those who wish to preserve rural and natural areas for their ecological values (Jackson 2002).

Another hopeful result indicates that “naturalistic golf courses,”—those that use the natural environment of a region as a development template and retain native vegetation, land form, soils, and typical habitat units—compare favorably with “unnatural” golf courses (Terman 1997). A naturalistic golf course is specifically managed for environmental integrity, public involvement, integrated pest management, wildlife food and cover enhancement, and water conservation and enhancement (Terman 1997). If nothing else, a naturalistic golf course may act as a complement to nearby wild areas and may be a better alternative to more urban or disturbed areas (Brennan 1992; Terman 1997).

We could not find studies that directly compared these different classes of golf courses, but two studies exist comparing golf courses and non-golf courses, in terms of bluebird breeding efforts and the quality of young produced in these different locations. Fluctuating asymmetry (FA, the deviation from perfect bilateral symmetry as a result of environmental stress) (Moller and Swaddle 1997) was used to compare the growth of chicks on and off golf courses in Virginia. Non-golf course chicks exhibited greater FA than golf course chicks, indicating that environmental stresses were actually *less* on golf courses than in natural sites (LeClerc et al. in press). Other aspects of breeding, including the condition of the young and the food delivery rates of the parents, were found to be equal across the sites (LeClerc et al. in press).

Although this study indicates that golf courses produce enough young bluebirds to act as a source to neighboring landscapes, other research apparently indicates the opposite. In North Carolina, bluebirds on golf courses initiated clutches later, laid smaller clutches, and produced nestlings of significantly poorer quality than those born in control areas (Stanback and Seifert in press). The authors hypothesize that food was the limiting factor but suggest that disturbance and chemical contamination could also play a role in altering the birds' life histories (Stanback and Seifert in press).

To more fully understand how beneficial or detrimental golf courses may be, it is necessary to understand whether individuals on golf courses are reproducing or whether they are "floaters;" whether golf courses are traps that look appealing but do not contribute to metapopulations; and whether wildlife on courses is exposed to contamination in the form of pesticides and other human disturbances (Tietge 1992; Terman 1997; Tanner 2005). Although the two bluebird studies took the important step of measuring demographics and taking a preliminary look at differences in bird behavior across golf course and non-golf course sites, they were unable to study why variation might occur.

We have attempted to address this gap in our knowledge by measuring basic demographics of Eastern bluebird breeding success and conducting observations to compile time budgets of Eastern bluebird parents and quantify disturbance regimes at their nest boxes (see Chapter 2 for methodology). Our total sample size of 52 nests included 19 golf course boxes and 33 non-golf course boxes. We used analysis of variance tests to compare demographics, parental time budgets, and

disturbance regimes across sites, then compared differences in relationships of these three factors between golf course and non-golf course sites.

We hypothesized that golf courses would experience higher levels of disturbance, with disturbance events occurring more frequently and closer to the box than at non-golf course sites. We believed that this, in turn, would result in adults spending comparatively less time on both self-maintenance and chick care. Further, we hypothesized that they would increase the amount of time spent on vigilance, defensive, and evasive maneuvers. We thought this would negatively impact the young, with golf course chicks exhibiting slower growth rates, poorer condition, and a lower survivorship than their non-golf course counterparts.

## CHAPTER 5

### RESULTS OF COMPARISON OF GOLF COURSES AND NON-GOLF COURSES

#### 5.1 ANOVAs for Fitness Metrics and PCs

We tested for significant differences in the fitness metrics, adult behaviors, and disturbance PCs of golf course and non golf course bluebirds using analysis of variance. No significant differences were found for any of these measurements (chick fitness conditions Table 5.1; values controlled as discussed for all-sites analysis; disturbance characteristic PCs Table 5.2; adult behavior PCs Table 5.3).

#### 5.2 Differences in Relationships Between Disturbance PCs and Fitness Metrics

Neither golf courses ( $-0.418 < r < 0.475$ ,  $n=17$ ,  $p > 0.054$ ) nor non-golf courses ( $-0.297 < r < 0.253$ ,  $n=30$ ,  $p > 0.111$ ) showed significant relationships between disturbance PCs and fitness metrics.

#### 5.3 Differences in Relationships Between Disturbance and Behavior PCs

On golf courses, Defense and Foraging showed a U-shaped relationship to Longer/More Variable Length ( $F_{2,14}=8.48$ ,  $p=0.004$ ) (Fig. 5.1).

<b>Fitness Metric</b>	<b>F<sub>1,48</sub></b>	<b>P</b>
Brood Growth	1.38	0.247
Brood Condition	1.99	0.165
Number of Fledglings	1.13	0.294
Brood Survival	0.390	0.535

Table 5.1: Results of multivariate analysis of variance comparing fitness metrics of chicks on and off golf course sites.



<b>Disturbance Characteristic PC</b>	<b>F<sub>1,46</sub></b>	<b>p</b>
Longer/More Variable Length	0.586	0.448
Frequent-Short-Predictable	0.678	0.415
Close	0.590	0.446
Variation in Proximity	0.069	0.794

Table 5.2: Results of multivariate analysis of variance comparing Disturbance Characteristic PCs on and off golf course sites.

<b>Adult Behavior PC</b>	<b>F<sub>1,50</sub></b>	<b>p</b>
Self-Maintenance and Perching	0.026	0.872
Box Visits	0.091	0.764
Reduced Calling	0.005	0.943
In the Box	0.593	0.445
Defense and Foraging	0.182	0.672

Table 5.3: Results of multivariate analysis of variance comparing adult behavior PCs on and off golf course sites.

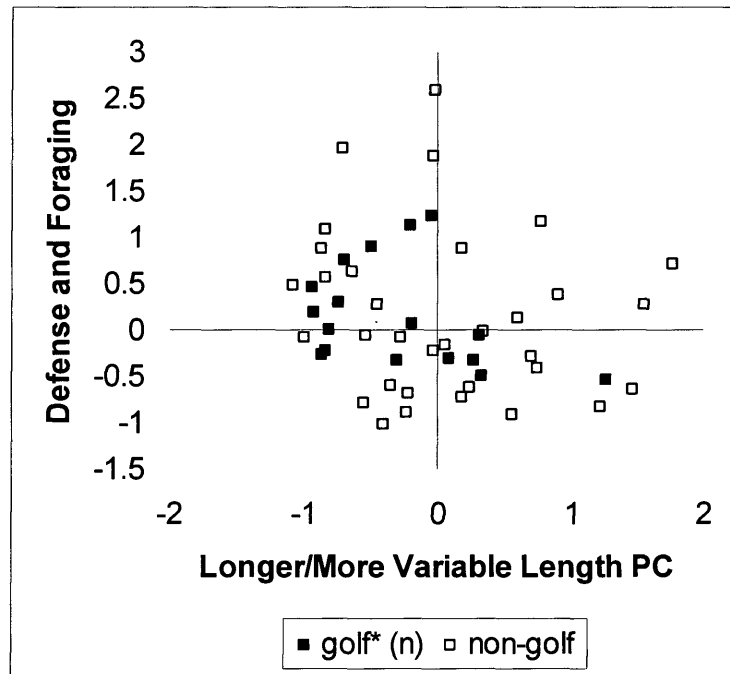


Fig. 5.1: Differences in the relationship between Longer/More Variable Length PC and Defense and Foraging PC at golf course and non-golf course sites (\* indicates significant correlation; l=linear and n=nonlinear).

Reduced Calling was related to a disturbance PC at both types of site. On golf courses, it was positively related to Close disturbance ( $r=0.492$ ,  $n=17$ ,  $p=0.045$ ) (Fig. 5.2), while off golf courses it was nonlinearly related to Variation in Proximity ( $F_{2,28}=8.59$ ,  $p=0.001$ ) (Fig. 5.3). Whereas high levels of disturbance on golf courses decrease vocalizations from bluebird parents, it is intermediate levels of disturbance that create the same response at non-golf course sites. This may indicate a habituation response to disturbance at non-golf course sites. Additionally, the differences in which disturbance PCs were related to calling behaviors may indicate that birds in different locations adapt to particular types of disturbance regime, such that the increasing proximity of disturbances is more threatening on golf courses, while the spatial variability is more threatening at non-golf course sites.

There were no other significant relationships between disturbance and behavior at golf course ( $-0.393 < r < 0.397$ ,  $n=17$ , all  $p > 0.117$ ) or non-golf course ( $-0.330 < r < 0.345$ ,  $n=31$ , all  $p > 0.057$ ) sites.

#### 5.4 Differences in Relationships Between Behavior PCs and Fitness Metrics.

Both golf course and non-golf course sites showed significant relationships to Defense and Foraging behaviors. Off golf courses, this PC showed a negative linear relationship to brood growth ( $r=-0.577$ ,  $n=19$ ,  $p=0.010$ ) (Fig. 5.4). Defense and Foraging on both types of sites was negatively nonlinearly related to number of fledglings ( $F_{2,16}=4.91$ ,  $p=0.022$ ;  $F_{2,28}=4.98$ ,  $p=0.014$ , respectively) (Fig. 5.5).

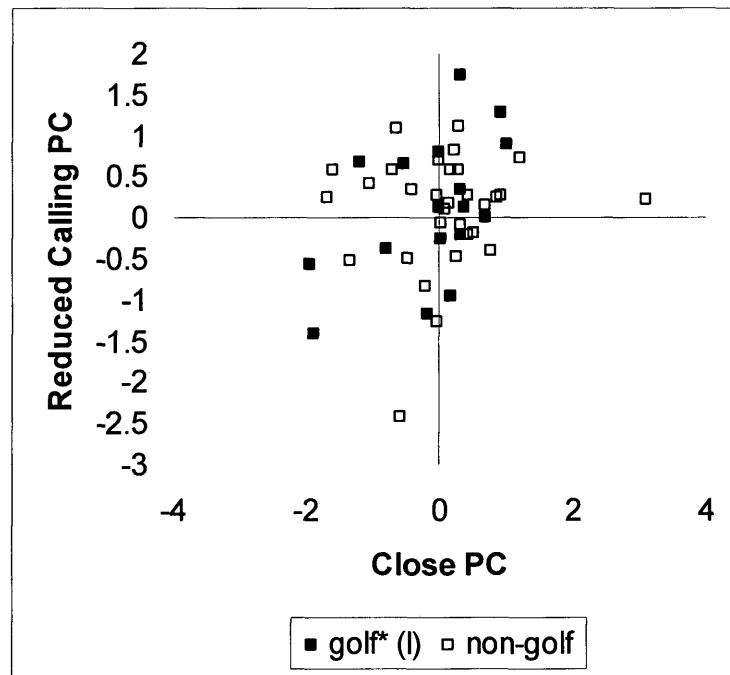


Fig. 5.2: Differences in the relationship between Close PC and Reduced Calling PC at golf course and non-golf course sites (\* indicates significant correlation; l=linear and n=nonlinear).

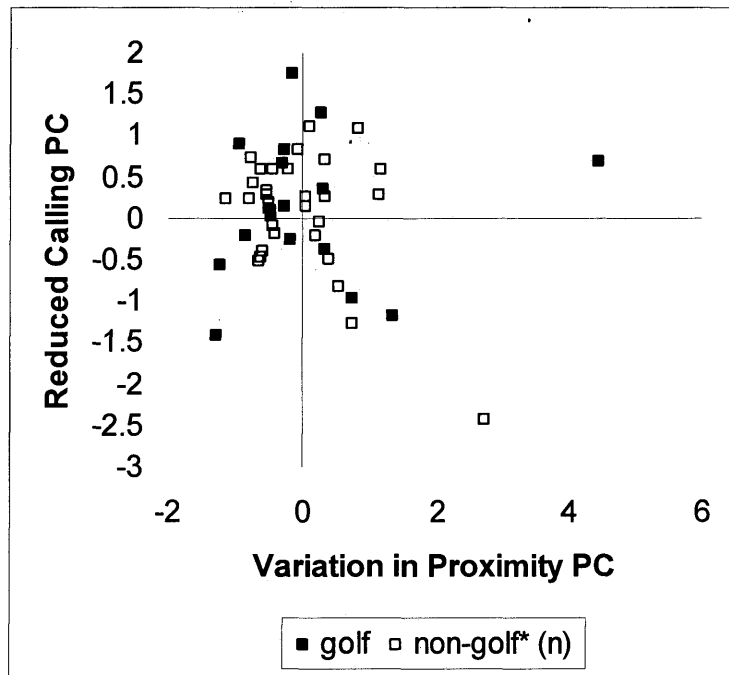


Fig. 5.3: Differences in the relationship between Variation in Proximity PC and Reduced Calling PC at golf course and non-golf course sites (\* indicates significant correlation; l=linear and n=nonlinear).

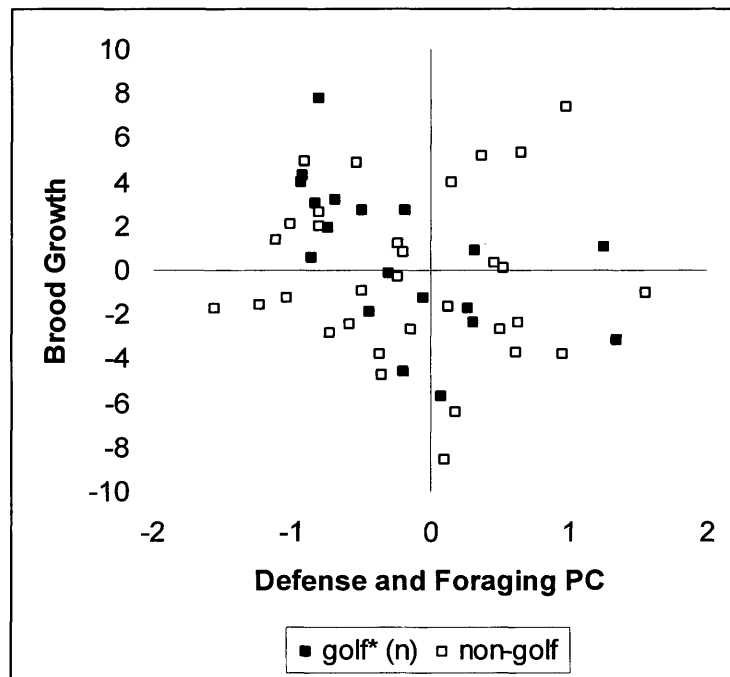


Fig. 5.4: Differences in the relationship between Defense and Foraging PC and brood growth at golf course and non-golf course sites (\* indicates significant correlation; l=linear and n=nonlinear).

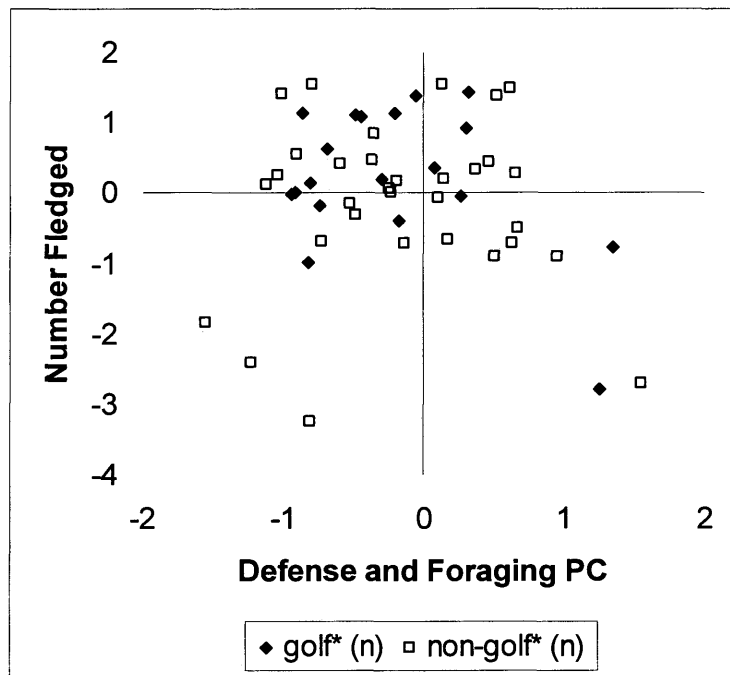


Fig. 5.5: Differences in relationships between Defense and Foraging PC and number fledged at golf course and non-golf course sites (\* indicates significant correlation; l=linear and n=nonlinear).



Non-golf course sites also showed a significant negative linear correlation between Defense and Foraging behaviors and condition ( $r=-0.420$ ,  $n=32$ ,  $p=0.017$ ) (Fig. 5.6). These relationships indicate that, regardless of disturbance regime or location, defensive behaviors are costly. They either require a sacrifice in time that cannot be made up for later with increased chick care, or they reduce the condition of parents such that they are simply not able to properly care for their young. An alternate possibility is that sites with enough natural threats to create a defensive response in parenting bluebirds reduce overall productivity.

At non-golf course sites, In the Box was negatively related to both number fledged ( $r=-0.390$ ,  $n=32$ ,  $p=0.027$ ) (Fig. 5.7) and survival ( $r=-0.410$ ,  $n=32$ ,  $p=0.020$ ) (Fig. 5.8). Although In the Box is a form of chick care, it does not encompass the hunting and feeding behaviors found in the Box Visits PC. The negative relationships seen here may indicate a time budget trade-off between more passive forms of chick care (e.g. sitting on the nest) and the more active forms required for feeding young. The fact that only non-golf course sites display these relationships perhaps suggests that prey items are more abundant, or nearer the nest boxes, on golf courses. This could allow golf course parents to more evenly engage in both forms of chick care behaviors. If this is true, it still remains to be seen whether prey items are higher quality on golf courses or merely can be located and/or caught more easily.

Self-Maintenance and Perching behavior was also negatively related to number fledged ( $r=-0.392$ ,  $n=32$ ,  $p=0.027$ ) at non-golf course sites (Fig. 5.9) and to survival at golf course sites ( $r=-0.505$ ,  $n=19$ ,  $p=0.027$ ) (Fig. 5.10). These

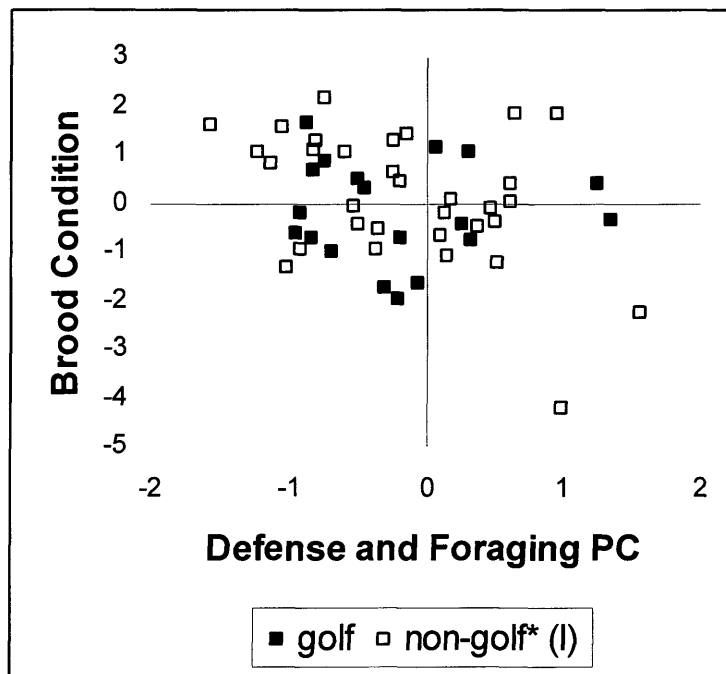


Fig. 5.6: Differences in the relationship between Defense and Foraging PC and brood condition at golf course and non-golf course sites (\* indicates significant correlation; l=linear and n=nonlinear).

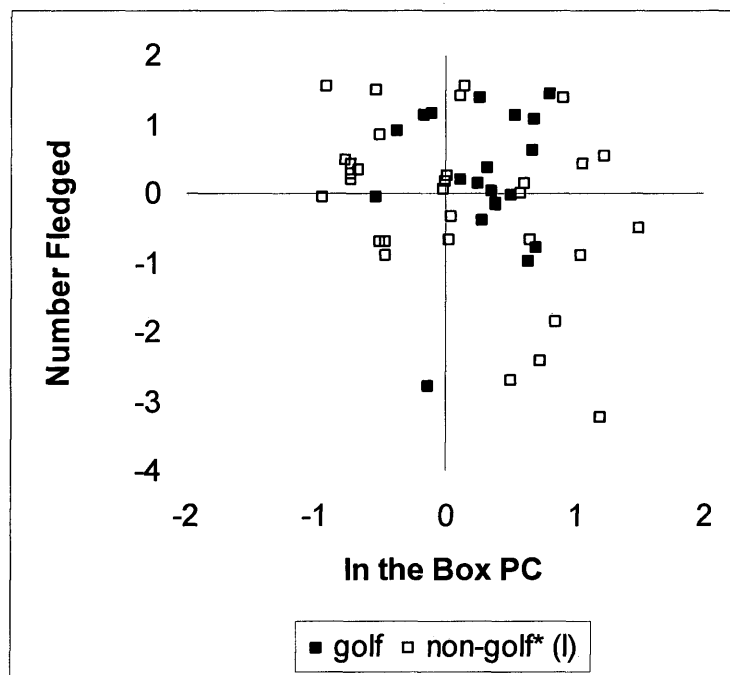


Fig. 5.7: Differences in the relationship between In the Box PC and number fledged at golf course and non-golf course sites (\* indicates significant correlation; l=linear and n=nonlinear).

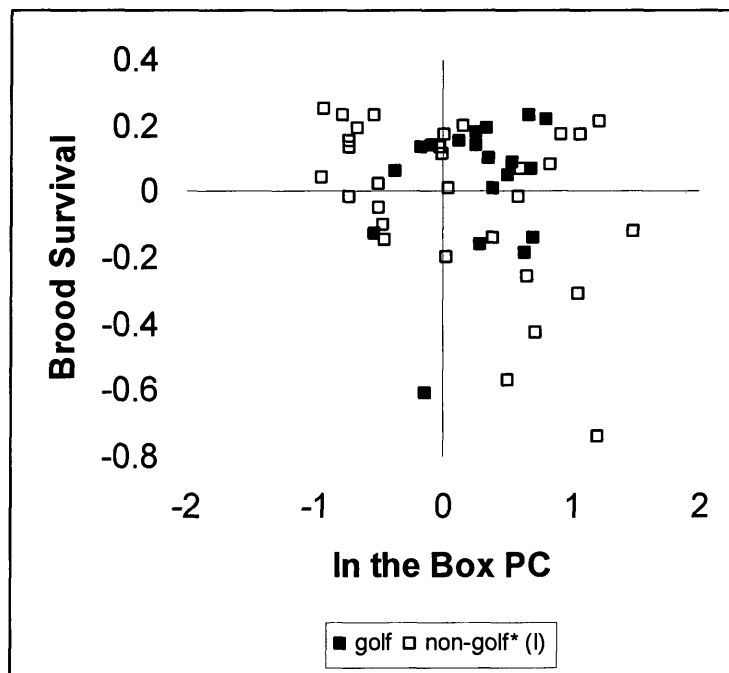


Fig. 5.8: Differences in the relationship between In the Box PC and brood survival at golf course and non-golf course sites (\* indicates significant correlation; l=linear and n=nonlinear).

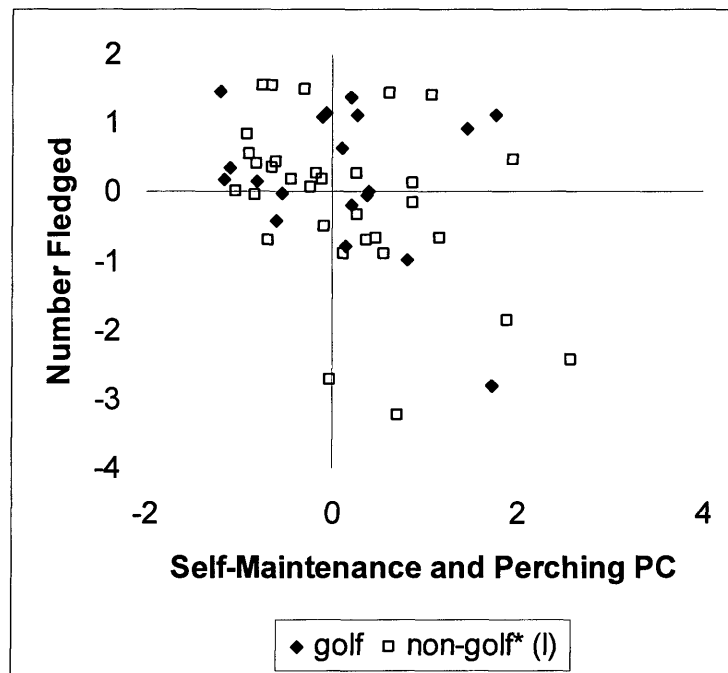


Fig. 5.9: Differences in the relationship between Self-Maintenance and Perching PC and number fledged at golf course and non-golf course sites (\* indicates significant correlation; l=linear and n=nonlinear).

relationships indicate that both golf and non-golf course parents experience significant trade-offs between adult health and fitness.

There were no other significant relationships between behavior PCs and chick fitness metrics on golf course ( $-0.401 < r < 0.441$ ,  $n=19$ ,  $p > 0.059$ ) or non-golf course ( $-0.299 < r < 0.243$ ,  $n=32$ ,  $p > 0.096$ ) sites.

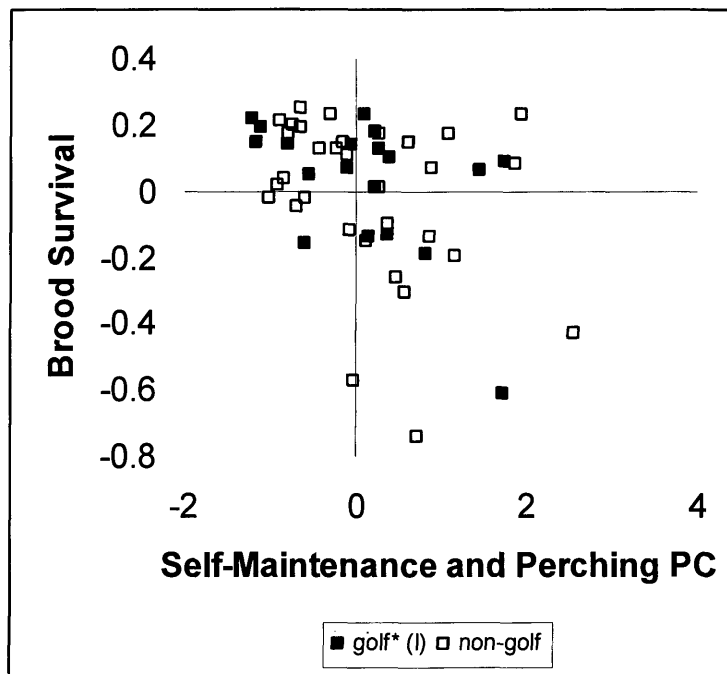


Fig. 5.10: Differences in the relationship between Self-Maintenance and Perching PC and brood survival at golf course and non-golf course sites (\* indicates significant correlation; l=linear and n=nonlinear).

## CHAPTER 6

### DISCUSSION

#### 6.1 What are the effects of disturbance on chick fitness metrics?

When correlating four chick fitness metrics against four Disturbance Characteristic and six Disturbance Source PCs, only two significant relationships were found—and neither of these was particularly strong. An increase in Frequent-Short-Predictable disturbance was correlated to an increased number of fledglings, and intermediate levels of Trail Vehicle disturbance were correlated to reduced brood growth rate. These relationships do indicate that environment has some effect on the fitness of bluebird chicks. However, the much stronger relationships between adult behavior and fitness indicate that the chicks may be more affected by contact with their parents than by direct interaction with the environment outside their nest box.

It is interesting that the Disturbance Source PCs only yielded one significant relationship to chick fitness. This suggests that bluebird young are more affected by disturbance in general, as opposed to particular sources of disturbance (e.g. golf cart, lawn mower, animal, etc.). On the other hand, we only measured four fitness parameters; there may be others that would yield more significant correlations with type of disturbance.



The lack of distinction between chicks born on and off golf courses is an interesting result that both supports and refutes previous work done on Eastern bluebirds (see Chapter 4). Clearly, more work will have to be done to resolve these discrepancies. In particular, future work should focus on delineating the effects of pesticide use on Eastern bluebird life histories. It is also important to extend studies over multiple years in order to account for variation in environmental and climatic conditions, which have previously been thought to influence breeding success (LeClerc et al. in press). This field in particular would benefit from expanding research to other species with different life histories, especially in terms of breeding and feeding habits. Results from such studies would elucidate whether bluebirds can be used as bioindicators on golf courses or whether these sites have diverse effects on different faunal species.

## 6.2 What are the effects of disturbance on adult time budgets?

Two important relationships emerged between disturbance and adult behavior. First, proximity is a key factor in determining whether, and how, adult bluebirds will react to disturbance. Variable proximity was significantly related to both Box Visits and Reduced Calling, while Close was significantly related to Box Visits. While adult bluebirds appear to habituate to disturbance at near but predictable proximity, they appear to decrease certain behaviors when disturbance is more variable. This is particularly interesting since variability is not a metric frequently used to gauge the effects of human disturbance on wildlife behaviors.

Second, disturbance is related to an increase in adult bluebird vocalizations and box visits, as well as the successful production of young that are fairly sheltered from outside disturbance. In general (though not significantly correlated to particular disturbance factors), adults sacrificed self-maintenance behaviors by reducing time spent resting, preening, and hunting, rather than sacrificing behaviors that are more directly related to chick maintenance and parental care.

When these analyses were conducted for golf courses and non-golf courses separately, we found that parent bluebirds in both locations altered vocalization behaviors in response to disturbance. On golf courses, proximity of disturbance was significantly related to this behavior, while off golf courses, vocalizations were affected by variability. Although golf course bluebird parents sacrificed self-care behaviors in response to disturbance (Longer/More Variable Length), no similar trade-offs occurred among non-golf course bluebirds.

These differences reflect years spent living and breeding in different disturbance regimes. The site fidelity of recaptured birds in our study certainly suggests that bluebird parents are returning to their natal territories to breed—or may never leave after fledging (Swaddle and Kight unpublished data). Thanks to the placement of bluebird trails, bluebirds have been breeding on golf courses for generations—enough time for self-sacrificing behaviors to have been selected for in these locations. The disparity in selective forces on and off courses would also explain why golf course and non-golf course birds alter their vocal behaviors in response to different types of disturbance.

Both the all-sites and golf vs. non-golf analyses yielded nonlinear relationships. The U-shaped and inverse U-shaped trend lines are reminiscent of Connell's (1978) intermediate disturbance hypothesis, which states that species diversity is higher at intermediate levels of disturbance due to the relaxation of competition. Although many studies have examined diversity and abundance in relation to intermediate levels of disturbance (Garstecki and Wickham 2003; Ikeda 2003; Lenz et al. 2004; Li et al. 2004; Magura et al. 2004; Rejmanek et al. 2004; Shea et al 2004; Anderson et al. 2005), we could not find any that investigate whether intermediate disturbance levels impact the behavior or fitness of wildlife.

It has been suggested that bird communities could withstand intermediate levels of human disturbance such as golfers (Tanner and Gange 2005). We found that, adult bluebirds are most vocal at intermediate levels of variation in proximity and visit the nest box least at intermediate levels of Non-GC Road Traffic. In addition, intermediate levels of Trail Vehicle and Frequent-Short-Predictable disturbances were associated with elevated brood growth rate and number of fledglings, respectively. Additionally, intermediate levels of adults' Defense and Foraging behaviors corresponded with the most fledglings and the highest brood survival. Clearly, an intermediate "disturbance" hypothesis, whether it focuses on the interactions between adults and disturbance or adults and their young, should be further investigated in the context of bird behavior.

### 6.3 Evolutionary Implications

Terman (1997) wrote that some evidence exists indicating that many birds can coexist with human recreational activity, particularly in areas where adequate habitat is provided and human interference is scheduled around sensitive times in the birds' life histories. However true this may be, evidence—in this paper and elsewhere—also suggests that coexistence may come with a price, whether it be increased mortality of young (see Chapter 1) or suboptimal changes in life histories. The increasing rates of human modifications to the natural environment may ultimately force us into contact, and therefore conflict, with wildlife, regardless of our good intentions towards protecting them from our activities.

Our study provides evidence that human-bluebird interactions have altered bluebird behaviors. The delicate balance between adult body condition and chick-rearing capabilities have been well-studied (Guinn and Batt 1985; Blums et al. 1997; Thomas et al. 2001; Tveraa and Christensen 2002; Castro et al. 2003; Markman et al. 2004; Pearse et al. 2004). Our research goes one step further by illustrating how adults can behaviorally adapt to some forms of disturbance, however unpredictable and intense it may be, seemingly to buffer their chicks and maintain their breeding success.

By sacrificing self-maintenance, adults are likely suffering costs of disturbance while shielding their young. These tradeoffs could accumulate over multiple breeding seasons and detract from future breeding attempts, by forcing adults to take time off from future breeding, producing lower-quality clutches later in life, or even by decreasing life expectancy. Cumulative effects of disturbance have

been studied in terms of avian richness and abundance (Riffell et al. 1996) but not in terms of behavior or reproductive success. Although it may be difficult to do against the background of normal breeding stress, future studies should attempt to gauge the change in condition throughout the breeding season of parent birds across a disturbance regime. It is also important to study breeding patterns over the long-term and to quantify fitness consequences over multiple breeding seasons. Over the long term, tradeoffs such as those documented in this study have the potential to alter population dynamics and reduce viability.

Living in disturbed habitat may select for certain behaviors, such as the inclination to reduce self-maintenance, that allow or even predispose individuals to inhabit or breed in specific regimes across the disturbance gradient. Another behavior that may be affected by disturbance is mate selection. One characteristic bluebirds may use to choose mates is blue feather coloration (Siefferman and Hill 2003). Juvenile birds produce their adult feathers while living at their natal territory, and adult birds molt at the end of the breeding season, at the natal territory of their young. If coloration is affected by stress or lack of nutrients, then birds growing “substandard” feathers while living in disturbed locations may be selected against in the following breeding season. This could be tested by conducting spectrophometric analyses on feathers sampled across the disturbance gradient, and by capturing mated and unmated adults to assess whether particular hues, chromas, and/or intensities affect likelihood of breeding.

The impact of both behavioral and sexual selection may be compounded by site fidelity, which could lead to separate bluebird populations with life histories that

differ in disturbance tolerance levels, breeding behaviors, and mate preferences. As mentioned earlier, this sort of fidelity may be responsible for the differences we report between the time budgets of golf course and non-golf course parents. In the future, it will be interesting to follow banded individuals in order to map the distances particular birds travel between their natal territories and breeding grounds.

Such studies will be aided by geographic information system software (GIS), which will allow us to calculate the distances between potential bluebird territories so that we may eventually understand bluebird metapopulation dynamics and therefore begin to model population movements and habitat use on a larger scale. During most of our time budget observations, parent bluebirds flew out of territory at least once, some traveling as far as a quarter mile away from the nest box. Our current study does not account for the potential effects of disturbance on bluebird adults during these forays outside the 50-m radius around the box. However, GIS landscape analysis will be useful in elucidating where the adults go, how they use the habitat, and whether they come into contact with human disturbances while in these locations. Understanding the effects of disturbance on this larger, landscape level, may clarify how large a buffer breeding bluebirds may need in order to preserve their “natural” time budgets and, potentially, the health of their young.

The discrepancy between chick fitness metrics in bluebirds and chickadees suggests that not all species are equally capable of coping with the kinds of environmental stress measured here (see section 6.4). Management plans must be tailored for organisms demonstrating *all* levels of sensitivity to human disturbance. In the future it will therefore be important to monitor multiple study organisms living

at the same disturbance level and to quantify how different regimes impact the behaviors and reproductive success of different individuals, species, or guilds.

#### 6.4 Conservation and Management Implications

Nest box trails have had undeniable success in reestablishing Eastern bluebird populations across North America (Gowaty and Plissner 1998; nabluebirdsociety.com 2005). Boxes have been placed across a variety of habitats with the goal of preserving bluebird population numbers, rather than preserving individual bluebirds' conditions or behaviors. Enough studies—including the one presented here—now question the logic of nest box placement that it is time to rethink our methods. Keeping in mind the effects of both the Disturbance Source and Disturbance Characteristic PCs in this study, it would be wise to reevaluate the structure of bluebird trails and, potentially, the placement of other species' (e.g. wrens, wood ducks) nest boxes: In order to minimize the impacts of human disturbance, boxes should be moved away from areas where disturbance is closest and most variable.

Our study also makes three important conceptual contributions to the field of behavioral ecology. First, we have shown that variation, rather than mean level, of disturbance alters bluebird time budgets and chick fitness. However, most current research measures only number, length, and proximity of disturbance. Variability will be important to measure in future research looking to elucidate the role and impact of human disturbance on life histories.

Second, we found that Eastern bluebirds and Carolina chickadees respond differently to the same disturbance regimes. This illustrates how individual life histories of study organisms must be taken into consideration when designing studies. Bluebirds may naturally attempt three clutches per season (Gowaty and Plissner 1998), whereas chickadees usually attempt only one (Mostrom et al. 2002). We also documented a higher predation rate for chickadees than for Eastern bluebirds (Swaddle and Kight, unpublished data). Such differences highlight the need to select a variety of organisms within an area of interest in order to more fully understand how human modifications to a natural environment can affect behavior and reproductive success (Furness 1993).

Third, and perhaps most importantly, the effects of disturbance on adult bluebird behaviors indicates that simply measuring brood health and productivity will not necessarily indicate environmental consequences on the larger population. For future research, we need integrated study designs incorporating metrics of disturbance, behavior, and reproduction, over the course of multiple breeding seasons. This type of study design will paint a much larger and more accurate picture, which in turn will allow managers to assess and develop plans for different environments and species across a range of human modified habitats.



APPENDIX I:

TABLE OF LOADING FACTORS FOR DISTURBANCE SOURCE PCA

	Component					
	1	2	3	4	5	6
vpother*	-.301	.295	4.228E-02	.413	.205	6.901E-02
mpother	-.359	.256	-.046	.724	.383	.104
cpother	-.349	.244	-.054	.722	.380	.104
mtother	-.286	.172	-.037	.706	.408	7.985E-02
ttother	-.353	.259	-.001	.723	.412	8.565E-02
vpbike	.484	.390	.211	-.050	4.883E-02	.203
mpbike	.575	.162	.558	.107	-.057	.177
cpbike	.550	.123	.555	.119	-.066	.174
vtbike	.556	.526	.106	-.062	-.009	.261
vpanim	3.129E-02	-.245	-.041	-.186	.444	-5.337E-02
mpanim	.128	-.144	-.182	-.331	.666	.111
cpanim	.131	-.037	-.178	-.263	.509	.155
vtanim	.122	-.260	-.013	-.055	.618	-.113
mtanim	.150	-.132	-.148	-.165	.751	-.113
ttanim	.153	-.175	-.137	-.176	.801	-.128
vpgc	-.585	.440	.202	8.948E-02	8.382E-02	.118
mpgc	-.711	.368	.178	-.036	-.060	.373
cpgc	-.661	.267	.135	-.022	-.062	.458
vtgc	-.684	.366	.130	-.088	-.055	.364
mtgc	-.704	.361	.128	-.053	-.057	.393
ttgc	-.710	.362	.155	-.069	-.064	.386
vpcar	.554	2.784E-02	.379	.206	.186	3.680E-02
mpcar	.614	-.061	.450	.343	-.078	-.117
cpcar	.539	-.048	.380	.301	-.137	-.123
ttped	.198	.570	-.502	.210	-.149	-.352
mtped	.123	.540	-.491	.234	-.115	-.389
vtped	.239	.613	-.410	1.007E-02	-.066	-9.028E-02
cpped	.137	.391	-.432	.302	-.218	-.458
mpped	.170	.489	-.481	.299	-.195	-.406

vpped	.168	.588	-.389	3.863E-02	-.018	2.719E-02
ttpeda	.509	.527	-.322	-.264	.177	.228
mtpeda	.505	.523	-.294	-.260	.163	.208
vtpeda	.386	.419	-.240	-7.002E-02	-5.783E-02	.330
cppeda	.489	.550	-.302	-.249	.139	.154
mppeda	.509	.569	-.307	-.243	.128	.180
vppeda	.397	.426	-.228	-6.539E-02	-5.875E-02	.338
ttcar	.645	-4.574E-02	.442	.303	-1.234E-02	-5.534E-02
mtcar	.668	-7.779E-02	.376	.258	9.899E-02	-3.759E-02
vtcar	.551	-9.063E-02	.311	.168	.207	2.270E-02
ttom	-.364	.540	.488	-.294	.146	-.380
mtom	-.352	.536	.505	-.288	.125	-.391
vtom	-.361	.482	.368	-.208	7.556E-02	-.391
ctom	-.236	.505	.503	-.247	.164	-.385
mpom	-.262	.556	.506	-.246	.163	-.406
vpom	-.209	.550	.267	-.153	8.751E-02	-.314
ttbike	.637	.368	.426	2.634E-02	-4.689E-02	.185
mtbike	.654	.353	.435	3.215E-02	-3.536E-02	.225

\*"Vtother" could not be used in this analysis because all values were null.

<b>KEY:</b>
TT=total time disturbed
MT=mean time disturbed
VT=variability in time disturbed
CP=closest proximity
MP=mean proximity
VP=variability in proximity
Other=projectiles
Bike=bicycles
Anim=animal (wild or domestic)
GC=golf cart
Car=automobile (including motorcycles, buses, trucks, etc.
Ped=pedestrians (without pets; includes runners and walkers alike)
Peda=pedestrians with animals (includes runners and walkers alike)
Om=other motorized disturbance

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