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MALE REPRODUCTIVE STRATEGIES AND MATING DISPLAYS IN THE OCELLATED
TURKEY (*MELEAGRIS OCELLATA*)

Master of Science

Department of Biology

Edward M. Hanlon

August 2013

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ABSTRACT

Animal mating systems are often characterized by intense competition for mates and resources. Despite how common this conflict is, mating systems exist in which some adult males of breeding age seem to not participate. These apathetic males may be exhibiting alternative reproductive strategies, or simply delaying maturation to conserve resources for future breeding attempts. In populations of the poorly studied, near-threatened Ocellated Turkey (*Meleagris ocellata*), males have been reported to be either “breeding” or “non-breeding,” apparently irrespective of age, although empirical data are scarce. This thesis has three main objectives for establishing a better understanding of the Ocellated Turkey’s mating system. The first objective is to create an ethogram of Ocellated Turkey mating behavior to facilitate comparisons between studies and with its well-studied congener, the Wild Turkey (*Meleagris gallopavo*). The second goal is to use behavioral data, along with measures of individual condition, to investigate the existence of dichotomous male strategies and correlates of female preference for males. The final aim is to investigate the effects of inadvertent human disturbance on the mating system of the Ocellated Turkey, in addition to the fitness of wildlife in general. In the present study, I create the first formal ethogram of Ocellated Turkey action patterns, using behavioral data from turkeys in Orange Walk District, Belize. Behavioral data were used, along with measures of sexual ornamentation and parasite load, to investigate the veracity of multiple male reproductive strategies existing, and also to uncover which behaviors and morphological characteristics of males are attractive to females in this species. I report that, despite a small sample size, there is

support for alternative reproductive tactics in the Ocellated Turkey. In addition, human disturbance seems to fundamentally alter the turkey's mating structure. A meta-analysis of recent studies addressing how inadvertent human disturbance affects wildlife is also included here, which suggests a negative impact of disturbance on the fitness of individual wildlife.

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TABLE OF CONTENTS

Title Page	pg. i
Abstract	pg. ii
Acknowledgements	pg. iv
List of Tables	pg. vi
List of Figures	pg. viii
Chapter I: An Ethogram of Reproductive Behaviors in the Ocellated Turkey	pg. 1
Chapter II: Male Reproductive Strategies and Mating Displays in the Ocellated Turkey	pg. 33
Chapter III: Behavioral Responses to Inadvertent Human Disturbance	pg. 69
References	pg. 97
Appendix I	pg. 110
Vita	pg. 115

LIST OF TABLES

Chapter 1

Table 1. Research Locations	pg. 7
Table 2. Male Call Rates	pg. 10
Table 3. Strut Durations	pg. 18
Table 4. Parallel Striking Durations and Outcomes	pg. 24
Table 5. Behavioral Matrix of Kinematic Diagram	pg. 29

Chapter 2

Table 1. Dietary Composition	pg. 40
Table 2. Wild and Ocellated Turkey Behavioral Comparison	pg. 42
Table 3. Field Work Dates and Locations	pg. 48
Table 4. Year and Location of Turkey Captures	pg. 48
Table 5. Fecal Parasites and Male Class	pg. 53
Table 6. Blood Parasites and Male Class	pg. 54
Table 7. Feather Ornamentation and Male Class	pg. 55

Table 8. Head Ornamentation and Male Class	pg. 58
Table 9. Alpha Male Behavioral Distinctions	pg. 60
Table 10. Male Display and Female Visitation	pg. 62
Table 11. Feather Ornamentation and Parasite Load	pg. 62
Table 12. Fecal Parasites and Female Visits	pg. 63
Table 13. Relationship of Female Visitation to Male Call Rate and Fecal Parasite Load	pg. 63
Chapter 3	
Table 1. Study Selection Criteria Example	pg. 82
Table 2. Important Variables	pg. 84
Table 3. Studies Included in Meta-Analysis	pg. 86
Table 4. Results from Random Effects Models	pg. 87
Table 5. Akaike Information Criterion Scores of Best Models	pg. 90

LIST OF FIGURES

Chapter 1

Figure 1. Flattening Behavior	pg. 11
Figure 2. Half Boxy Behavior	pg. 12
Figure 3. Full Boxy Behavior	pg. 14
Figure 4. Expo Behavior	pg. 15
Figure 5. Wag Behavior	pg. 16
Figure 6. Strut Behavior	pg. 18
Figure 7. Kinematic Diagram of Courtship Behaviors	pg. 28
Figure 8. Typical Progression of Courtship Behaviors	pg. 30

Chapter 2

Figure 1. Ocellated Turkey Head Ornamentation	pg. 49
Figure 2. Principal Components Analysis of Feather Ornamentation	pg. 56
Figure 3. Principal Components Analysis of Head Ornamentation	pg. 59
Figure 4. Call Rate and Female Visitation	pg. 61

Chapter 3

Figure 1. Fitness Performance Effect Size

pg. 88

Figure 2. Average Effect Size in Relation to Diet

pg. 89

I. AN ETHOGRAM OF REPRODUCTIVE BEHAVIORS IN THE
OCELLATED TURKEY

Introduction

Animals behave to maximize individual fitness. These behaviors vary in type and quantity depending on environmental and life history traits (Hamilton 1964). Thus, description and classification of behaviors are fundamental in studying how animals react to their environment (MacNulty et al. 2007). Individual action pattern descriptions (the fundamental components of behavior (Barlow 1977)) comprise an ethogram. Action patterns in an ethogram exhibit four general similarities: they are objective, separate, usually exhibit only slight variations in execution, and include sampling on numerous occasions from multiple individuals. Complex suites of behavior, however, may be too fluid for segregation in this manner (Bond et al. 1985). To better reflect how individuals interact with their environment, action pattern sequences can be amalgamated into broader behavioral progressions (kinematic diagrams).

This chapter has three main objectives. The first objective is to create an ethogram of Ocellated Turkey courtship and mating action pattern descriptions. Behaviors are described and quantified, with sequential suites of action depicted as a kinematic diagram. My second objective is to contrast some notable reproductive behaviors of the two species in the genus *Meleagris*, the tropical *M. ocellata*, and the temperate *M. gallopavo*. By contrasting the mating behaviors of these two similar species inhabiting very different environments, it may be possible to identify how selective pressures differ between them. Third, I present preliminary data on how human disturbance may alter male Ocellated Turkey mating behavior.

Ethogram value

The ethogram is at the foundation of the study of animal behavior because behaviors must be described before they can be analyzed (Mather et al. 2010). Ethograms are useful for studying

animal behavior in four ways (Tinbergen 1963). The first way is in exploring the mechanisms through which behavior occurs. Second, the adaptive nature of specific behaviors can be investigated using ethograms. Next, behavioral descriptions can help identify evolutionary patterns through comparisons of populations and species. Lastly, responses to environmental change can be documented.

Mechanisms of behavior

The first of the four ways that ethograms are useful is in identifying the mechanisms through which behavior occurs. After describing common action patterns, it is possible to investigate the physiological environment associated with observed behaviors. For example, Golden-Collared Manakin (*Manacus vitellinus*) males perform acrobatic mating displays, generating characteristic noises thought to attract females during the mating season. Descriptions of these action patterns allowed Day et al. (2006) to study how male display is regulated. They found that experimentally augmenting male testosterone levels significantly increased display frequency. Another example of ethogram practicality comes from the Ring-tailed Lemur (*Lemur catta*), a social mammal exhibiting female dominance. Action patterns of lemur social interactions enabled the discovery that males are socially subordinate. This realization led to an investigation of the proximate causes for this uncommon mammalian hierarchy. Drea (2007) found that circulating androgens are positively correlated with aggression and social dominance in both sexes, but females exhibit relatively high levels compared to other species. While facilitating the discovery of mechanisms that underlie behavior, ethograms also reveal why certain action patterns may be adaptive.

Behaviors as adaptive

Ethogram construction permits exploration into the adaptive nature of behaviors. For example, some species defend territories perennially. In the Pied Babbler (*Turdoides bicolor*), comparisons of defense behavior throughout the year revealed that individuals are more aggressive when breeding. This realization led to the discovery that reduced food availability makes vigorous defense of a territory prohibitively costly outside of the reproductive season (Golabek et al. 2012). The adaptive significance of different territory-guarding intensities was revealed through comparisons of action pattern descriptions at different points of the year. Another example is found in the social behavior of Geoffroy's Tamarins (*Saguinus geoffroyi*). This species is cooperatively polyandrous, with multiple adult males mating with a single female and raising her offspring. Ethograms of these behaviors are puzzling because males usually compete for mating opportunities and limit parental care (Orians 1969). Diaz-Munoz (2011) investigated this abnormal system by coupling behavioral and genetic data, which revealed that cooperative male groups were closely related. The indirect fitness benefits gained by the polyandrous males offer an explanation of why this behavior is adaptive. Describing behavior can also provide insight into why broader evolutionary patterns exist in nature.

Ethograms and evolutionary patterns

Ethograms allow quantifiable contrasts of behavior between species (Norris & Hosie 2005). Contrasting behavior between species or populations is valuable for at least two reasons. First, it helps to identify evolutionary patterns across taxa that have resulted in the diversity of life on Earth. One way to uncover these patterns is by identifying when behavior may be influencing a divergence of populations into separate species. For example, two tropical populations of

Rufous-collared Sparrows (*Zonotrichia capensis*) exhibit asynchronous breeding behavior due to local weather differences, despite being separated by only 25 kilometers (Moore et al. 2005). A comparison of reproductive behaviors found that males from opposite populations differed in their mating calls, which may partially explain how females choose locally-adapted mates. Over time, these differences in behavior could result in speciation. A second reason for contrasting behavior among species is to better understand what is adaptive in specific environments for similar species. For example, across avian species tropical breeders suffer higher nest failure rates than temperate breeders (Remes et al. 2012). Contrasting the reproductive behaviors of closely-related temperate and tropical species may reveal how populations have evolved in response to local patterns of juvenile mortality. For example, warblers from the genus *Sylvia* inhabit both tropical and temperate regions of the Old World. Tropical species have smaller clutches and exhibit longer incubation and post-fledgling parental care behaviors when compared to their temperate congeners (Schaefer et al. 2004). Because tropical species have higher nest failure rates, these behaviors probably help to improve offspring survival by increasing parental investment in each egg. Without ethograms cataloging parental care patterns, it would not be possible to contrast behaviors and identify environmental sources of this behavioral dichotomy. Through comprising behavioral sequences, it is also possible to identify how species may respond to changing environmental conditions (Greenberg 2003).

Ethograms and environmental change

If behaviors are first understood within their original evolutionary context, it is possible to identify when they may become maladaptive. Humans are rapidly altering Earth's environments (Sekercioglu et al. 2011; Trevors & Saier 2009). Ethograms help reveal how animals react to their environments, and as humans alter the earth, previously adaptive behaviors may actually

reduce survival and reproduction (Buchholz & Hanlon 2012). Well-defined action patterns help identify the stimuli that precede them, and can benefit management officials attempting to reduce maladaptive behaviors in response to human disturbance. For example, wildlife can react to predators and humans similarly, even when animal harvest is not our intent (Frid & Dill 2002). Anti-predator behaviors are adaptive (Blumstein 2006), but overstimulation through repeated human disturbance can reduce time engaged in other important behaviors (e.g. feeding or mating) (Frid & Dill 2002). An example of this phenomenon is seen in the King Penguin (*Aptenodytes patagonicus*), which increases vigilance behaviors in response to helicopter overflights (Hughes et al. 2008). Elk (*Cervus elaphus*) also alter behavior in response to human disturbance (i.e. ATVs and mountain biking), travelling greater distances per day and foraging less often when exposed (Naylor et al. 2009). Ecotourism creates opportunities to interact with nature, but more information is needed to understand how we may inadvertently have negative effects on wildlife. My three study locations (see methods) are valuable ecotourist destinations, so quantifying human behaviors that may impact turkey fitness is valuable for conservation. In the Ocellated Turkey, reducing harmful behaviors is especially important because of the vulnerability of populations. For a number of years, the Ocellated Turkey has been listed as near threatened (BirdLife International 2010, Species factsheet: *Meleagris ocellata*). Once found from the Petén region of Guatemala, to central and northern Belize, and throughout Mexico's Yucatán peninsula extending west into Chiapas and Tabasco (Steadman et al. 1979), habitat loss and overhunting have drastically reduced populations. The Ocellated Turkey has now been extirpated from northern Yucatán, western Campeche, eastern Tabasco and north-eastern Chiapas, Mexico (BirdLife International 2010). Constructing an ethogram of Ocellated Turkey action patterns will facilitate further research into the mechanisms, adaptive nature, evolutionary origins, and

plasticity of turkey behaviors, hopefully leading to improved conservation and knowledge of the species.

Methods

I observed behaviors during research at La Milpa (N 17 50.487 W 89 01.106) and Hill Bank (N 17 36.047 W 88 42.065) field stations in the Rio Bravo Conservation and Management Area (Orange Walk District, Belize), and the adjacent Gallon Jug Estate (N 17 33.634 W 89 02.801). Data collection took place over two field seasons (Table 1). Behavioral observations were

Research Locations

Year	La Milpa	Hill Bank	Gallon Jug
2011	March 6-20 May 3-June 13 July 3-15	March 21-May 2	June 14-July 2
2012	April 1-8	N/A	April 9- June 15

Table 1. Location and dates of field research over two years in Orange Walk District, Belize.

conducted using Eagle Optics Ranger 10x50 Binoculars (Eagle Optics, Middleton, WI) and a Bushnell Model 78-1700 Spotting Scope (Bushnell Corporation, Overland Park, KS). Behaviors were recorded at all hours of daylight, with most observation occurring in the morning (05:00:00 to 10:00:00) and evening (14:00:00 to 19:00:00) when the birds were most active. Ocellated Turkeys were often located in clearings near the forest. Sampling took place from cover behind the forests’ tree line, or from a distance that did not elicit vigilance behaviors, which depended on the individual bird (c. 20 meters to c. 75 meters). Focal animal sampling was used to assess

variation in behavior, until relatively stereotyped behaviors were identified. Action pattern descriptions were generated from field notes, which included precise times, durations, frequencies, and rates of behaviors coupled with illustrations. Many behaviors were witnessed a countless number of times, and sample sizes refer to the observation number after which novel, notable variations were no longer detected. For the following behaviors, N denotes the number of individuals observed prior to ethogram construction, while n refers to the total number of times the behavior was witnessed until cessation of novel variations.

Data concerning the effects of human disturbance on mating behavior were also collected. Recorded disturbances included events in which vehicles passing could affect male Ocellated Turkeys who were displaying in the road. The following data were recorded: vehicle size (1-5, 1= motor bike, 5= loaded 18-wheeler), vehicle speed, distance to cover, and duration until resumption of normal (previous) male behavior.

Results

N-Normal Posture-For brevity, a bird or particular body part may be referenced as exhibiting normal posture in the descriptions below. Normal posture is defined as the standing bird having the head anterior to the body, with the neck at an angle of 45° to 90° from parallel. The mantle and back are parallel to the ground, with the tail anywhere from a 45° angle, to parallel with the earth. Wings are folded and held against the flank, as the breast creates a 45° angle with the ground, while the belly and ventral surface are nearly parallel to it.

Male mate signaling behavior

The following behaviors were exhibited by males during the breeding season (March-July), and are assumed to signal females of their willingness to mate.

C-Call (“Gobble” Steadman et al. 1979) -A male adopts an erect posture with head pointed forward so that the beak makes a 90° angle with the anterior side of the neck. The neck is straightened, resulting in a 90° angle with the male’s dorsal surface. The body begins in Normal Posture, with the dorsal and ventral sides of the male nearly parallel to the ground. Wings are folded and held against the body, with the tarsi at a near 45° angle with the ground. The breast feathers are erected seconds before the entire body begins vibrating. Next, a high pitched chirping whistle is emitted at a rapidly increasing rate. As the rate increases over a period of approximately two seconds, the chirping is augmented into a rattling-honk that maintains the same rapid pace. As soon as the final rattling-honk is emitted, the male rapidly pulls its head back into its body so that the neck makes an “S” shape, with the posterior part of the head touching the mantle. The head is kept in this position for about 1.5 seconds before returning to a normal, relaxed position. Steadman et al. (1979 pg. 19) roughly translated the call as “whump-whump-whump-pum-pum-pum-peedle-glunk.”

Calling differs slightly when performed from a tree. A male stands in an erect posture with head pointed skyward and neck straight, so that its entire dorsal surface creates a 45° angle with the ground below. The wings are folded and held against the body, and the tarsi make a 45° angle with the ground. The breast feathers are erected seconds before the entire body begins to vibrate. Next, a high pitched chirping whistle is emitted at a rapid and increasing rate. As the rate increases over a period of approximately two seconds, the chirping switches to a rattling-honk that adopts the same rapid pace. As soon as the final rattling-honk is let out, the male rapidly pulls its head back into his body, so that the neck makes an “S” shape, with the posterior part of the head touching the mantle. The head is held in this position for around 1.5 seconds before returning to a normal, relaxed posture. **Occurrence:** Calling from a tree occurs only at dawn or

dusk. With sufficient light, a male was always witnessed Calling from the ground. Ethogram Call data: N= 14, n= 100. Average Call rates of 13 males are listed in Table 2.

D- Two-Note-Drum (“Drum Tones” Williams et al. 2010 pg. 66) – In between Calls, territorial males may emit two deep drum tones totaling one second in duration, roughly translated as “duh-dum.” This drum tone closely resembles the notes that immediately precede Calling behavior.

Male Call Rates

Male Identification	Average Call Rate (per minute)	SE (+ or -)
Tomas	1.289	0.148
Bajo	1.205	0.11
Lagun	1.281	0.167
Charlie	1.755	0.162
Gov	1.240	<u>0.225</u>
V	0.960	0.068
Phoenix	1.403	<u>0.105</u>
Killer	1.195	<u>0.066</u>
The J	1.375	<u>0.093</u>
Twin Spot	1.328	<u>0.001</u>
M. Domesticus	1.798	<u>0.146</u>
BWBOC	1.255	<u>0.028</u>
ChuckD	1.240	0.131

Table 2. Average Call rates for 13 male Ocellated Turkeys in Orange Walk District, Belize. Underlined standard errors were calculated from Calling performed on a single day (observation time ranging from 20 to 60 minutes), using the standard deviation from the first and second half of the total observation period. All other standard errors were calculated using the standard deviation of Call rates averaged from multiple days of sampling.

The males’ body posture matches that seen in the first few seconds of Calling behavior, with the only major difference seen in tail posture. While the first note is released, the males’ tail briefly raises a few centimeters before dropping down to its original position (usually a 45° angle with the ground) with the ending of the second note. **Occurrence:** The Two-Note-Drum was

witnessed only in territorial males, in between Calls during territorial patrol. Ethogram Two-Note-Drum data: N= 3, n= 50. Average rate of Two-Note-Drum tone= 0.81/minute (N= 2, n= 64).

F- Flattening (“Crouching” Williams et al. 2010 pg. 27) - Male crouches down, so that his ventral surface contacts the ground. The wings are folded against the body, or kept a few centimeters away from the flank. The head may be retracted, making an “S” shape, with the caudal side of the skull nearly making contact with the mantle; alternatively, the head can also be positioned anteriorly, farther away from the body than the normal angular range (45° to 90 degrees) in relation to the ground, or lowered nearly to the earth. The back feathers are raised slightly, while the uppertail coverts lie flat. The tail is folded with the tip near, or touching, the ground. Typically, the crown and snood are enlarged. **Occurrence:** This behavior is performed in close proximity to a female, and is almost always exhibited before and after Calling, Half Boxy, and Full Boxy behaviors (Figure 1) (Figure 7). Ethogram Flattening data: N= 5, n= 17. Average Flattening duration: 1:07.3 min.

Flattening Behavior



Figure 1. Male Ocellated Turkey in “Flattening” posture.

HB- Half Boxy- Male stands erect or leans slightly forward, with its neck extended in the normal range (45° to 90° angle with the ground, and head pointed anteriorly). The wings are folded and held against, or nearly against the body. The breast feathers are partially erected, so that the anterior half of the bird's ventral surface bulges, as if swollen. The dorsal surface remains flat and parallel to the ground, while the tail is in a normal position, close to a 25° angle with the ground. **Occurrence:** Half Boxy is almost always adopted during Calling bouts. Additionally, it is often the preferred body position when an alpha male is patrolling its territory, especially in the morning and evening. When in the presence of a female, Half Boxy almost always precedes Full Boxy and Expo (see below) behaviors (Figure 2) (Figure 7). Ethogram Half Boxy data: $N= 3$, $n= 20$.

Half Boxy Behavior



Figure 2. Adult male Ocellated Turkey exhibiting Half Boxy behavior

FB- Full Boxy (“Hunched” Williams et al. 2010 pg. 27)- Male stands erect or slightly crouches, with its ventral surface ranging from half a meter above, to nearly touching the ground. Breast

feathers are partially or fully erected, with the center-most feathers forming an inverted “V” shape (when viewed from the front) with an apex around 15 cm below the neck line when maximally erect. The inverted “V” reflects little light, and contrasts sharply against adjacent, iridescent breast feathers. Wings are folded, or slightly extended ventrally and held against, or nearly against the flank. Feathers of the mantle, back, and uppertail are also erected, giving the turkey a rotund appearance. The uppertail coverts form an arch near the tail, which may extend higher than the head, depending on neck and body positioning. Caudal to the uppertail covert mound, the tail feathers are folded and positioned downward, making a 45° angle with the ground (Figure 3a), or slightly outspread and nearly parallel to the ground (Figure 3b). The head can be positioned in two general ways: normally, with an outstretched neck making a 90° to 45° angle with the ground (Figure 3b), or retracted, with the neck forming an “S” shape, and the caudal end of the skull nearly making contact with the mantle (Figure 3a). Crown and snood are typically enlarged. **Occurrence:** This behavior is exhibited during Calling sessions in the morning or evening, or when in the presence of a female, when it is usually followed by Flattening and Calling behavior, which may herald Strutting. This body position is sometimes adopted immediately prior to intrasexual conflict. Ethogram Full Boxy data: N= 4, n= 25. Average percentage of time spend in Full Boxy while in the presence of a female was 57% (N= 4, n= 7)

EX- Expo- A male slightly crouches, with his ventral surface nearly touching the ground. Breast feathers are partially or fully erected, with the center-most feathers forming an inverted “V” shape with an apex around 15 cm below the neck line when fully erect. The inverted “V” is non-reflective, and its black color contrasts sharply against adjacent, iridescent breast feathers. Wings are folded and held against, or nearly against the flank. Feathers of the mantle, back, and

Full Boxy Behavior



Figure 3a (left) and 3b (right). Male Ocellated Turkeys displaying variations in Full Boxy body posture.

uppertail coverts are also erected, giving the turkey a rotund appearance. The uppertail coverts form a mound near the tail, which may extend higher than the head, depending on neck positioning. Caudal to the uppertail covert mound, the tail feathers are folded and positioned downward, making a 45° angle with the ground. The head is retracted, resulting in the neck making an “S” shape, and the caudal end of the skull pointing skywards. The beak points towards the ground, so that the extended snood hangs perpendicular to the earth. The crown and snood are enlarged. **Occurrence:** This behavior is exhibited when in close proximity to a female (Figure 4), and is usually preceded and followed by Flattening and Calling behaviors (Figure 7). For all witnessed Expo behaviors, the male’s head was oriented towards a female. Ethogram Expo data: N= 2, n= 8.

W- Wag (“Tail Wagging” Williams et al. 2010 pg. 28) – A male slightly crouches, with ventral surface about 25cm above the ground, and tarsi forming nearly a 45° angle with the earth. The

wings are held close to the body and extended ventrally with the first couple primaries barely touching the ground. Each wing is alternately vibrated, rapidly, against the body, resulting in a

Expo Behavior



Figure 4. Male displaying Expo behavior.

loud flapping noise. As each wing is alternately flapped, the foot on the corresponding side is tapped on the ground in rhythm. The head is pointed down, with the beak almost perpendicular to the ground and the neck slightly recoiled. Tail feathers are fanned out, making anywhere from a 45° to 130° angle with the back. The tail is then oscillated from side to side, in rhythm, like a metronome with a rate close to 1.5 times per second. Occasionally, the tail is lowered parallel to the ground and oscillated more slowly, before again being raised to its previous position after a few seconds, where the faster rate is then resumed. The crown and snood are extended, and the breast feathers are typically erected, sometimes to the extent that the inverted “V” shape is formed. More caudally located back feathers and uppertail coverts are also erected, forming an arch just anterior to the tail. **Occurrence:** This behavior (Figure 5) most often precedes a

Strutting performance when in the presence of females, with no standard orientation position in relation to individual hens. Less frequently, a Wag is executed near a female but no Strut follows. This behavior is sometimes exhibited immediately prior to intrasexual conflict.

Ethogram Wag data: N= 5, n= 10.

S- Strut- A male extends its snood and enlarges his crown, before fanning out its tail perpendicular to the dorsal surface of his body. The wings are held close to the flank and extended ventrally, with the first few primaries touching the ground. The feathers of the breast are erected so that light does not reflect off a large portion of the center, resulting in a large, dark

Wag Behavior



Figure 5. Male Ocellated Turkey performing Wag behavior.

equilateral triangle whose apex is around 15 cm below the neck line. The head is pulled back into the body, with the posterior part of the skull resting against the mantle and the neck in an “S”

shape, so that the apex of the triangle is nearly parallel with the head. The back feathers and uppertail coverts are also erected, with the iridescent coloration generating a contrasting background for the blue head and neck. The male then walks towards an adjacent female, or among a group of females, focusing its attention on one or two at a time. The wing facing away from the female of interest is slapped vigorously against the body, making a loud flapping noise. The male approaches females while presenting his lateral side, with the bright, extended wing nearest the female contrasting with the dark chest-triangle. In this position, the tail is turned in order to present the dorsal side containing ocelli to the female. As the male switches his presented side, the opposite wing then begins flapping, and the tail is pivoted so that its dorsal side remains visible. Periodically, a male will Call while Strutting. **Occurrence:** Strutting (Figure 6) (Table 3) occurs in the presence of females, and is directed at them. On one occasion, a male directed strutting at a Black Vulture (*Coragyps atratus*) and on another, at a human (*Homo sapiens*) female. In one rare instance, a territorial male began Strutting at two males entering his territory. The intruding males were driven away, and the strut lasted 03:07.0 minutes. Ethogram Strut data: N= 7, n= 9. Average Strut duration was 05:34.2 minutes (N=7, n=9).

E- Extending (“Tiptoe” Williams et al. 2010 pg. 29) - A male may temporarily interrupt a Strutting display by extending his body skyward and in the direction of a female when in close proximity. The male stands raised up on its toes, with the neck outstretched over the female, making a 160° angle with his dorsal surface. The head and neck are angled in the direction of the female, so that the majority of the male’s weight is supported by the foot nearest the female. The

Strut Behavior



Figure 6. Three photos of male Ocellated Turkeys exhibiting Strutting behavior.

Strut Durations

Male Identification	Strut Duration (minutes)
Charlie	09:42.4
Gov	00:21.0
Killer	05:34.0
Killer	06:08.0
Lagunita	03:03.0
Tomas	07:37.0
Tomas	04:07.0
V	08:02.0
Yalbecα	05:34.0

Table 3. Observed Strut durations for seven male Ocellated Turkeys.

wings are extended ventrally, and make a near 30° angle with the male's lateral surface. If occurring in the middle of a Strut (as is typical), the tail is usually fanned out in the manner

described for Strutting behavior, with the dorsal side angled towards the female, or dropped slightly nearer the ground. The entire sequence is completed in under two seconds. **Occurrence:** On all but one occasion, this behavior was exhibited by a Strutting male. The lone aberration was a juvenile male that performed the behavior on a female as an alpha male was Strutting about a meter away. Ethogram Extending data: N= 3, n= 4. Average frequency of Extending behavior (when witnessed at least once) was 3.75 per Strut (N= 3, n= 4).

T- Pointing- A males' head is retracted, with the back of the skull nearly touching the mantle, and the beak pointed skyward at a 45° angle with the ground. The back and belly are nearly parallel with the ground, with the feathers of the breast (as in Half Boxy posture) and back (not enough to create uppertail-covert mound) erected. The tail is pointed downward at a 45° angle with the ground, and the wings are folded against the flank. **Occurrence:** This behavior was exhibited by males when in close proximity to females. Almost always, a non-territorial, adult male was observed Pointing near a female. On two occasions late in the breeding season (July), territorial males Pointed in the presence of a female. Ethogram Pointing data: N= 6, n= 7.

In Figure 7 (Table 5) (Figure 8), a kinematic diagram of male display behavior reveals common behavioral progressions when in the presence of a female. In the chapter titled “Male Attractiveness and Display Behavior in the Ocellated Turkey,” specific differences in display behaviors between males (e.g. Calling rates when in the presence of a female) are investigated in greater depth.

Pre-copulatory behavior

P- Presenting- A female drops to the ground, with her ventral surface resting against the earth. The tail and wings are folded in, with the head and neck in a typical resting posture, around 110°

from her dorsal surface (about 45° angle with the ground). **Occurrence:** This behavior is very similar to simply resting on the ground, except that it immediately follows a male Strutting, and precedes Mounting and Copulation behaviors (see below). Ethogram Presenting data: N= 1, n= 1.

M- Mounting- A male exhibits this behavior immediately before Copulation. With the female in Presenting position, the male approaches from behind and steps onto her back. The male has his snood extended, tail feathers fanned out perpendicular to his dorsal side, and wings extended ventrally with the first primaries touching the female. The male is leaning slightly forward, with his neck partially stretched out anteriorly, and head pointed so that a 45° angle is made with the ventral side of the neck. The male shifts its weight from leg to leg while in this position, appearing as if he is attempting to maintain balance. The female may support her body by pressing the alulae against the ground, seemingly to brace against the weight of the male.

Occurrence: Precedes Copulation. Ethogram Mounting data: N= 1, n= 1.

CP- Copulation- While atop a female, the male crouches down until his belly nearly touches her back. The male has his wings extended at 45° angles to his lateral side, with the first primaries barely touching the ground. Leaning forward, the male's head is pointed so that a 45° angle is made with the ventral side of the neck, with its neck partially stretched out in the female's anterior direction. The toes of the male grip the anterior end of the female's scapulars, with the tarsi creating 90° angles with the feet. The female supports her body by pressing her alulae against the ground. The female's head and neck point forward, making a 180° angle with her back, and hovering about two centimeters above the ground. Both birds move their tails to opposite sides of their body (relative to one another), so that the male can position his cloaca

against the females. After about three seconds, the male dismounts towards the female's anterior end. Ethogram Copulation data: N= 1, n= 1.

Male intrasexual mating behavior

EN- Encircling- This behavior was always exhibited by two males, with one appearing socially dominant over the other. The dominant male adopts a Half Boxy posture, and slowly walks in a tight circle around the socially-subordinate male. The dominant male will periodically stop, turn, and continue the circular walk in the opposite direction. While being Encircled, the subordinate male stands erect, with his chest and belly nearing a 60° angle with the ground. His legs are also straight, with the tail slightly dorso-ventrally raised at an angle near 20° with the ground. The subordinate male exhibits vigilance-like behavior, with his head and neck quickly retracted and outstretched over alternating sides of his body, or aggressively preens. The vigilance-like behavior of the subordinate male may also be accompanied by an “alarm cluck,” which is also emitted when in the presence of a perceived predator (Williams et al. 2010 pg. 73). The subordinate male may also flap both wings twice in quick succession while being Encircled by the dominant male. Throughout the duration of Encircling behavior, a subordinate male may execute two or three rapid hops in sequence, typically travelling about 2 meters in the opposite direction of the dominant male. After this movement, the dominant male will walk over to the subordinate male and begin Encircling him again. **Occurrence:** Encircling behavior was always observed between males, but involved multiple classifications. For example, territorial males would Encircle non-territorial, adult males. These non-territorial, adult males were also witnessed Encircling juvenile males. Territorial males were never observed Encircling juvenile males. This behavior was witnessed more often during the late stages of the breeding season (July). Ethogram Encircling behavior: N= 4, n= 7.

G- Ground Flick- A male lowers his head with neck outstretched, contacting the ground with its beak, and then rapidly turns the head laterally to one side or the other, as if sifting through leaf litter while foraging. During this time, the wings are held against the body, and the ventral surface of the bird is parallel to the earth to facilitate the beak reaching the ground. Tail can generate anywhere from a 45° to 20° angle with the ground. **Occurrence:** This behavior is most often seen immediately preceding a fight, during a fight, or after a fight has taken place in which both males are still visible to one another. Ethogram Ground Flick data: N= 9, n= 25.

L- Lateral Walk- Two males walk with their sides facing each other. Their wings are folded and held slightly away from the body, so that an angle of about 20° is made with their lateral side. Their heads are held upright (beak facing forward), with the neck making around a 100° angle with the mantle. Each bird points its beak straight ahead, periodically tilting its head to change the roll angle and view the other male's lower body. The breast feathers are partially erected, and the tail is slightly fanned out and parallel to the flank, but slightly raised at a near 160° angle relative to the back. The ventral surface of each male makes a 45° angle with the ground. The males walk about a meter in one direction, separated by less than that distance, and then turn to face the other direction while adopting the same posture with the opposite lateral sides facing each other. The walk and turn is repeated multiple times. Typically, the turn may be preceded by Ground Flicking behavior by one or both individuals. **Occurrence:** This behavior typically precedes fighting between two males. Ethogram Lateral Walk data: N= 7, n= 20.

X-Spur Extension- A male drops his tail so that it makes a 45° angle with the ground, while concurrently raising his ventral surface, resulting in the breast having an angle slightly greater than 45° with the ground. Simultaneously, the male bends his legs to balance the shift in weight. Next, a forceful extension of the legs, coupled with a shift in body weight away from the

intended target propels the tarsi sideways with the head and neck almost becoming parallel to the ground. Often, the extension of the legs is coupled with a vigorous flap of both wings, generating extra lift, which results in the tarsi extending forwards a meter or more off the ground, and the bird nearing inversion of its body before landing. **Occurrence:** Spur Extensions were only witnessed between males, typically during a fight. On three occasions, males directed this behavior at a non-territorial (n= 2) or juvenile male (n= 1). Ethogram Spur Extension data: N= 6, n= 20.

PX- Parallel Striking (“Fighting” Williams et al. 2010 pg. 41) - Two males stand with their sides facing each other about a meter apart, and wings held slightly away from the body at an angle of about 20°. Wings are folded, or slightly extended towards the ground, partially covering the flank and upper tarsus. Body posture is erect, with the ventral side of each bird making an angle slightly larger than 45° with the ground. The head and neck are positioned upright (neck nearly straight and beak facing forward), close to a 90° angle with the ground. While still facing the same direction, each male shifts weight from one side to another while shuffling its feet to maintain balance. During this time, the head and neck remain relatively stationary as the body vacillates. Periodically, males will turn 180°, almost simultaneously, and resume the same relative posture with opposite sides facing each other. Males will alternately feign a Spur Extension, but complete the action only if the intended recipient fails to guard against it. When a Spur Extension is executed, it is performed in the manner described above (X-Spur Extension). Most Spur Extensions do not make contact, and the Parallel Striking behavioral sequence typically continues afterwards. **Occurrence:** Parallel Striking was most often observed between territorial males guarding adjacent territories. Later in the breeding season (mid-July), yearling males were observed Parallel Striking with each other, or with adult, non-territorial males.

Although Parallel Striking behavior was fairly stereotyped, the behaviors that preceded and followed it were not. Directly before Parallel Striking commenced, males were observed alternatively Calling in close proximity, Wagging, or sprinting directly at an opposing male. Following a Parallel Striking event, multiple behaviors were also witnessed (Table 4). Occasionally, one male would successfully spur the other. The injured male would then run or fly away, often while being chased by the other male. On other occasions, Parallel Striking behaviors would abruptly stop, or slowly lose intensity until cessation, sometimes without an obvious victor. Ethogram Parallel Striking data: N= 7, n= 8.

Parallel Striking Durations and Outcomes

Males Involved	Outcome	Duration
Bajo and Tomas	Bajo flies away while being chased	0:04:18
Lagunita and Tomas	Slow de-escalation until Tomas walks away	1:26:23
Sly and Vulture	Slow de-escalation until Vulture walks away	0:10:00
Sly and Vulture	Abrupt stop as Vulture walks away	0:01:20
Lagunita and Tomas	Abrupt stop as Lagunita quickly walks away	0:00:33
Yearling and NT male	Slow de-escalation until one male walks away	2:08:00
Yearling and NT male	Slow de-escalation until one male walks away	0:10:18

Table 4. Observed durations and outcomes of seven Parallel Striking bouts. All named males are territorial, NT stands for non-territorial, adult male.

Human disturbance of mating behavior

Open areas are rare in the forest, but required by males for most display behaviors. Because of the local habitat, roads are the primary display areas for some populations and vehicular

disturbance may reduce male display rates. In my preliminary study, vehicle size ranged from 2-5 (1= motor bike, 5= loaded 18-wheeler), and velocity from 3.02 m/s to 17.37 m/s, with an average velocity of 6.85 m/s. The average distance to vegetative cover for disturbed turkeys was 11.93 meters. Overall, males took an average of 58.6 seconds to resume normal behavior, but individual samples were highly variable (SD= 45.8 sec). Individual male averages for resuming normal behavior were also variable (1:32.6 min; 0:35.0 min; 0:27.3 min). Despite the small sample size (n= 7), vehicle speed and volume had similar effects on behavior, with large vehicles and faster speeds preceding longer durations of disturbed male behavior (Large= 01:31.8 min, Small= 0:45.3 min; Fast= 01:11.5 min, Slow= 0:48.9 min). Response based on distance to cover did not follow reasonable assumptions, as turkeys farther from cover had shorter affected periods (0:29.1 min; 1:37.2 min).

Discussion

The male reproductive behaviors of the Ocellated Turkey seem characteristic of a resource-defense, polygynous mating system. Males guard territories, presumably with the most dominant males occupying territories with the best access to females. This pattern was also reported by previous authors (Williams et al. 2010 pg. 24; Steadman et al. 1979). This Ocellated Turkey ethogram facilitates investigation into three areas relevant to my research. First, these elaborate male action patterns seem energetically costly, and, therefore, should be adaptive and increase mating opportunities. Second, behavioral comparisons with the temperate Wild Turkey may reveal how local selective pressures have resulted in the divergence of male mating behaviors. Lastly, if reproductive display behaviors are energetically costly and adaptive, human disturbance, like other forms of disturbance, could have harmful effects on turkey populations.

Adaptive nature of Ocellated Turkey behavior

The observed action pattern descriptions may be adaptive for three reasons. First, with one exception (adult male with no territory), only territorial males were observed displaying to or mating with females. Mating success alone is evidence of the adaptiveness of male display behaviors. Second, elaborate male display behaviors often attract females (Loyau et al. 2005). Because male movement is limited by guarding territories, conspicuous displays may serve to attract females and prolong their presence in a males' territory. Longer, more vigorous courtship displays are associated with higher male mating success in other species (Alonso et al. 2010). This pattern may exist because these action patterns reveal information females use to choose a mate. For example, male calling may advertise morphological characteristics that females prefer in a mate. Lower-pitched mating vocalizations are often preferred by females across species (Felton et al. 2006), and in some bird populations, larger males are able to call at a lower pitch (Hall et al. 2013). Male Ocellated Turkey calls may broadcast information about individual size, which could indicate an ability to find food and avoid infection. A third reason that these observed behaviors may be adaptive is intrasexual signaling. While serving to attract females, displays might also inform other males. For example, mating vocalizations can signify social dominance, with lower-pitched calls coming from larger, more dominant males (Vannoni & McElligott 2008). A males' call frequency and rate may inform rivals of his condition. In my observations, Calling often preceded intrasexual conflict (e.g., Parallel Striking). In addition to attracting females, male display vigor could also indicate social dominance. Indeed, display behaviors (i.e. Wagging, Strutting, Full Boxy) were observed between males prior to territorial challenges. If more elaborate and vigorous display behaviors attract females and deter rival males, they are most likely costly to an individual. Contrasting the costly display behaviors of

the temperate Wild Turkey may reveal how environmental differences have influenced adaptiveness, resulting in the divergence of these two species.

Meleagris ocellata and Meleagris gallopavo

Ocellated Turkey courtship differed from Wild Turkey courtship in multiple ways. For example, Ocellated Turkeys were observed Wagging their tails before exhibiting Strutting behavior, slapping the wing opposite a female against their body while Strutting, and Flattening in the presence of females. Steadman et al. (1979 pg. 34) also reported these behaviors, while noting that they did not occur in Wild Turkeys. Additionally, I observed male Ocellated Turkeys guarding territories rather than females, the opposite of male Wild Turkey behavior, which has also been reported by Williams et al. (2010 pg. 31). These differences in male behavior between the two species result broadly from reproductive isolation, and specifically from environmental disparities.

Ocellated and Wild Turkeys are geographically and reproductively isolated from each other. Because the two species are not interbreeding, mutation alone could be responsible for some observed differences in behavior. In addition, the polygynous mating systems of both species could facilitate the spread of these novel mutations. Resource-defense polygyny provides an opportunity for rapid change in heritable male display behaviors because few males obtain a large percentage of total matings (Wade 1995). Although Ocellated and Wild Turkeys are superficially similar morphologically, the speed at which evolutionary change occurs in their mating systems may help explain how courtship behaviors have diverged since isolation. Environmental differences between the two geographically-isolated species should also change

Kinematic Diagram of Courtship Behaviors

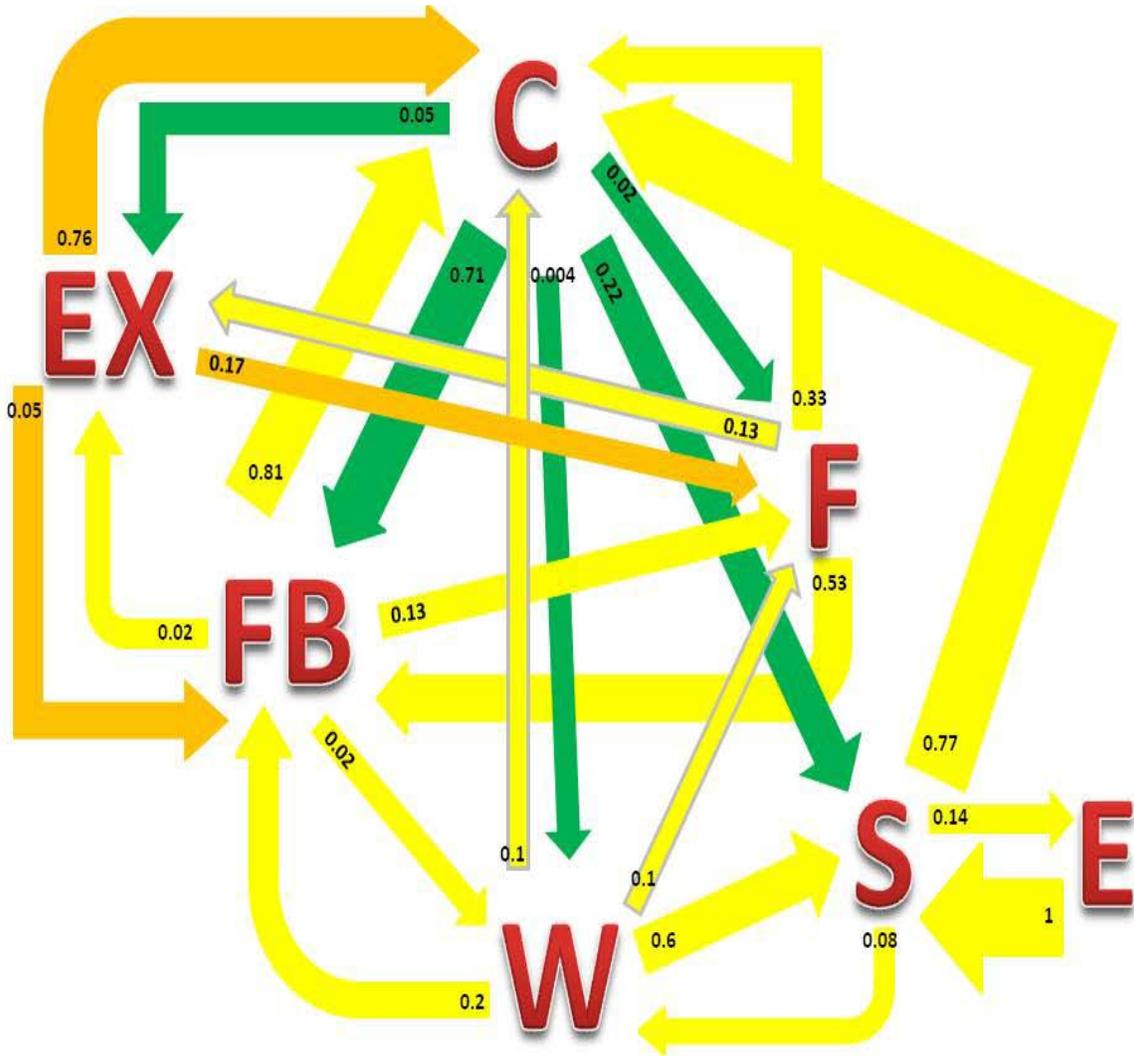


Figure 7. Kinematic diagram of territorial male behavioral progressions in the presence (within 20 meters) of females. Behavioral matrix with sample sizes is listed in Table 5. Action patterns and abbreviations are listed in Results section above. Numbers represent probabilities of specific behavioral transitions, with arrow size depicting magnitude. Only one mating event was observed, which followed strutting behavior. Different arrow shades were used only to help individual differentiation. Behavioral transitions are based on observations of four males from March 13th to April 29th 2011. Although combined transition probabilities total 1 for each behavior, only two digits were included after decimals for display purposes.

Behavioral Matrix of Kinematic Diagram

	Call	Full Boxy	Flattening	Wag	Expo	Strut	Extending	TOTAL
Call	0	156	4	1	12	48	0	221
Full Boxy	149	0	24	4	5	0	0	182
Flattening	10	16	0	0	4	0	0	30
Wag	1	2	1	0	0	6	0	10
Expo	13	1	3	0	0	0	0	17
Strut	48	0	0	5	0	0	9	62
Extending	0	0	0	0	0	9	0	9
TOTAL	221	175	32	10	21	63	9	

Table 5. Behavioral matrix used to construct kinematic diagram (Figure 7). The leftmost column designates the action pattern preceding the behavior listed in the top row, with numbers indicating n for that specific behavioral transition. The rightmost column reports total occurrences of behavior for each row.

the selective pressures experienced by each, resulting in different behavioral adaptations.

Many environmental differences between species may cause behavioral divergence. Different predators, parasites, food availability, climates, or habitat types could result in dissimilar adaptations of behavior. In the Ocellated and Wild Turkey, for example, habitat may contribute to differences in display behaviors. In tropical habitats with dense vegetation, loud, frequent calling may better attract females (Yorzinski & Anoop 2013). The thick undergrowth of the Belizean forest may explain why territorial males call almost non-stop in the early mornings and late evenings. Vegetation density may also elucidate why males guard territories. The display behavior with the greatest energetic investment (Strutting) requires an area without extensive ground vegetation (Williams et al. 2010 pg. 28-29). Because open areas are rare in the forest, guarding them (rather than females) may increase mating opportunities as females congregate in these areas to assess potential mates. Male Ocellated Turkeys invest

considerable time and energy into courtship, and this may increase vulnerability to human disturbance during the mating season.

Typical Progression of Courtship Behaviors

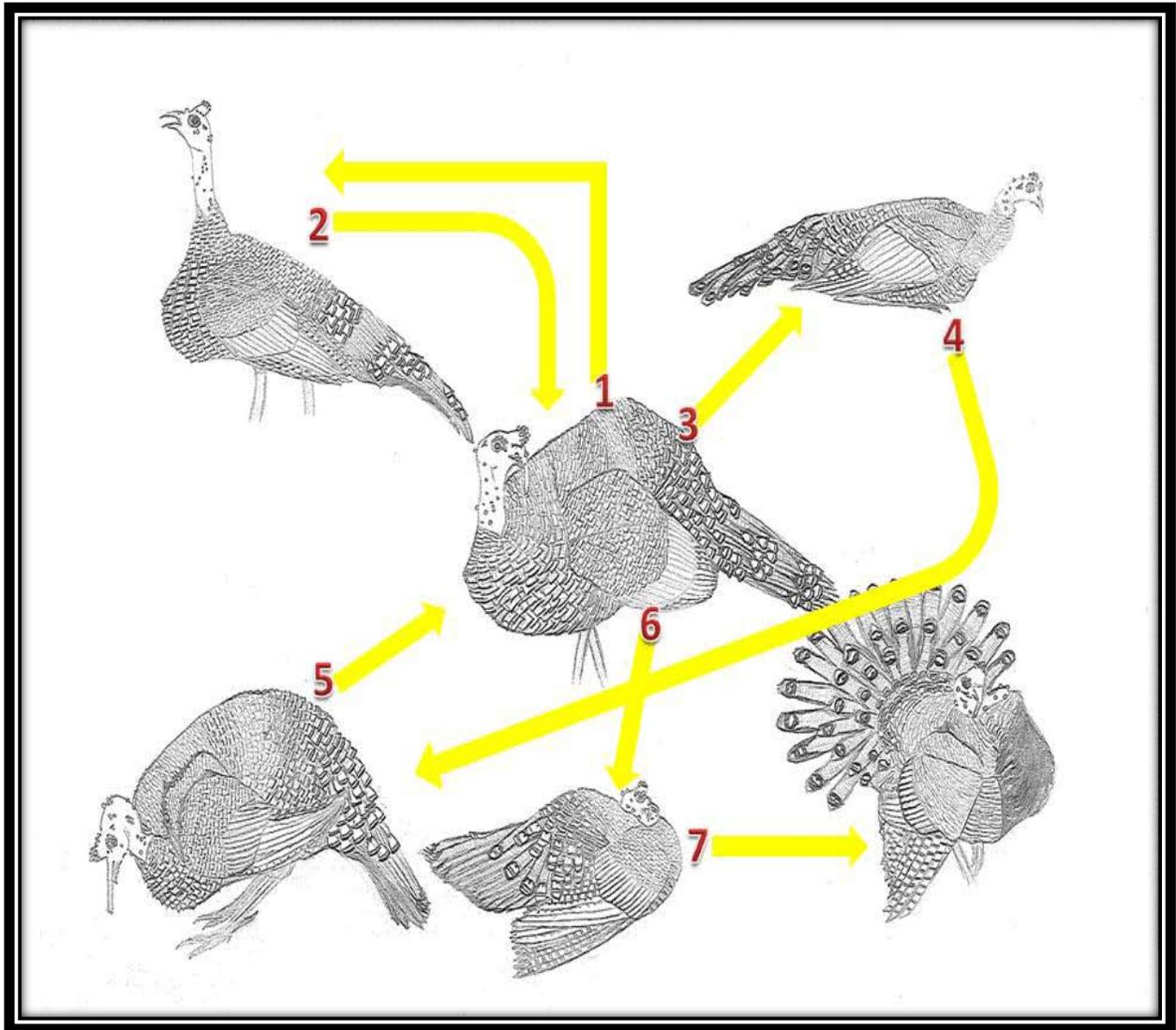


Figure 8. A typical progression of male display behaviors when in the presence of females. Clockwise from top left: Call, Flattening, Strut, Wag, Expo, with Full Boxy in the center.

Human disturbance and mating behavior

As previously mentioned, on multiple occasions I witnessed male Ocellated Turkeys displaying to human females. While this maladaptive change in normal mating behavior may not be harmful at low rates, if tourism increases, males may waste substantial energy displaying to humans in vain. The energetic costs of displaying to humans frequently might also reduce the quantity (and quality) of displays to females, reducing female's capacity to detect the best potential mates. Human disturbance that interrupts courtship may have the same effect. If male display behaviors are disrupted chronically, females may not be able to gather sufficient information on males before temporal constraints force mate selection. The behavioral disturbance data reported here are limited in explanatory power (due to small sample size). However, this information is an important initial step in the identification of non-antagonistic human behaviors that may reduce fitness in Ocellated Turkeys, and other species in Rio Bravo and Gallon Jug. If ecotourist visitation increases, ensuring the continued survival of tourist-attracting species is essential to sustainability. In the chapter titled: "Behavioral Responses to Inadvertent Human Disturbance," this topic is explored in greater depth.

Conclusion

In order to understand how animals react to their environment, it is first necessary to objectively categorize the different behaviors exhibited by individuals. Ethograms of common action patterns are valuable in four ways. The first way is in identification of the mechanisms through which behavior is performed. Ethograms can also provide information about how behaviors are adaptive to individuals. The elaborate displays of male Ocellated Turkeys likely serve as inter- and intrasexual signals of individual condition. The third way behavioral description is useful is

to identify selective pressures that have resulted in divergence, through comparisons between species. The observed differences in Wild and Ocellated Turkey courtship may be influenced by habitat. Lastly, ethograms can identify how species respond to environmental change. Human disturbance alters Ocellated Turkey reproductive behavior. Further study is needed to uncover whether anthropogenic changes in behavior may endanger populations of this near threatened, Central American endemic.

II. MALE REPRODUCTIVE STRATEGIES AND MATING DISPLAYS IN
THE OCELLATED TURKEY

Introduction

Mating systems

The structure of a mating system is heavily influenced by resource heterogeneity, mate availability, and other ecological factors (Verner and Willson 1966; Orians 1969). This explanation characterizes a mating system as an adaptive response to environmental constraints, and therefore, able to change structurally along with the environment (Emlen and Oring 1977). The particular structure of a mating system at any point in time is the result of individuals within the system acting adaptively. Within a mating system, selective pressures often differ between sexes due to disproportionate parental investment, with a larger burden typically falling on females of a species (Trivers 1972). The tradeoff of higher resource allocation to each offspring by females is that they must spend a reduced amount of time receptive during each mating cycle. Emlen and Oring (1977) explained that this increased parental investment by females skews the ratio of males and females that actually reproduce (Operational Sex Ratio (OSR)), so that the proportion differs from the 1:1 ratio of the population. If one sex has fewer options for selecting a mate, competition over mating opportunities will be higher in that sex (Kvarnemo and Ahnesjö 1996). According to Arnqvist and Rowe (2005), greater mate competition may also alter the selective pressures on each sex during courtship and copulation. For example, Weir et al. (2011) performed a meta-analysis to investigate how mating behavior changes in response to an increasingly biased OSR. They found that as the OSR increased, so did competitive aggression, mate guarding (by the non-limited sex), and copulation duration. For the limiting sex, behaviors like mate guarding can decrease the capacity to evaluate extra-pair mating opportunities. Because each sex's fitness is not always maximized in the same way (e.g. higher parental investment in females vs. better intrasexual competition in males), behaviors may evolve that

increase fitness in one individual at the expense of its mate (sexual conflict). In response to such influential and divergent selective pressures, some individuals show plasticity in their reproductive behavior (West-Eberhard 1989).

Alternative reproductive tactics

Male reproductive success is characterized by greater variance than female reproductive success in many mating systems (Bateman 1948). When true, the intrasexual fitness skew in these mating systems should put a premium on any male method of maximizing copulations. Genetic and environmental heterogeneity within populations, however, may limit the potential of certain methods for each individual. This efficacy differential can lead to the coexistence of multiple fitness-maximizing tactics (Gross 1996). Alternative tactics provide clues about how individuals can maximize fitness even though they do not employ the dominant mating strategy. These individuals are altering their behavior in response to selective pressures. Describing particular selective pressures that generate alternative tactics is informative because evidence for multiple tactics has been described in numerous, unrelated taxa, with varying types of parental care, and in temperate, tropical, terrestrial, and aquatic systems alike. For example, individual male House Finches (*Carpodacus mexicanus*) may choose to live in groups with reduced competition for mates. Because females prefer to mate with males exhibiting colorful plumage, less attractive males are able to increase their odds of mating by switching to flocks in which they are relatively more attractive (Oh and Badyaev 2010). Due to the energetic and opportunity costs associated with searching and sampling multiple groups, only individuals with the greatest potential benefits should switch flocks often. Ornament elaboration predicted mating success, so more ornate males do not need to incur the costs of switching groups in order to effectively compete for mates. Less elaborate males switch social groups more often, and the most socially mobile

“dull” males have the greatest success at pairing with females. Rather than compete for mating opportunities with birds displaying superior plumage, some males increased their fitness by reducing a selective pressure (intrasexual competition) imposed by their species’ life history trait of communal living.

A mammalian example of alternative male reproductive tactics is found in the Orangutan (*Pongo pygmaeus*) (Atmoko and Van Hoof 2004). There are two sexually mature male morphs in this species: the socially-dominant form, with large cheek flanges and a coat of long hairs, and the unflanged, socially-subordinate form. Although female preference was associated with the dominant form, the subordinate males still father a large percentage of offspring by sexual coercion. Subordinate males also change tactics and become dominant males, sometimes after decades of using the alternate strategy. Both the finch and Orangutan alternative mating tactic examples are what Gross (1996) called condition-dependent tactics; males in the population are genetically monomorphic (do not exhibit more than one generalized morphology). Adoption of a particular tactic must, therefore, be controlled by prevailing internal and external environmental conditions. A reproductive tactic should be an adaptive response to best maximize the potential fitness of an individual in its current environment (Schradin et al. 2012). Alternative tactics are most often seen in mating systems where intra-specific competition for mating opportunities is strong, and individual reproductive success is highly variable (Shuster and Wade 2003). Under these conditions, multiple tactics may persist because the composite structure of the mating system is evolutionarily stable (Smith and Price 1973), or because certain reproductive tactics are rendered ineffectual for some individuals by phenotypic and environmental limitations. Studies in which data are gathered on environmental heterogeneity and mating tactics concurrently can uncover which trade-offs influence the adoption of one tactic over another.

Determination of tactics by the environment

If the adoption of a particular mating tactic is influenced by the environment, any reproductive strategist should be considering both its external and internal environmental conditions. For example, male African striped mice (*Rhabdomys pumilio*) may adopt one of three tactics: communally living and territorial, communally living and natally philopatric, and roaming while living solitarily (Schradin et al. 2009). Body mass predicts male type, with territorial males largest, followed by roamers, and philopatric males weighing the least. Males can switch tactics during the breeding season as their weight changes. The relative fitness of each tactic is associated with population density (Schradin and Lindholm 2011).

During a year of high population density, territorial males have the highest paternity; in some cases, the territorial paternity success rate can be 10 times greater than roaming male paternity, and 102 times higher than philopatric paternity. When population density is intermediate, however, territorial and roaming tactics have similar fitness values. Interestingly, no philopatric males are observed during this time. Both the territorial and philopatric tactics are absent during low population densities, and there is high variance in roaming males' reproductive success, with 56% of reported males failing to reproduce, while one male was observed fathering 29 offspring from 10 different females. It appears that when females are sufficiently clumped, defending a territory yields the highest fitness, but only large males seem to have the energy reserves to do so. As female availability decreases, a males' fitness is limited most by his ability to find mates, during which acquisition and defense of a territory would be an unproductive use of resources. Although mass predicted male tactic, differences in mass within groups did not account for fitness variances. The authors suggest that female choice might explain why body mass and fitness were not highly correlated within groups because 40% of

offspring from “guarded” communal groups were fathered by other males, and large males were not preferentially chosen for these matings (Schradin and Lindholm 2011). If mass alone were a reliable predictor of general male tactic, however, what underlying factors contribute to general differences in mass? Other than reporting that philopatric males have high corticosterone levels, the authors do not address this. However, in another mammal with two male mating tactics (territorial and non-territorial), the internal environment of individuals differs predictably between groups.

In the Chamois (*Rupicapra rupicapra*), the fecal parasite loads of territorial males increase after the initiation of the rut (Corlatti et al. 2012). This pattern is not observed in non-territorial males. The stressful reproductive season revealed differences between males, showing that some could not afford the trade-off between mating effort and immune function. In addition to social structure and individual condition, differences in habitat have also been shown to influence the dynamics of alternative tactics. For example, Atlantic salmon (*Salmo salar*) exhibit two anadromous male reproductive tactics influenced by natal habitat quality (Fleming 1998). The multisea winter tactic (MSW) is seen in males that spend two or more years at sea, after which they return to freshwater to spawn. The second tactic is characterized in males known as grilse, who return to freshwater to spawn earlier, after only one year at sea. MSW males are larger than, and socially dominant to grilse. The social sub-dominance of grilse is reflected in their satellite mating behavior near a nesting female, where they wait on the periphery of a territory until the eggs are released, and then surreptitiously attempt to fertilize them after rushing in at the last moment (Fleming 1998). Juvenile growth rate is the main determinant of subsequent mating tactic, and offspring produced in smaller streams are larger than those from portions of a main river (Garant et al. 2003). Furthermore, although growth rate

is heritable, it is much higher in streams compared to wider stretches of river. Garant et al. (2003) suggest that food availability and quality is greater for young salmon in smaller stream habitats, resulting in the higher rates of growth. In some species, alternative tactics are only exhibited under certain environmental conditions.

In a well-studied North American endemic, the Wild Turkey (*Meleagris gallopavo*), the mating system is variable and seems to change due to habitat-specific spacing patterns (Krakauer 2008; Krakauer 2005). Eastern Wild Turkeys, for example, typically exhibit male dominance polygyny, with rank dictating access to receptive females (Williams and Austin 1988 pg. 95). Eastern turkeys have also been described as displaying a harem defense system, similar to that found in large, herding artiodactyls (Healy 1992 pg. 47). In one southern population in Texas, Watts and Stokes (1971) described a mating system similar to a lek that contained coalitions of males that defended and displayed to groups of females. These coalitions maintained a strict dominance hierarchy, with only the highest ranking male permitted to mate. This alternative male behavior by subordinates was interpreted as kin selection by the authors, a claim later supported by genetic data from male coalitions in another population (Krakauer 2005). Despite being closely related, the Neotropical congener of the Wild Turkey seems to exhibit a very different alternative male mating tactic, and a paucity of data precludes a kin selection explanation.

Natural History of Meleagris ocellata

The Ocellated Turkey (*Meleagris ocellata*) is a highly ornamented, polygynous species without male parental care (Williams et al. 2010 pg. 24; King and Bol 2004). The male's ornaments include an extendable "snood" above the nostrils, a knob-like crown atop the head, red-orange

caruncles scattered across the head and neck, formidable leg spurs, and strikingly iridescent feathers all over the body (Figure 1). For a number of years, the Ocellated Turkey has been listed as near threatened (BirdLife International 2010, Species factsheet: *Meleagris ocellata*) in its lowland, tropical forest range including parts of southeastern Mexico, Belize, and Guatemala (Figure 2). Within its range, Gonzalez et al. (1998) reported that the turkeys use open or cleared areas during breeding and nesting, and retreat to taller forest habitats during the remainder of the year. Ocellated Turkeys are mostly herbivorous within their limited Central American range (Table 1).

Dietary Composition

Food Item	Percentage of Total Contents
Seeds	77
Grit	22
Fruit Pulp	11
Leaves	10
Flower/Stem/Animal	<3

Table 1. Upper digestive tract contents of Ocellated Turkeys (*Meleagris ocellata*) n=181, with percentage of total volume included for each item (Modified from Baur 2008).

Mating system

Adult male Ocellated Turkeys exhibit multiple behaviors during the mating season (Steadman et al. 1979). Williams et al. (2010 pg. 11) maintained that there are adult males, certainly old enough to breed, who do not engage in any mating behavior. Steadman et al. (1979) also

observed males who, despite being around females, would not engage in courtship behavior. Dominant males tolerate these apparently “non-breeding” adult males, even in the presence of females, while at the same time they fiercely defend their territory from other breeding (territorial) males. It is not clear whether the “non-breeding” males are exhibiting alternative mating tactics, or truly abstaining from reproduction.

Comparison with the Wild Turkey

With so many factors influencing the origin and maintenance of alternative mating tactics, using well-researched species in comparative studies can be an effective way to gain insight into poorly understood mating systems. A comparison of closely related species occupying different environments helps reveal selective pressures responsible for shaping the evolution of disparate life-histories (Gill and Haggerty 2012). Among North American birds, the Wild Turkey possesses an impressive assortment of behaviors and morphological features that seem suited only for attracting mates (Buchholz 1995), and its congener, the Ocellated Turkey, exhibits similar secondary sexual characteristics with some notable differences (Figure 3). Male behavioral displays contrast even more strikingly between the species (Table 2).

Despite the variable structure of the mating systems of Wild Turkeys, males have never been observed guarding territories, rather than females. Likewise, males have never been reported as non-participatory during the mating season after reaching adulthood. In contrast, individual male Ocellated Turkeys may appear to occupy opposite ends of the competitive spectrum for (at least) the duration of a mating season, with some males fighting for territory as others avoid intrasexual competition (Williams et al. 2010 pg. 11).

Wild and Ocellated Turkey Behavioral Comparison

Behavior	<i>Meleagris gallopavo</i>	<i>Meleagris ocellata</i>
Males call while “strutting” for females	No	Yes
Breeding males tolerate juveniles near mating performance	No	Yes
Breeding male is territorial	No	Yes
Males form mating “alliances”	Sometimes	No
Flocks segregate by age class and sex	Strictly	Only Slightly
Hens and immature males roost together in spring	No	Yes

Table 2. A behavioral comparison between congeners *Meleagris gallopavo* and *M. ocellata*. (Modified from Williams et al. 2010 Table 2-5. pg. 31)

Objectives and hypotheses

The current understanding of *M. ocellata* mating systems is limited and based on few studies, some of which are decades old and restricted in sample size. The available evidence suggests that male Ocellated Turkeys exhibit alternative mating tactics which differ from those seen in its congener, the Wild Turkey (Williams et al. 2010 pg. 11; Steadman et al. 1979). Unfortunately, most studies of Ocellated Turkey behavior are somewhat anecdotal, lacking individual

identification and quantification. The primary objective of my research is to identify the factors (behavioral and non-behavioral) responsible for the alternative mating tactics used by males of this species. My second objective is to identify characteristics of individual males that are associated with mating success. The main goal of this research is to establish a strong foundation for future studies of the mating system of the Ocellated Turkey, using objective data from individually-recognized birds. Hopefully, these data will provide a better understanding of how natural and sexual selection have molded this tropical, Central American endemic differently than the more commonly known, temperate, and widely ranging Wild Turkey.

Objective 1: Describing male mating strategies.

Are there dichotomous male strategies?

In theory, alternative reproductive tactics can be discrete or continuous, permanent or facultative, and purely behavioral or morphologically influenced (Gross 1996). Williams et al. (2010 pg. 11) claimed that mature male Ocellated Turkeys exist in discrete behavioral types: breeding or non-breeding; but they lacked sufficient data to support this contention. Steadman et al. (1979) provided some data on individual males during the breeding season, with at least two males (N=6) never engaging in mating displays. As this study is the only known quantification of individual male Ocellated Turkey display behavior, I predict that individually-identifiable males will either a) actively defend a territory and commonly engage in courtship displays, or b) never display or guard a territorial boundary. Alternatively, there may be intermediate classes of males representing additional discrete strategies, or facultative adjustment of male tactics depending on local social conditions.

Causes and consequences of male behavioral types

In some species, alternative male mating tactics are associated with variance in male condition. Males may differ in age, body size, or health, so that some strategies (e.g. territoriality) are an impractical means of achieving mating success when compared to others (e.g. surreptitious copulation) (Plaistow et al. 2004). I propose two alternative hypotheses explaining how male behavioral type will be indicated by condition.

The **Condition-Dependent Hypothesis** states that males use specific mating strategies based on their body condition. Males in superior condition will be able to endure the costs of defending a territory and constantly displaying, while males in inferior condition will employ the less costly non-territorial strategy. This hypothesis has four predictions:

- a) beta (“non-breeding” (Williams et al. 2010 pg. 11)) males will have lower body mass : tarsus ratios than alpha (territorial) males
- b) beta males will have higher blood and fecal parasite loads than alpha males
- c) beta males will be younger than alpha males
- d) beta males will have lower quality plumage and head ornamentation than alpha males

Alternatively, the **Burden Hypothesis** states that the energetic costs of maintaining territory and displaying are physiologically burdensome to alpha males. As a result, alpha males will exhibit inferior body condition when compared to the beta males whose strategy is less physically costly. This alternative hypothesis makes the following three predictions:

- a) beta males will have higher body mass : tarsus ratios than alpha males

- b) beta males will have lower blood and fecal parasite loads than alpha males
- c) beta males will have better quality plumage and head ornamentation

Objective 2: Female choice and male mating success.

How do females select a mate?

Females choose mates based broadly on two types of potential benefits they receive from males. Direct benefits increase female fitness tangibly (e.g. male parental care, territory quality), while indirect benefits increase fitness by augmenting offspring quality (through males' genetic contribution) (Kotiaho and Puurtinen 2007). When males of a species provide parental care within a defended territory, females can be expected to choose a mate based on the quality of both a male and his territory. In the polygynous mating system of the Ocellated Turkey, males provide no parental care (Williams et al. 2010 pg. 24). Females in this system can only receive indirect benefits from males. Hypotheses concerning indirect benefits exist in two general classes, both of which predict that more exaggerated male traits (i.e. mating displays and ornamentation) are preferred by females. Good genes explanations of female choice predict that courtship displays and sexual ornamentation indicate male genetic quality (Zahavi 1975). Arbitrary preference models, conversely, propose that despite being preferred by females, these characters do not indicate the heritable qualities of males. Instead, male displays and ornamentation that may have once indicated quality are genetically linked with a preference by females for those traits, solely because they more efficiently stimulate the sensory biases of females (Fisher 1958). Because most females in a population prefer these elaborate traits, the offspring of males exhibiting them should still experience greater mating success.

Female preference and male reproductive success are most accurately quantified using molecular genetic methods of measuring parentage of offspring. Without genetic data, which are difficult to obtain and costly to produce, behavioral indicators of female preference can be used. If female Ocellated Turkeys are choosy about their mates, I predict that females will associate more often with certain territorial males than others. If females mate at random, hens should be equally distributed across all male territories.

If females mate non-randomly, two hypotheses may explain their preferences. The “**Good Genes**” **Hypothesis** states that females assess the quality of territorial males using their secondary sexual ornaments (e.g. plumage quality, crown, snood, and caruncles) and courtship displays. Under this hypothesis, I predict that:

- a) there will be a positive correlation between female visitation to a male’s territory and his display rate and ornament quality
- b) parasite load will be negatively correlated with male display rate and ornament quality

Alternatively, females may prefer males that are highly ornamented because their sensory systems are predisposed to react to those male features due to non-sexual selection (e.g. females that detect orange fruits better have higher caloric intakes , but as a consequence also prefer the orange coloration present in some male’s caruncles). The predictions of this **Sensory Bias Hypothesis** overlap with those of the good genes hypothesis as follows:

- a) there will be a positive correlation between female visitation to a male's territory and his display rate and ornament quality
- b) display and ornament quality does not indicate male condition

Methods

After collection permits were obtained from the Belize Forestry Department (Ref. No. CD/60/3/12(19)), research was conducted at La Milpa (N 17 50.487 W 89 01.106) and Hill Bank (N 17 36.047 W 88 42.065) field stations (Rio Bravo Conservation and Management Area, Programme for Belize) and the adjacent Gallon Jug Estate (N 17 33.634 W 89 02.801), of NW Belize. Data collection took place over two field seasons (Table 3). Turkeys were captured using a variety of methods: Walk-in traps (**1/11 birds**) (V-shaped traps tied along tree-line into which birds are funneled. Approximate dimensions: Face (front): 10m, height: 1.5m, depth: 3.5m), drop nets (**1/11 birds**) (Approximate dimensions: square, 3m length), foot nooses (**1/11 birds**), hand nets (**1/11 birds**), and drugged (**7/11 birds**) (α -chloralose dosage: 1g per cup of whole corn or rice) bait. Individuals showed wide variance in tolerance to α -chloralose, dosages were often augmented for birds exhibiting relative resistance. Doses were incrementally increased by a weight of 0.3g until the desired level of intoxication was achieved. Turkeys were captured from different locations as presented in Table 4. Standard body measurements and measures of male ornaments (Figure 1) were modified from those described by Buchholz (1995) for the Wild Turkey. Male snood length measurement was standardized by stretching the relaxed snood with 30g of tension using a clip attached to a 100g spring-scale (Pesola AG, Baar, Switzerland). Male

Field Work Dates and Locations

Year	La Milpa	Hill Bank	Gallon Jug
2011	March 6-20 May 3-June 13 July 3-15	March 21-May 2	June 14-July 2
2012	April 1-8	N/A	April 9- June 15

Table 3. Dates and locations of field work performed during 2011 and 2012.

Year and Location of Turkey Captures

Year	La Milpa	Hill Bank	Gallon Jug
2011	4	3	0
2012	0	N/A	4

Table 4. Study year and location of Ocellated Turkeys captured for sampling.

crown height was measured at the center of the crown's front side. Males were aged by spur length for division into three categories: < 2.54cm (yearlings), c. 3.81cm (2 years), and \geq 4.45cm (3 years or older), according to Williams et al. (2010). For all male birds, caruncle counts were taken from the entire crown, left head side, right head side, and neck, along with body weight. Tarsus lengths were also recorded from the tibiotarsus/tarsometatarsus joint extending to the first unbending scale of the middle toe when feet were clenched.

Parasite Quantification

Blood was collected by syringe from each turkey via the alar vein (underside of the wing) and placed on a microscope slide as a blood smear, then fixed in methanol by coating the slide with two or three drops before drying. Slides were treated with Wright Stain (Polysciences, Inc., Warrington,

Ocellated Turkey Head Ornamentation

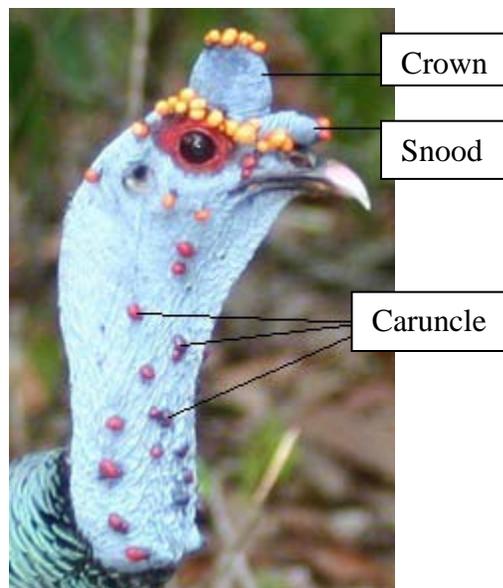


Figure 1. Example of male Ocellated Turkey head ornamentation quantified after capture.

PA) to facilitate microscopy. Polysciences, Inc. Wright Stain Procedure protocol was modified. Slides were flooded with Wright Stain for 1.5 minutes, before being covered with buffer mixture (15mL Wright Stain/ 75mL Stain Buffer) for 6 minutes. Slides were then submerged in buffer mixture for an additional 1.5 minutes, and then rinsed with distilled water. Scanning for a suitable investigative area began at the top left portion of the slide near the origin of the smear. At 100 x, each slide was assessed along the y-axis, moving towards the right, until a section of

erythrocytes one layer thick was discovered. Blood parasite abundance was assessed per 10,000 erythrocytes under oil immersion at 1000 x by investigation of each cell for abnormalities associated with infections (Campbell 1995 pg. 30-34). Fecal samples (5.75mL- 0.718mL) were collected opportunistically from individuals with a scoop of known volume, and placed in 30mL water containing 1g potassium dichromate for preservation. The percentage of the scoop's volume filled by each fecal sample was used to calculate fecal volume. Samples were exposed to the atmosphere for six hours prior to preservation to facilitate coccidian (common intestinal parasite) oocyst sporulation for identification. For analysis, methods described by Buchholz (1995) were modified. A 1mL portion of each fecal solution was placed in a 15mL centrifuge tube and filled to the top (no air bubbles were present) with 1.28g/mL (56%) sucrose solution, so that a coverslip adhered to the solution and created a seal during 12 minutes of centrifugation at 2000rpm. Parasites with lesser densities than the solution were forced onto the coverslip, allowing for microscopic analysis. The entire cover slip was scanned at 100 x, and parasite genera and abundance were recorded for all known. Parasites of greater densities than the solution were forced to the bottom of the tube, and inspected with a dissecting microscope at 20 x. Unidentified parasites that occurred commonly were given a designation, quantified, and used in analyses. Atkinson et al. (2008) was consulted to differentiate pathogenic organisms from other organic matter present in the samples.

Feather samples were collected in pairs from four locations: five rows above mid-speculum in marginal coverts, dorsal-most feathers of speculum with complete "copper" coloring, center feathers of uppertail coverts in line with tips of folded primaries, and central breast feathers parallel to wrist joint of folded wing held in normal posture. An Ocean Optics (Dunedin, FL) USB2000 fiber optic spectrometer and PX-2 pulsed xenon light source were

equipped with Spectrasuite[®] operating software (version 2.0.162) to quantify spectral reflectance, after calibration with Labsphere Spectralon[®] (North Sutton, NH). An incident light source probe (PX-2) was secured at a 45° angle, with the collecting probe at 90°, in an RPH-1 anodized aluminum probe holder (Ocean Optics, Dunedin, FL). The collecting probe was retrofitted with a piece of aluminum by the University of Mississippi Physics Department Machine Shop to secure immobility within the 90° angle slot. Three measurements were taken from each feather region, with the incident light source positioned farthest from the rachis. The first measurement was taken from the edge of the feather, and the next two were taken by moving in 2 millimeter increments towards the center (rachis). For feathers with multiple, distinct regions of coloration, this process was repeated. Reflectance curves were analyzed to decide which color variables were appropriate for analysis. Areas of the spectrum which showed little to no reflectance (except for black feathers) were not used in analysis.

Captured turkeys were each fitted with a yellow identification tag (4" x 6" yellow cattle ear tags attached to one wing patagium) and/or leg bands (as dictated by regional protocol). Male display rates and frequencies, associations with females, fights with other males, and other notable behaviors were quantified during behavioral observation. Focal animal sampling was used whenever suspected reproductive behaviors were exhibited, with all occurrences of behavior recorded. Call rates were recorded for an observation period of 20-60 minutes. Cases where males left the area or were disturbed before 20 minutes had passed were not included in my analysis. Recorded male courtship interactions with females began as soon as the birds were within 20 meters of each other, and lasted until birds were no longer visible, or the female departed and the male ceased pursuit (when distance between them again reached 20 meters). Because males occupied territories, observations were scheduled (quantity determined by

number of territorial males in study area) for specific males each week so that all males could be observed equally. At the La Milpa and Hill Bank study sites, few males (N= 4) were present, so total observation durations for each bird were much higher than at Gallon Jug. When a scheduled male could not be located, an adjacent male territory was searched, which resulted in a sampling bias towards the more available, human-tolerant birds nearer the research camps.

Instantaneous/Scan sampling was used to establish time percentages of certain activities (forage, walk, stand, rest) for both marked and unmarked individuals at intervals of 5 minutes. Care was taken to record data from all individuals during similar hours of the day and weeks of the breeding season. The Animal Care Committee at the University of Mississippi reviewed and accepted the methodology of this proposal (Protocol no. 11-005). I used unique patterns of head ornamentation for individual identification of turkeys that were not captured for marking.

Statistical methods

The open source software program R (<http://cran.r-project.org/>) was used for all statistical tests. Non-normal data were log transformed, when necessary, for specific analyses. Logistic regression was used to compare parasite loads to male class. Spur lengths, activity patterns, and ornamentation of the feathers and head in alpha and beta males were analyzed with One-Way Monte-Carlo Permutation tests. Principal Components analyses were also used to compare head and feather ornamentation data in males, and to compress those data for use in regression analyses.

Independent regression analyses were used to assess the value of certain male predictor variables (Call rate, display rate, ornamentation, and parasite load) on female visitation rate.

Regression analyses were also used to assess how parasite load affects male Call rate and feather reflectance.

Results

Condition Dependent and Burden Hypotheses

Body mass: tarsus ratios were virtually identical between alpha ($\bar{x} = 0.337$, $n = 5$) and beta males ($\bar{x} = 0.335$, $n = 3$), both of which were slightly higher than the average ratio for all birds (including females and juveniles) combined ($\bar{x} = 0.319$, $n = 11$). A logistic regression analysis of fecal parasite loads of alpha and beta males did not significantly (Table 5) differentiate between male class for either coccidian or other common parasites (described in Appendix I), although both were higher in beta males. Standardized (by sample volume) raw averages of parasite loads

Fecal Parasites and Male Class

Logistic Regression Analysis				
Parasite Type	Slope Estimate	Error	z-value	p-value
Coccidian	-0.051	0.158	-0.324	0.746
Other	0.261	0.268	0.972	0.331
Descriptive Fecal Parasite Statistics				
Male Class	\bar{x} Coccidia	σ Coccidia	\bar{x} Other	σ Other
Alpha	1.19	1.25	1.43	1.54
Beta	17.93	35.07	2.07	2.05

Table 5. Regression scores for fecal parasite loads of alpha (N= 12) and beta (N= 4) male Ocellated Turkeys, with averages and standard deviations listed below. Counts are divided by sample volume for standardization.

are listed in Table 5 below regression scores, along with standard deviations. Similarly, blood parasite loads were not significantly different between male classes (Table 6), although raw values were slightly higher in beta males (Table 6). Male age (spur length) did not predict mating strategy ($z = 1.296$, $p = 0.260$, $n = 5$ (alpha), $n = 3$ (beta), One-Way Monte-Carlo Permutation Test), but average spur length was higher in alpha males ($\bar{x} = 4.18$, $\sigma = 0.356$) than in beta males ($\bar{x} = 3.77$, $\sigma = 0.503$). Because of a small sample size, feather ornamentation was also tested using One-Way Monte Carlo Permutation Tests, treating each tristimulus variable separately (CLR 1.05, Montgomerie 2008) (Table 7). A Principal Components Analysis was also performed, using tristimulus variables calculated from all birds captured (Figure 2). Alpha and beta head ornamentation were analyzed in two different ways. First, One-Way Monte Carlo Permutation Tests were employed for each head ornament category (Table 8), with left-side head caruncles being significantly different between groups.

Blood Parasites and Male Class

Logistic Regression Analysis				
Parasite Type	Slope Estimate	Error	z-value	p-value
<i>Haemoproteus</i>	0.264	0.274	0.961	0.336
Descriptive Blood Parasite Statistics				
Male Class	\bar{x} <i>Haemoproteus</i>	σ <i>Haemoproteus</i>		
Alpha	4.3	2.11		
Beta	6.67	5.01		

Table 6. Regression scores for blood parasite loads of alpha (N= 5) and beta (N= 3) male Ocellated Turkeys, with average *Haemoproteus* blood parasite load (per 10,000 erythrocytes) included below with standard deviation.

Feather Ornamentation and Male Class

Feather	Tristimulus Variable	α Average (%)	β Average (%)	Test Statistics
Marginal Coverts	B1 (brightness)	26.11	28.72	$z = -0.767$, p-value = 0.464
Speculum	B1 (brightness)	31.44	24.74	$z = 0.764$, p-value = 0.523
Tail Coverts (gold region)	B1 (brightness)	20.18	34.18	$z = -1.58$, p-value = 0.148
Tail Coverts (blue region)	B1 (brightness)	18.44	15.72	$z = 0.988$, p-value = 0.356
Tail Coverts (black region)	B1 (brightness)	4.72	6.0	$z = -0.573$, p-value = 0.618
Marginal Coverts	S1G (saturation λ 510-605)	33.44	31.13	$z = 0.921$, p-value = 0.444
Tail Coverts (blue region)	S1B (saturation λ 400-510)	46.04	39.43	$z = 1.21$, p-value = 0.269
Speculum	S1Y (saturation λ 550-625)	32.66	27.6	$z = 0.969$, p-value = 0.503

Table 7. Tristimulus variables calculated for specific feather regions (Montgomerie 2008) for alpha (N= 5) and beta (N= 3) male Ocellated Turkeys. Test statistics refer to One-Way Monte Carlo Permutation Tests for each variable and male class.

Principal Components Analysis of Feather Ornamentation

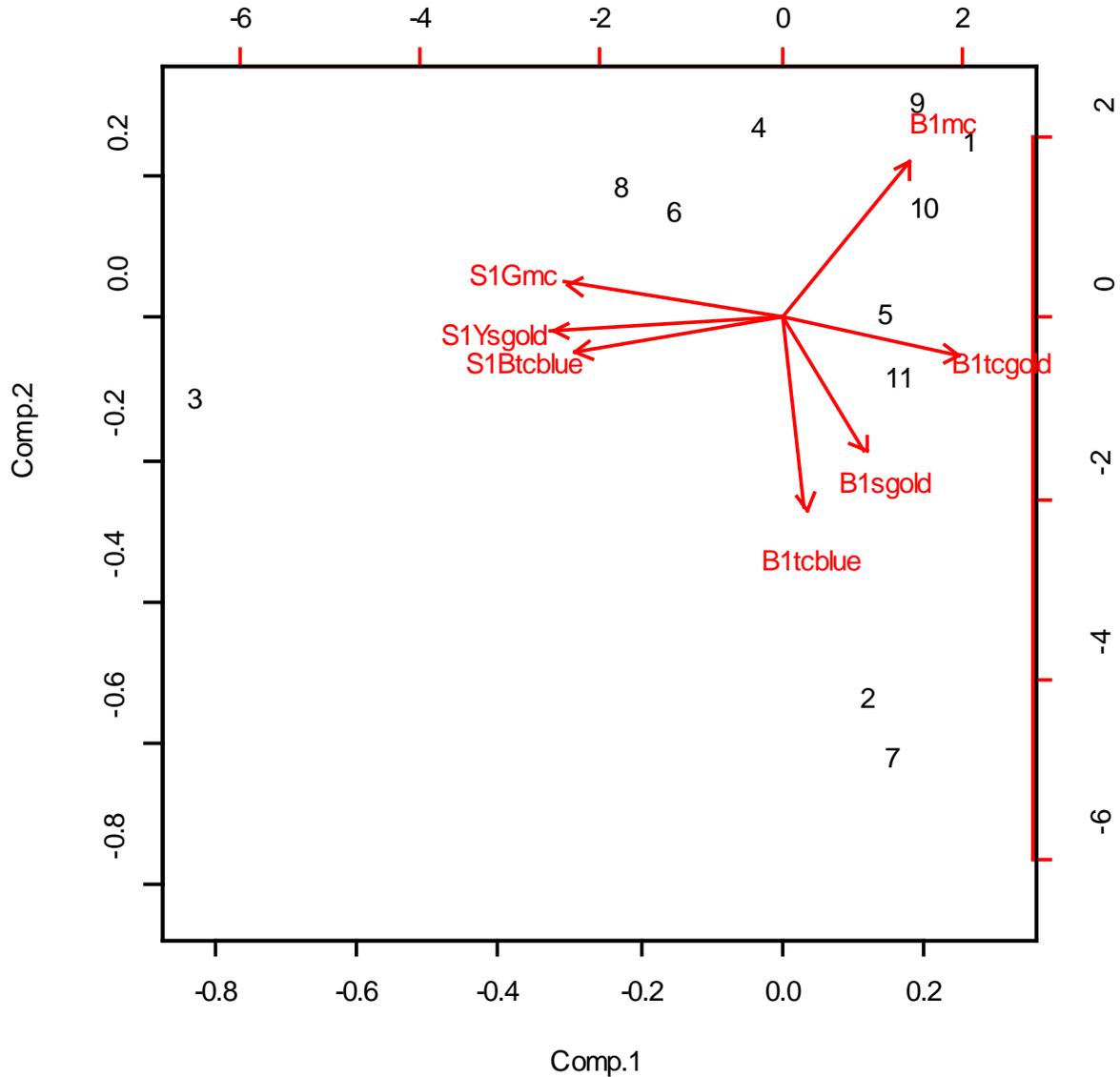


Figure 2. Principal Components Analysis using tristimulus variables (Montgomerie 2008) calculated from specific feather regions for all birds captured. Variables signify the following: B1= brightness, S1G= saturation (λ 510-605), S1B= saturation (λ 400-510), S1Y= saturation (λ 550-625). Feather types are designated by the following: mc= marginal coverts, tc= tail coverts, s= speculum, with specific color regions measured on each feather listed thereafter (if multiple exist). Numbers refer to individual birds of the following classes: 1 (female), 2 (alpha), 3 (alpha), 4 (beta), 5 (female), 6 (alpha), 7 (juvenile male), 8 (alpha), 9 (beta), 10 (alpha), 11 (beta).

The second method incorporated photographs of known male turkeys that were not captured, in order to increase sample size. These new measures of ornamentation were used in a Principal Components Analysis (Figure 3) that did not reveal a discernible pattern between turkey class and head ornamentation. Data on male activity patterns were also gathered, and One-Way Monte Carlo Permutation Tests were used to identify behavioral differences (other than in mating displays and territoriality) between alpha and beta males. Tests on all five categories of behavior did not reveal any significant patterns (Table 9).

“Good Genes” and Sensory Bias Hypotheses

In order to assess the “Good Genes” and Sensory Bias Hypotheses (why females prefer certain males), two approaches were used due to small sample size. First, data on female preference and male ornamentation and condition were analyzed separately to assess biological patterns. In addition, multiple regression analysis was employed, using male ornamentation and condition data that provided the largest sample size.

A regression analysis revealed that male Call rate significantly influenced female visitation to his territory ($r^2 = 0.26$, $t = -2.3$, $p = 0.042$, $m = -6.024$, $N = 13$) (Figure 4), with lower call rates experiencing higher visitation. Regression analyses were also used to assess the relationship between female visitation and the percentage of time spent performing specific display activities (see chapter titled: “An Ethogram of Reproductive Behaviors in the Ocellated Turkey”) when in the presence (within 20 meters) of a female (Table 10); however, no overall pattern was evident. Another regression analysis using Principal Components Analysis axis scores (see Figure 3) of male ornamentation did not reveal a significant trend regarding female visitation ($r^2 = 0.113$, $t = 0.626$, $p = 0.559$, $m = 0.518$, $N = 7$).

To identify whether male condition influenced display ability, a regression analysis of male Call rate and fecal parasite load (coccidian and other combined) was performed. This combined analysis was performed due to sample size restrictions and no notable patterns were revealed ($r^2 = 0.028$, $t = 1.13$, $p = 0.287$, $m = 0.027$, $N = 11$). Similarly, measures of condition based on parasite load influencing feather reflectance (Table 11) were not significant.

Head Ornamentation and Male Class

Monte Carlo Permutation Tests	Snood	Crown Height	Head Caruncles (right side)	Head Caruncles (left side)	Crown Caruncles	Neck Caruncles
Test Statistics	$z = 0.081$, $p = 0.962$	$z = 0.954$, $p = 0.437$	$z = -1.317$, $p = 0.188$	$z = -1.97$, $p = 0.037$	$z = -0.036$, $p = 1$	$z = -0.227$, $p = 0.854$
Descriptive Statistics (matching columns above)						
Alpha \bar{x} ; σ	$\bar{x} = 3.8$; $\sigma = 1.07$	$\bar{x} = 1.32$; $\sigma = 0.25$	$\bar{x} = 18$; $\sigma = 4.42$	$\bar{x} = 14.6$; $\sigma = 3.36$	$\bar{x} = 15.2$; $\sigma = 6.46$	$\bar{x} = 18.4$; $\sigma = 4.56$
Beta \bar{x} ; σ	$\bar{x} = 3.73$; $\sigma = 1.47$	$\bar{x} = 1.17$; $\sigma = 0.153$	$\bar{x} = 23.67$; $\sigma = 7.23$	$\bar{x} = 23.33$; $\sigma = 5.86$	$\bar{x} = 15.33$; $\sigma = 2.3$	$\bar{x} = 19$; $\sigma = 2$

Table 8. Results of six Monte Carlo Permutation Tests using head ornamentation of alpha ($n = 5$) and beta ($n = 3$) males, with average head ornamentation and standard deviation values included. All distance measurements are in centimeters. Caruncle measurements are count data.

Principal Components Analysis of Head Ornamentation

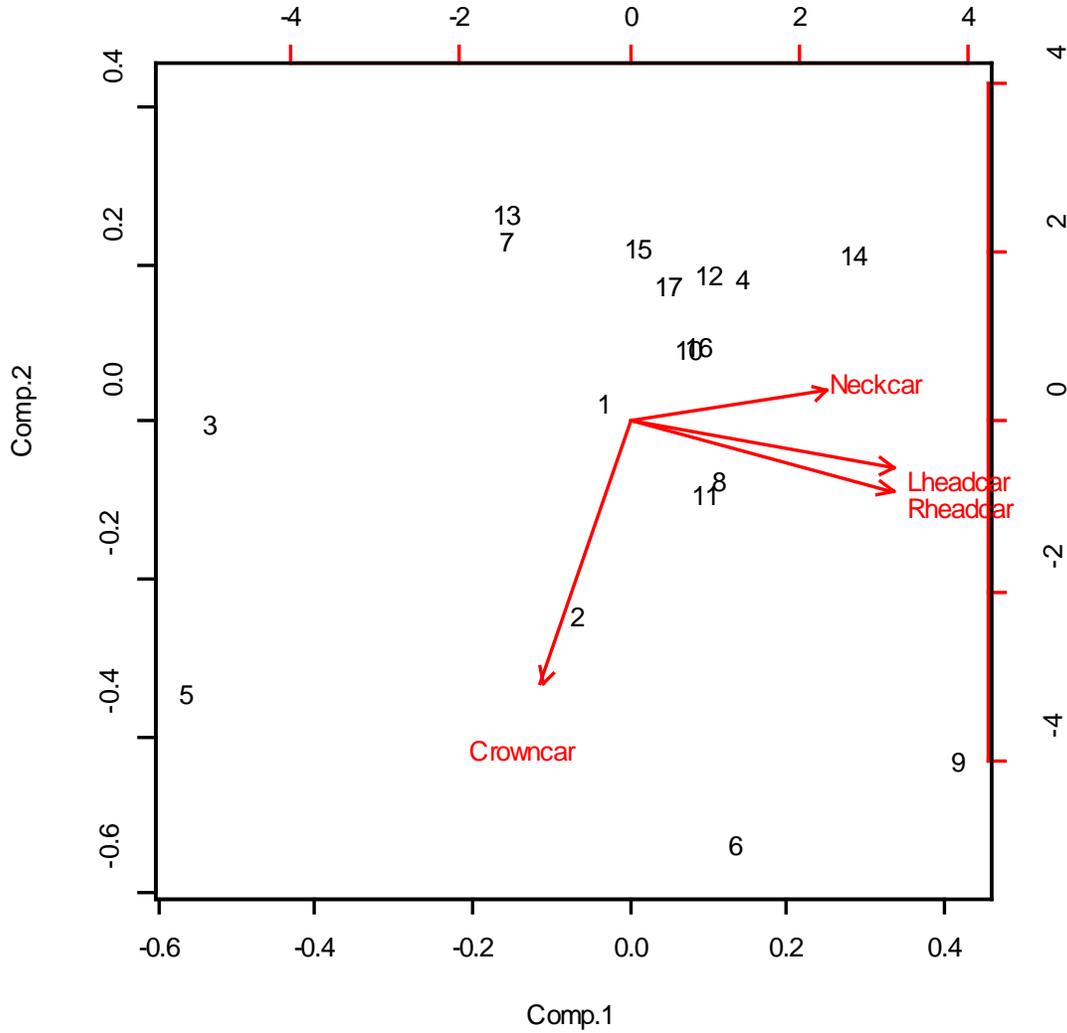


Figure 3. Principal Components Analysis using four measures of head ornamentation. Measurements include captured, photographed (known individuals), male, female, and immature individuals. All four measures are caruncle counts from the neck, crown, right side of the head, and left side of the head. Numbers refer to individual birds of the following classes: 1 (alpha), 2 (alpha), 3 (female), 4 (juvenile), 5 (female), 6 (alpha), 7 (alpha), 8 (beta), 9 (beta), 10 (alpha), 11 (beta), 12, (beta), 13 (alpha), 14 (alpha), 15 (alpha), 16 (alpha), 17 (alpha) .

Two multiple regression analyses were used to investigate the relationship between female visitation and alpha male quality. The first multiple regression analysis revealed no significant pattern between alpha male fecal parasites (condition) and female visitation (Table 12). The second multiple regression included female visitation, with male fecal parasite load and Call rate as predictors (Table 13), and a negative relationship between Call rate and female visitation was apparent, but non-significant.

Alpha Male Behavioral Distinctions

Monte Carlo Permutation Test	Forage	Walk	Preen	Stand	Rest
Test Statistics	z= -0.527 p = 0.608	z= 1.13 p= 0.266	z= -0.725 p = 0.479	z= -1.39 p = 0.173	z= 1.49 p = 0.101

Table 9. One-Way Monte Carlo Permutation Tests of behavioral differences between alpha (N= 8) and all other classes (including females and juveniles) (N= 15) during similar hours of the day. Resting consists of lying on the ground when not exhibiting Flattening display behavior.

Discussion

Are there dichotomous male strategies?

Based on my behavioral observations alone, multiple male strategies seem to exist. Individual males were identified and followed throughout the breeding season, and on almost all occasions, were observed adhering to either the alpha or beta male strategy as described

previously (Williams et al. 2010 pg. 11, Steadman et al. 1979). Here, I documented two noteworthy exceptions to the dichotomous male strategy model. First, on two occasions involving different males, a known beta was observed repeatedly calling in the territory of an alpha male. On the first occasion, the supposed beta male stopped calling, abruptly, after the local alpha male approached him. During the second occurrence, calling ceased voluntarily after

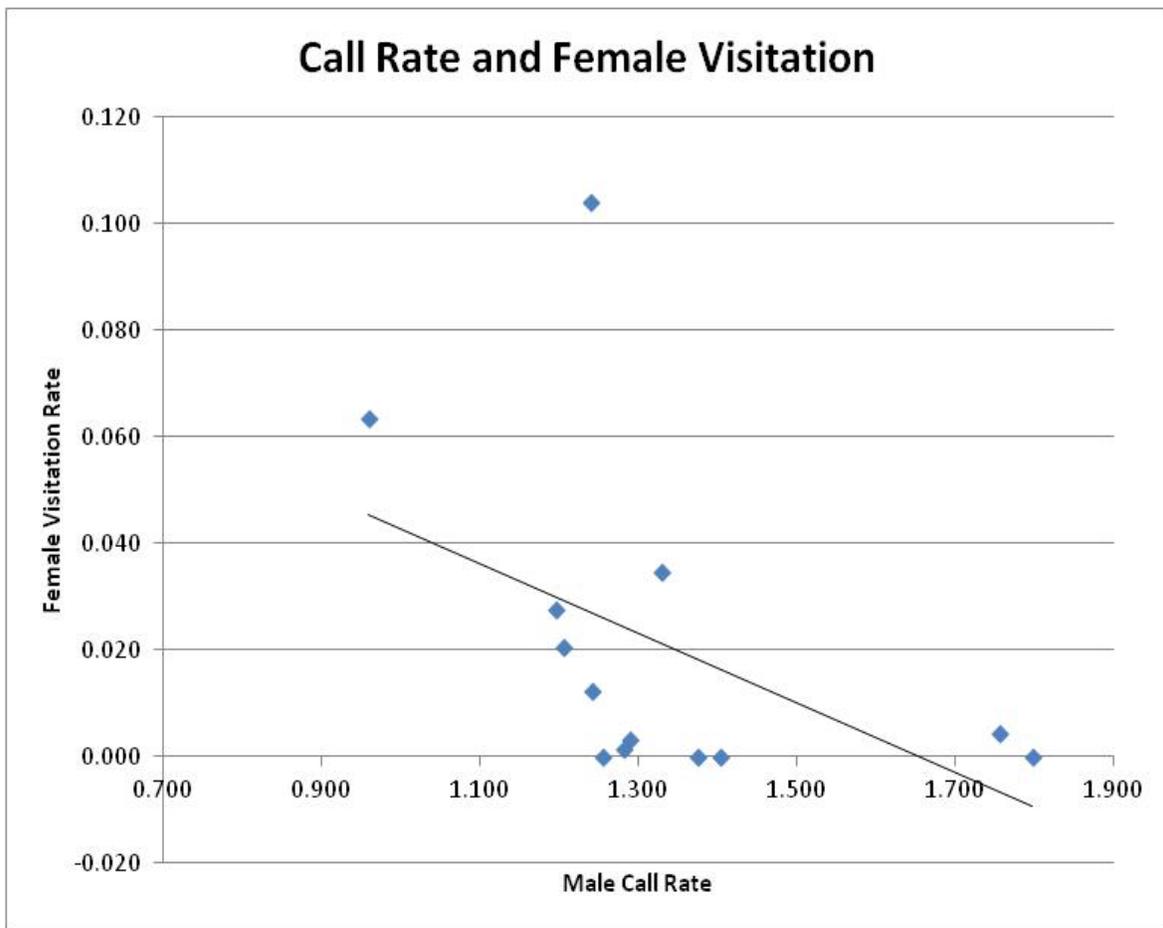


Figure 4. Male Call rate per minute of observation time plotted against the number of females visiting a males' territory (within 20 meters of the male) per minute of total observation time, with trendline (N= 13).

Male Display and Female Visitation

Display Behavior	r ²	Slope Estimate	Error	t- value	p-value	N
Boxy	0.113	-0.503	1.75	-0.288	0.781	10
Flattening	0.107	-0.952	1.67	-0.569	0.590	8
Strut	0.142	-0.051	0.994	-0.051	0.961	9

Table 10. Results of individual regression analyses of female visitation rate and percentage of total display time males spent in Boxy, Flattening, or Strut behaviors.

Feather Ornamentation and Parasite Load

Response Variable	Predictor Variable	r ²	Slope Estimate	Error	t-value	p-value
Feather Axis 1	<i>Haemoproteus</i>	0.107	0.025	0.142	0.177	0.864
Feather Axis 1	Coccidia	0.07	0.685	0.568	1.21	0.282
Feather Axis 1	Other (fecal)	0.153	0.161	0.357	0.452	0.67
Feather Axis 2	<i>Haemoproteus</i>	0.165	0.138	0.079	1.73	0.118
Feather Axis 2	Coccidia	0.164	-0.121	0.308	-0.391	0.712
Feather Axis 2	Other (fecal)	0.12	-0.203	0.151	-1.35	0.235

Table 11. Results of individual regression analyses using Principal Component Analysis axis scores (axes 1 and 2) of feather tristimulus variables and *Haemoproteus* (N= 11), coccidian (N= 7), and other fecal parasite (N= 7) loads.

Fecal Parasites and Female Visits

Fecal Parasites	Slope Estimate	Error	t- value	p-value	r²
Coccidia	-0.065	0.161	-0.406	0.694	0.20
Other	0.016	0.158	0.101	0.922	

Table 12. Multiple regression scores for coccidian and other (Appendix I) fecal parasite loads of alpha males and rates of female visitation (N= 12).

Relationship of Female Visitation to Male Call Rate and Fecal Parasite Load

Predictor	Slope Estimate	Error	t-value	p-value	r²
Fecal Parasites	0.104	0.162	0.643	0.538	0.183
Call Rate	-4.34	2.11	-2.06	0.074	

Table 13. Multiple regression of female visitation, using male Call rate and fecal parasite load (total combined) as predictors (N= 11).

about 50 minutes. The second exception to the two-male-strategy hypothesis was observed on three occasions, always in an area (50 m² or less) containing at least four adult males. All three instances suggested a gradient of male strategies, rather than two discrete male types. Typical alpha male display behavior was witnessed in some individuals, while others exhibited the characteristic beta strategy. Multiple males, however, were observed engaging in display behaviors less vigorously than nearby alpha males. These individuals displayed Full Boxy and Wagging behaviors only, never Calling, Flattening, or Strutting. Also, this third class of male only displayed when separated from females and alpha males by 30 meters or more. Regardless

of whether there are two or three male mating strategies, non-behavioral data should reaffirm the observed differences in male behavior.

Causes of male behavioral types

Behavioral observations support the existence of at least two male strategies in the Ocellated Turkey. The small sample size of this study made identification of biological patterns difficult; however, there are three non-behavioral trends that support dichotomous male behavior, the first two of which are in support of the Condition-Dependent Hypothesis. First, although logistic regression analyses of male class and parasite loads did not reveal any strong trends, average blood and fecal parasite loads were higher in beta males. Furthermore, calculations of effect size ($d = (\bar{x}_1 - \bar{x}_2) / \sigma_{\text{pooled}}$) Cohen 1992) revealed a pattern of beta males having higher coccidian ($d = 0.97$) and *Haemoproteus* ($d = 0.61$) loads after using Hedges' bias correction factor (Hedges and Olkin 1985). Cohen (1992) suggested that medium effect sizes are around 0.5, with large values near 0.8. Despite a small sample size, this evidence suggests an important difference in parasite loads between alpha and beta males.

The second trend in support of multiple strategies is the age of each class of male. Once again, small sample size reduced the power to detect a significant difference between alpha and beta males. According to the spur-aging recommendations of Williams et al. (2010), however, the average age of beta males was around two years, while alpha males were closer to three years of age. In mating systems that involve multiple male strategies, younger individuals often adopt the socially-subordinate mating strategy (Atmoko and van Hoof 2004). Younger turkeys may use the beta strategy in order to attain a greater size before defending territories and displaying to females. In addition, younger age classes often have higher parasite loads (Garamszegi et al.

2005), which is supported by the first major trend mentioned. Still, this interpretation is contradicted by the almost identical average measures of condition (body mass: tarsus ratio) between the classes, and a larger sample size is needed for further analysis.

The final trend supporting the existence of multiple male mating strategies is habitat. The three study locations can be separated based on the degree of human disturbance to the landscape as follows: La Milpa (low), Hill Bank (moderate), Gallon Jug (high), resulting in Gallon Jug having the highest percentage of open area. Turkey populations were highest in Gallon Jug, and lowest where landscape disturbance was minimal. Throughout the two-year study period, beta males were only observed where open habitat and turkey density were highest (Gallon Jug). Thus, it seems likely that the adoption of multiple male strategies may be an adaptation to increased competition. Population density is known to alter mating strategies in multiple taxa (Ribeiro et al. 2010; Hardling et al. 2004). If beta males truly are younger than alphas as spur length suggests, this pattern may result from high concentrations of turkeys increasing the benefits of delaying sexual maturity. Although genetic data prevent validation in this study, kin selection may also explain why some adult males adopt a beta strategy. In an unusual (densely populated) Wild Turkey (*Meleagris gallopavo*) mating system, Krakauer (2005) found that kin selection explained the existence of certain male coalitions that defended females together, although only one male ever mated. Late in the breeding season (July), I observed three occurrences of a male-duo, where one male acted in a typical alpha fashion, while the other aided in the defense of his territory while never displaying to females. This counterintuitive behavior is adaptive from a kin selection perspective, but further study is needed.

Feather and head ornamentation data were mostly inconclusive. Once again, small sample size limited the power of analyses, although the number of caruncles on the left side of

the head was significantly different between groups. In support of the Burden Hypothesis, beta males had a greater number; however, no other analyses of ornamentation supported this pattern. Individual tests using feather tristimulus variables, along with Principal Components Analyses did not reveal any measurable differences between male classes.

How do females select a mate?

Measures of male display and ornamentation did not reveal any discernible patterns regarding female visitation, with one notable exception. Males with lower Call rates experienced higher female visitation. While this finding may seem counter-intuitive, three explanations may be offered. First, lower call rates may reflect random sampling error in regards to display effort based on female presence. Male Greater Sage Grouse (*Centrocercus urophasianus*), for example, increase display rates when in close proximity to females (Patricelli and Krakauer 2010). If male turkeys were sampled on numerous days without female visitation, and then multiple females were subsequently recorded during a few observation periods, recorded Call rates could be biased. A second explanation may be intrasexual conflict over high-quality territories. When males guard territories, mating success is often dependent on their quality (Forstmeier 2002; Pribil and Searcy 2001) because females are attracted to superior territories. Male Ocellated Turkeys able to secure favorable areas may not need to display as vigorously in order to attract females. If true, much of an alpha males' reproductive effort would be allocated to defending his territory. The final explanation for higher visitation to males with lower Call rates is sampling error due to population density. Because of its high turkey density, the majority of samples originated from Gallon Jug. In an effort to increase sample size and diversity, multiple alpha males were observed on fewer than four occasions, resulting in multiple (n= 5) recordings of

zero visitation. These limited observations skewed female visitation data without influencing average Call rates (Figure 4), and could have resulted in the observed inverse relationship.

Differences in habitat and turkey density may also have been responsible for non-significant findings between female visitation and other measures of male display and ornamentation. In general, many more females visited male territories in the disturbed, highly populated study site of Gallon Jug. In fact, males in highly disturbed areas experienced an average of over 2.5 times the number of female visits as males in undisturbed areas. The large difference in rates of female visitation between study sites calls into question the use of female visitation as a proxy for male attractiveness and mating success. Because of higher population density, males in Gallon Jug may simply encounter more females without experiencing greater mating success or paternity, although this may not necessarily occur. Patterns of female visitation and male ornamentation and display may more accurately measure female preference for males in areas of low population density.

Measures of male ornamentation similar to some used in this study are influential in female choice in the Wild Turkey (Buchholz 1995). Also, parasite loads in Wild Turkeys can significantly alter measures of plumage reflectance, with greater numbers of parasites reducing iridescent coloration (Hill et al. 2005). The small sample size in this study prevents excluding the possibility of these patterns existing in Ocellated Turkey mating systems as well.

Conclusion

Despite a small sample size, four patterns concerning the mating behavior of Ocellated Turkeys seem credible. First, multiple male strategies do exist in some populations. Second, beta males seem to have higher parasite loads than alpha males, as predicted by the Condition-Dependent

Hypothesis. Also in support of this hypothesis is the finding that beta males appear to be younger, on average, than alpha males, a trend further supported by younger age classes typically having greater parasite loads in other taxa. The final major pattern observed is that the percentage of open habitat and density of individuals drastically alters mating system structure. Specifically, a high density of breeding males (which occurs in open habitats) may reduce the benefits of early maturation in that sex.

Two other results are notable, but require further study for substantiation. First, rather than dichotomous male strategies, a gradient may be more representative of a high-population-density mating system. Territorial, alpha males occupy one end of the spectrum, with non-displaying betas at the other. The second notable finding is that alpha males with lower Call rates experience higher visitation. This trend may reflect female preference for high quality territories over male Call rates, or may simply be sampling error resulting from insufficient data. Future studies should seek to obtain data on offspring paternity to better assess female preference in the Ocellated Turkey.

III. BEHAVIORAL RESPONSES TO INADVERTENT HUMAN
DISTURBANCE

Introduction

Humans have direct and indirect impacts on wildlife. Since the Pleistocene, humans have been associated with the extinction of wild populations (Lyons et al. 2004). Currently, reductions in biodiversity greatly exceed rates found in the fossil record (Biggs et al. 2008). This recent, direct anthropogenic harm of wildlife is attributable to at least four direct sources, namely, altering landscapes (Sekercioglu et al. 2011), pollution (Trevors & Saier 2009), outright harvest (Rosser & Mainka 2002), and the introduction of exotic species (Banko et al. 2013). Often, the additive effects of these anthropogenic disturbances can exacerbate negative outcomes for biodiversity (Laurance and Useche 2009). Mitigating the effect of these direct sources is intuitive. To benefit wildlife, humans need to protect more land from development, pollute less, harvest only from sustainable populations, and reduce introductions of exotic species. It is more complicated, however, to properly identify and reduce our harmful indirect disturbance of wildlife.

Most studies concerning the effects of human disturbance on wildlife investigate changes in species abundance and range (Vanthomme et al. 2013; Paudel & Kindlmann 2012). While population size is valuable conservation information, human alteration of ecosystems also has indirect effects that change the way animals behave. These changes in behavior may, ultimately, result in reduced abundance and smaller ranges. In order to reverse the trend of pernicious human-wildlife interactions, we must identify maladaptive changes in behavior before population reductions occur (Wrege et al. 2010). Recently, greater attention has been devoted to understanding how human alteration of environmental stimuli influences wildlife behavior (Sih 2013; Lankau et al. 2011; Sih et al. 2011). Although these disturbances may not directly poison or kill wildlife, altering behavior indirectly might be harmful to individual fitness (Buchholz & Hanlon 2012). One major source of indirect disturbance that alters behavior is human intrusion

in which the goal is not to harvest the animal. Ecotourism, for example, aims to provide opportunities to experience natural environments with minimal impact, while generating funding to preserve wildlife for future generations (Shahwahid et al. 2013). Unfortunately, even ephemeral occupation of a habitat typically devoid of humans may change animal behavior and, unintentionally, ecotourists could be harming the fitness of wildlife (Buchholz & Hanlon 2012; Clemmons & Buchholz 1997, pg. 33). Understanding which factors influence a species' susceptibility to harm from inadvertent human disturbance (IHD) is critical to conservation efforts. A recent blueprint for understanding behavioral variation due to anthropogenic change suggests four main considerations (Sih 2013). Sih (2013) outlines four main points to clarify how species respond to direct sources of anthropogenic disturbance (i.e. human induced rapid environmental change (HIREC)). This framework for understanding behavioral responses to direct disturbance can be adopted to investigate reactions to indirect sources of human disturbance (IHD) as well. First, behavioral responses result from specific cue-response systems. These systems may involve behavioral decision-rules that are influenced by organisms' sensory biases. Second, maladaptive behavioral outcomes often result from incomplete or undependable information. Third, the behavioral flexibility of an individual affects responses to human disturbance. Lastly, evolutionary and ontological history shapes variation in responses. These four considerations provide a framework to identify general predictors of species' behavioral responses to IHD. This framework is also useful for revealing how study methodologies can yield data more indicative of the true effects on populations. By revealing the factors that result in studies collecting more valid data, or make a species more vulnerable to harm from IHD, conservation management decisions can be improved. In this chapter, I first review possible predictors of wildlife responses to IHD utilizing Sih's (2013) HIREC framework. I then perform

a meta-analysis of different studies, using data that measure fitness differences for similar populations in disturbed (by IHD) and undisturbed areas. Multiple predictors are investigated to account for variations in fitness values between groups.

Cue-Response Systems

If the behavioral responses of wildlife to IHD are dependent on local cue-response systems, factors that influence stimulus perception, like habitat and social structure, must be influential. Habitat heterogeneity should be an important consideration for at least two reasons. First, sound and light transmission are influenced by physical aspects of habitat (Bormpoudakis et al. 2013; Slabbekoorn et al. 2002; They 2001). The perception of visual and auditory signals, then, must differ depending on specific habitat. The physical appearance and acoustic characteristics of IHD do influence behavioral responses (Goudie 2006; Wrege et al. 2010), and similar disturbances may elicit divergent responses depending on habitat type (Stankowich 2008). Secondly, the amount of cover in a particular habitat should influence how much danger is associated with an IHD because it represents the perceived ease of escape. Indeed, the amount of and distance to cover influence responses to IHD (Wolf & Croft 2010; van Polanen Petel et al. 2007). The social structure of a species should also impact cue-response systems.

Social structure of a species should affect cue-response systems for two reasons. First, in social species, multiple individuals use sensory repertoires to simultaneously survey the environment. Earlier and more frequent detection of IHD by numerous individuals could increase the effect of each occurrence. Infrequent disturbances might result in harm additively, through latent reactions to behaviors of previously disturbed group members. Conversely, individual risk is reduced with increasing group size (Dilution Effect (Sorato et al. 2012)).

Despite experiencing IHD, individuals may not maladaptively alter their behavior because they experience greater safety in groups. Social species have been found to be less tolerant of human disturbance (Blumstein 2006). However, social species with larger group sizes have also shown reduced behavioral reactions to IHD (Martinez-Abraín et al. 2008). The relative importance of sociality in predicting behavioral responses to IHD is likely dependent on other factors. For example, regardless of sociality and habitat, the reliability of informational cues will impact wildlife responses to specific human disturbances.

Reliability of disturbance information

Wildlife should be expected to behave more closely to optimality as the reliability of environmental information increases (Sayers & Menzel 2012). Unreliable information about IHD can result from three sources. Two sources, variation in associated danger and insufficient exposure, concern the perception of wildlife. The third source of unreliability originates from the specific response variables measured in studies. First, variation in associated risk of IHD results from some disturbances being perceived as harmful by wildlife. This perception of jeopardy exists when species view humans as predators (Geist et al. 2005). The Risk-Disturbance Hypothesis states that anthropogenic disturbances elicit anti-predator behavior. The response to human disturbance should then be mediated by the same general cost-benefit decision rules as natural anti-predator behaviors; individuals must make trade-offs between disturbance avoidance and other fitness-elevating behaviors (e.g. time spent foraging or searching for mates) (Frid & Dill 2002). A major problem with well-intentioned disturbances like ecotourism, however, is that other humans may simultaneously be preying on wildlife (Bego & Malltezi 2011). Because activities like bird watching require the same hushed-stalking behaviors as many types of human hunting, populations exposed to both activities may never view IHD as harmless. Although

species are responding adaptively by fleeing from human hunters, fleeing from ecotourists who, though harmless, are nevertheless perceived as predators may reduce fitness. For example, species may flee numerous times throughout the day from IHD and human hunting when they both elicit anti-predator responses. This overstimulation of anti-predator behavior could deplete energy reserves and reduce time engaged in other advantageous behaviors. A second source of IHD information unreliability is exposure. As a population experiences similar, inadvertent human disturbances over time, wildlife should be expected to learn that there is no associated danger. Some species do habituate to IHD (Ellenberg et al. 2009). Other species, however, are not able to habituate (Ellenberg et al. 2006). Research of responses to IHD should utilize protracted study lengths, which better measure the true effects of disturbance over time. Greater study lengths alone, however, only provide more reliable information if the behavioral response measured has an effect on fitness.

The third source of misinformation about behavioral responses to IHD concerns study methodology. In particular, the type of behavioral response measured influences the quality of information. An overt behavioral response to disturbance does not mandate an individual fitness consequence. Similarly, a lack of behavioral response does not indicate a negligible fitness consequence. For example, some breeding birds may not exhibit a notable behavioral response to human observers, although measures of physiology (Ellenberg et al. 2009) and fecundity (Ibanez-Alamo et al. 2012) signify a reduction in fitness. Information relevance is increased when quantified behaviors (fitness proxies) better reflect actual fitness. For example, patterns of movement in response to IHD may alter energetic costs and decrease access to resources, which should reduce fitness (Neuman et al. 2010). Without a measure of actual energy expenditure or availability of adjacent resources, however, the degree to which fitness is actually altered will

remain unclear. Actual measures of physiology, such as stress hormone concentrations, better reflect changes in fitness resulting from IHD (Thiel et al. 2008). Still, because of genotypic variation, individual fitness may differ, despite similar physiological responses. The most reliable information about changes in fitness due to IHD results from measures of reproduction. Using measures of fecundity or survival rates of offspring as a proxy for fitness should most accurately reflect the impact of IHD on wild populations. For slowly-reproducing species, accurate information about offspring requires protracted study lengths. Length of study is also important for assessing habituation, but populations may differ in their ability to alter behavior. Over longer observation periods, certain species may reveal differences in the ability to alter behavior in response to IHD; this behavioral flexibility is also influenced by information reliability (Sih 2013).

Behavioral flexibility

In general, species that exhibit greater behavioral flexibility without detrimental fitness reductions are better able to adapt to IHD. The ability to alter behavior, however, is influenced by local environmental constraints. Therefore, behavioral flexibility of species exposed to human disturbance can be predicted in two general ways. First, foraging habits can determine the costs of altering behavior. Food limitation reduces survival (Railsback & Harvey 2011); therefore, foraging habits most impacted by IHD should be less behaviorally flexible. Second, the specific season during which behavior is recorded changes the costs and benefits of certain reactions. Diet can determine behavioral flexibility because it indicates the viability of alternative foraging locations and habits. The relative costs of being disturbed differ with foraging strategy. Diet can predict differences in IHD tolerance, but a clear pattern is not evident (Heil et al. 2007; Geist et al. 2005; Blumstein 2006). Predicting a specific response based on diet is difficult because

human disturbance alters diet composition in species with dissimilar foraging strategies (Jayakody et al. 2011; Henschel et al. 2011). Herbivores might experience reduced foraging costs from disturbance because food cannot escape, although reductions in foraging time may disproportionately limit energy intake because of the low caloric content of vegetation (Wilmshurst et al. 2000). Predicting the reaction of carnivores also requires multiple considerations. Carnivores may suffer greater foraging opportunity costs of disturbance because of the handling-time of prey items. Conversely, a high opportunity cost may be offset by a greater available calorie load (Snellen et al. 2007). An omnivorous diet is most flexible, and greater relative dietary options may reduce the costs of augmenting behavior in response to IHD. In omnivores, however, a diverse diet may be essential to energy maximization (Robbins et al. 2007), and this could limit the flexibility of behavior.

Behavioral flexibility also depends on local environmental conditions. The second general way to predict behavioral flexibility may be seasonality. During different seasons, the costs and benefits of behavioral responses to IHD are altered. For example, food availability changes with the season (Luiselli et al. 2011) and may limit the range of adaptive foraging behaviors. During the reproductive season, IHD could have additive negative effects as individuals are expending energy on intrasexual competition and parenting. For example, given that stress-hormone levels increase with group size in colonial-nesting Cliff Swallows (*Petrochelidon pyrrhonota*) during the breeding season (Raouf et al. 2006), ecotourist disturbance of a large group during nesting could result in more harm to individual fitness than visitation to small swallow groups. Solitary reproducers may also exhibit reduced behavioral flexibility during breeding seasons. With the added investment of offspring, wildlife may be more reluctant to eschew human disturbance and abandon an area. Studies of responses to IHD

that include multiple seasons should provide more valid data. Accuracy of information, however, also depends on the evolutionary and ontological history of a population.

Evolutionary and ontological history

The first three of Sih's (2013) considerations of behavioral response studies, specific cue-response systems, information reliability, and behavioral flexibility, all originate from the fourth major category. Specific considerations of evolutionary history and ontological development are highly influential in shaping behavioral responses to IHD. Three factors, generation time, mass, and human-disturbance exposure over time may all provide insight into the behavioral responses of wildlife.

The first two factors are closely related. Species with longer generation times usually attain greater size. These species may also have lower reproductive rates, and exhibit increased vulnerability to reductions in fitness associated with IHD (Blumstein 2006). Mammals and amphibians with lower reproductive rates and longer generation times do exhibit greater negative population responses to road and traffic density (Rytwinski & Fahrig 2011; Rytwinski & Fahrig 2012). Also, mass positively correlates with disturbance intolerance (Blumstein 2006). An alternative view currently lacking supportive evidence is that species with longer generation times usually have greater longevity, and may have more opportunities to habituate to IHD and reduce negative fitness impacts. The possible habituation potential of larger, long-lived species can be further investigated by examining the local history of IHD.

Just as a species' evolutionary history may predict certain behavioral responses to IHD, an individual's developmental history shapes its behavior (Robbins & Langkilde 2012). The specific history of IHD influences the opportunity wildlife has to change behavior because it

dictates the reliability of disturbance information. Longer periods of local IHD should result in more reliable information about risk to individuals, and local populations should adapt over time (Buchholz & Hanlon 2012). Alternatively, a history of disturbance from multiple sources (e.g. hikers, ATVs, and dogs), especially if fatal (e.g. from dogs), may decrease the perceived reliability of information and increase harmful responses to IHD. Just as human harvesting of wildlife might result in populations responding to all humans as they respond to predators, a history of multiple types of human disturbance could decrease the reliability of behavioral cues. For example, if unleashed dogs repeatedly chase wildlife, all humans walking with leashed dogs may eventually cause a flight response. It is also possible that the association between these pets and their owners could result in wildlife exhibiting anti-predator responses to humans in the absence of dogs. Repeated human disturbances could then overstimulate anti-predator behaviors and reduce fitness. Another example involves recreational use of ATVs. When driving near wildlife, humans may again be perceived as predators actively hunting and chasing prey. Occasionally, a driver may inadvertently harm wildlife directly, changing how human disturbance is perceived. Crushing the eggs of a ground-nesting bird, for example, might result in stimulation of anti-predator behaviors during all subsequent encounters with an ATV. Future nesting attempts may even be abandoned whenever an ATV is observed in the individual's home range.

Using Sih's (2013) four major considerations of behavioral responses to human disturbance, ten potential predictors have been identified: habitat, sociality, disturbance exposure (habituation), hunting pressure, fitness proxy, season, diet, generation time, mass, and history of specific disturbances. Many of these predictors are interrelated, and each may contribute

simultaneously to variation in behavioral responses to IHD. Analyses of behavior should consider all possible variables (and correlations) when assessing the responses of wildlife.

Behavioral analyses of IHD

The numerous confounding variables of behavioral disturbance studies necessitate objective comparisons of data. Meta-analysis can make these objective comparisons. The term meta-analysis refers to multiple statistical techniques that facilitate the assembly and contrast of data from similar studies. Relevant results from select studies are quantified in a common manner (effect size), allowing existing patterns to be identified. In this way, meta-analyses obtain a more objective view of the association between two variables (Viechtbauer 2010). A handful of studies have used meta-analysis techniques to quantify the impact of habitat disturbance on wildlife (Tilghman et al. 2012; Holloway and Smith 2011; Winfree et al. 2009). Only a few of these consider multiple, unrelated taxa simultaneously (Rytwinski & Fahrig 2012; Riffell et al. 2011). These previous meta-analytic studies are chiefly concerned with species richness and abundance data, and outline how our modification of natural environments degrades habitat-quality. Species abundance data alone, however, do not describe impacts on individual (and population) fitness. Presence in a seemingly suitable habitat may belie untenable occupation, as human disturbance events may result in negative fitness consequences. In addition, interpretation of immediate behavioral responses to disturbance can contradict more tangible measures of fitness (i.e. nest failure (Bouton et al. 2005)). To date, just two studies have used meta-analyses to investigate fitness effects of IHD (Ibanez-Alamo et al. 2012; Stankowich 2008); no studies on the subject have incorporated data from a broad diversity of taxa. Comparisons of the effects of human behavioral disturbance across different animal taxa could help identify if some fragile, biodiverse areas should forever severely limit human presence. Using meta-analytical techniques, I

investigated the impact of non-antagonistic human disturbance events on individual fitness across multiple taxa. Contrasting data from similar populations in human-disturbed and relatively undisturbed locations should yield an objective measure of specific fitness effects; comparing effect sizes to certain life history traits may, additionally, identify patterns useful for conservation.

Hypothesis and Predictions

I propose the Ecotourist-Effect Hypothesis, which states that innocuous human disturbance decreases individual fitness in wild populations. This hypothesis has two predictions. The first prediction concerns the relative importance of predictor variables. From nine (excluding hunting) predictors identified, I predict that length of study, generation time of species, and fitness-proxy measure will explain the most variation in wildlife responses to IHD. As the length of a study increases, I predict that the true effects of IHD will become more apparent, and longer studies will reveal more negative fitness effects on wildlife. The generation time of a study species will also be an important predictor. Some studies report a decrease in disturbance tolerance as generation time increases (Rytwinski & Fahrig 2012). However, I predict these species will better habituate to IHD because of increased experience due to longevity. The specific fitness proxy used will also explain significant variation in disturbance responses. Studies that record behaviors closely related to true fitness (e.g. fecundity) will reveal greater negative impacts of IHD than studies reporting on less-direct fitness proxies (e.g. patterns of movement). The second prediction is that a local history of hunting will increase the severity of negative fitness effects due to IHD. The Null Hypothesis states that there will be no significant relationship between fitness and disturbance level for the species studied.

Methods

The journal literature databases Biological Abstracts, Science Citation Index, and ScienceDirect were used to amass studies concerning anthropogenic behavioral change. The following keywords were used: disturbance, anthropogenic, human, and wildlife. Each study was reviewed and accepted for data analysis if it met the following seven criteria. First, only recent papers were investigated for inclusion (published in or after 2005) because the field of conservation behavior is nascent (Buchholz 2007) and older studies were not expected to include necessary information. Papers published after May, 2013 are also not included. Second, only empirical studies (no reviews) were included. Next, a study needed to be behavioral in nature. This behavioral component excluded population surveys, species richness, and species diversity research, regardless of whether human disturbance influenced these variables. Also, the behavioral component needed to include some measure of fitness. Fifth, only research on populations in a wild setting was considered. Additionally, studies that investigated only physiological responses to disturbance were not included if differences in habitat, even if due to human activity, comprised the only method of selecting study subjects. Lastly, data needed to be collected in both disturbed and undisturbed (or relatively undisturbed) populations, areas, or time periods (e.g. tourist locations during periods of high or low visitation). Examples of the rationale for inclusion of particular studies are shown in Table 1. Studies that included a local history of hunting the study species were treated separately. Research involving inadvertent human disturbances similar to hunting (e.g. randomly discharging a firearm) was not included in the primary analysis. A second analysis included these studies, to assess whether additive effects to fitness might result from changes in how wildlife perceives IHD (e.g. more extreme anti-predator responses). Some of these hunting data were gathered from the same studies, when information

on IHD and hunting-like disturbances were both included separately (Table 3). In total, 117 papers were identified using the above keywords. After careful review, only 39 papers were determined to be suitable for data analysis. Of these 39 papers, only 21 reported data appropriate for this meta-analysis, namely, a comparison of fitness parameters in disturbed and (relatively) undisturbed populations (Table 1) (Table 3). Five additional data points were added from

Study Selection Criteria Example

Lead Author/Year	Study Species	Response to Disturbance Measured	Suitable for Inclusion	Reason for Rejection
Larsen 2005	<i>Somateria mollissima</i> ; <i>Melanitta nigra</i>	Escape distance	No	No separate disturbed and undisturbed category
Vidya 2010	<i>Elephas maximus</i>	Degree of agitation (1= no response, 5= charge vehicle)	No	No separate disturbed and undisturbed category
Ellenberg 2009	<i>Megadyptes antipodes</i>	Increase in heart rate (beats/minute)	Yes	N/A
French 2011	<i>Zalophus californianus</i>	Offspring growth rate	Yes	N/A

Table 1. Examples of research appropriate for analysis, or excluded from study. Failure to include both disturbed and undisturbed population responses was the most common reason for rejection if a study investigated wildlife responses to IHD.

hunting-disturbance studies. From each study, behavioral responses to IHD that reflected individual fitness were collected. This information charted an averaged measure of performance (e.g. offspring provisioning rates in disturbed and undisturbed locations) in categories assumed to have a substantial influence on fitness. If multiple behaviors were recorded, the behavioral

category most closely tied to fitness was used (e.g. chicks fledged rather than time spent incubating). A log response ratio (LRR) was calculated using the ratio of performance without and with disturbance to measure effect size, and standardize fitness effects from different studies. In one instance (snowy plover chicks fledged in protected and unprotected beaches (Lafferty et al. 2006)), performance with disturbance was zero, so the performance value with disturbance was changed to 0.1 to facilitate calculation of the log response ratio. Because performance without disturbance was 72, this change had the effect of slightly reducing the size of the disturbance effect, although the effect size remained large. The LRR was transformed so that higher numerical values represent better fitness outcomes without disturbance. The transformation reflected the measure of fitness used in each study. An LRR was multiplied by -1 if the behavior recorded had a negative effect on fitness (e.g. percentage of time spent vigilant), or by 1 when the effect was positive (e.g. breeding success per nest). Studies were weighted based on sample size and study variance was taken into account. Both random and mixed effects models were used to calculate both the overall effect size and to ascertain the value of certain variables as predictors of response to disturbance. Values for predictor variables based on life history traits were collected from the University of Michigan's animal diversity database (<http://animaldiversity.ummz.umich.edu/>). Secondary sources were consulted if species information was unavailable from the primary source. To identify predictors explaining the most variation in behavior, models with all combinations including one, two, or three predictors were compared. Small sample size prevented comparisons of models using more than three predictors. Akaike information criterion (AIC) scores were used to identify the best overall model. Also, the 24 best (lowest) AIC-score models were compared to identify which predictors commonly explained the most variation (all other models had AIC scores nearly double these 24). The

results (r value) of one mixed effect model predictor (mass) were rounded to -0.001 (from -0.000) because the statistical program R (<http://cran.r-project.org/>) used for analysis (Metafor package) only displays the first three decimal places of r values in mixed effect meta-analysis models. This was not thought to change the interpretation of the results because the pattern (positive or negative) of the slope, rather than the magnitude, is most important in assessing biological trends. Because large ranges and variances in the units of predictor variables can diminish slope severity, the overall slope pattern is most important. Other important variables in this meta-analysis are described in Table 2.

The open source software program R was used for statistical analysis. The Metafor package (Viechtbauer 2010) was employed for meta-analysis calculations.

Important Variables

Variable	Describes	In this meta-analysis
μ	Average effect size estimate for all studies	Positive values signify higher individual fitness in undisturbed populations
I^2	True variation in effect sizes between studies (heterogeneity)	High percentages indicate importance of predictors not included in model
Q	Test of significance for heterogeneity between studies	Significant p-values indicate importance of predictors not included in model

Table 2. Short description of important variables used in this meta-analysis.

Results

Ecotourist-Effect Hypothesis

Overall, disturbed populations exhibited lower fitness ($\mu = 0.411$) in the random effects model when exposed to IHD. This model, however, yielded a non-significant p-value with a confidence interval that crossed zero ($z = 1.206$, $p = 0.228$, $n = 21$, $SE = 0.341$, 95% CI = -0.257 to 1.079) (Figure 1, Table 4). High heterogeneity among effects sizes ($I^2 = 98.87\%$) was not due to sampling error, but due to explanatory factors absent from the model ($Q = 4874.27$, $p < 0.0001$, $df = 20$), justifying the search for significant predictors. An unweighted analysis yielded very similar results to the weighted model, suggesting that my initial results were not skewed by a few studies with large sample sizes ($\mu = 0.403$, $z = 1.212$, $p = 0.225$, $n = 21$, $SE = 0.332$, 95% CI = -0.248 to 1.054) (Table 4). When studies involving hunting-like disturbances were included in the random effects model, disturbed populations experienced greater reductions in fitness from IHD ($\mu = 0.487$, $z = 1.702$, $p = 0.088$, $n = 26$, $SE = 0.286$, 95% CI = -0.073 to 1.048). High effect size heterogeneity, however, again suggested the importance of explanatory factors not in the model ($I^2 = 98.65\%$, $Q = 4904.38$, $p < 0.0001$, $df = 25$) (Table 4).

Variation in behavioral responses to IHD

All combinations of nine predictor variables (excluding hunting) were investigated, using one, two, and three moderators in mixed effect models. Overall, the model with the lowest AIC included three predictors: average mass of species, total length of study (days), and diet of study species (AIC = 31.49) (Table 5). Mass influenced fitness effects for disturbed and undisturbed populations ($p = 0.01$; $z = -2.54$); as species increase in mass, disturbed populations are less affected by IHD. The large range and variance in mass (min = 11.5g, max = 183,000g, SD =

52541.37) decreased slope magnitude ($r = -0.001$), although a trend was evident (large range and variance in predictor variables dilutes slope severity). Similarly, study length was an influential

Studies Included in Meta-Analysis

Study	Year	Measure of Fitness	Species	LRR
(1) Barron	2012	fledgling success per egg	<i>Cardinalis cardinalis</i>	0.1853111
(2) Bisson	2009	energy expenditure	<i>Vireo griseus</i>	-0.2564621
(3) Bouton	2005	chicks fledged	<i>Mycteria americana</i>	0.51082562
(4) Dooley	2010	probability of return to treatment area (over 5 days)	<i>Anas platyrhynchos</i>	0.06899287
(5) Ellenberg	2009	heart rate increase	<i>Megadyptes antipodes</i>	0.92374674
(6) Ellenberg	2006	breeding success per nest	<i>Spheniscus humboldti</i>	0.38698029
(7) French	2011	offspring growth rate	<i>Zalophus californianus</i>	-0.1355455
(8) Goudie	2006	proportion of time spent feeding	<i>Histrionicus histrionicus</i>	0.00554018
(9) Guillemain	2007	proportion of time spent feeding	<i>Anas crecca</i>	-0.6010319
(10) Holm	2009	number of breeding pairs per year	<i>Limosa limosa</i>	-0.7884574
(11) Hughes	2008	percentage of individuals exhibiting active behaviors	<i>Aptenodytes patagonicus</i>	0.14148182
(12) Jayakody	2008	percentage of individuals vigilant	<i>Cervus elaphus</i>	1.5293952
(13) Lafferty	2006	chicks fledged	<i>Charadrius alexandrinus</i>	6.57925121
(14) Margalida	2011	breeding success	<i>Aegypius monachus</i>	0.31015493
(15) Martinez-Abraín	2008	flight initiation distance	<i>Larus michahellis</i>	-0.9495767
(16) Muehlenbein	2012	fecal glucocorticoid metabolite concentrations	<i>Pongo pygmaeus</i>	0.31188721
(17) Pangle	2010	percentage of time spent vigilant	<i>Crocota crocuta</i>	-0.2113091
(18) Thiel	2008	corticosterone metabolite concentration	<i>Tetrao urogallus</i>	0.33976985
(19) Viblanc	2012	duration of maximum heart rate	<i>Aptenodytes patagonicus</i>	-0.5155
(20) Weston	2005	chick foraging time per hour	<i>Thinornis rubricollis</i>	0.43954442
(21) Zuberogoitia	2008	number of fledglings produced	<i>Neophron percnopterus</i>	0.18459318
(22) Broseth	2010	total homerange	<i>Lagopus lagopus</i>	0.19863714
(4) Dooley	2010	probability of return to treatment area (over 5 days)	<i>Anas platyrhynchos</i>	0.53551824
(23) Neumann	2010	diurnal activity range	<i>Alces alces</i>	2.44956728
(17) Pangle	2010	percentage of time spent vigilant	<i>Crocota crocuta</i>	0.63305401
(24) Rumble	2005	average movement per hour	<i>Cervus elaphus</i>	0.29577424

Table 3. List of studies included in random and mixed effect models. Studies are listed by lead author and year. The behavioral measure of fitness used is listed, along with species (n.b. if multiple species data were averaged, the species with the most data is listed). Log response ratios (LRR) were used as a measure of fitness, and positive values represent higher fitness in undisturbed environments. The five studies involving hunting-like disturbances included in the separate analysis are listed below the partition. Complete authorships correspond to numbers above: (1) Barron, D.G., Brawn, J.D., Butler, L.K., Romero, L.M. and Weatherhead, P.J. 2012; (2) Bisson, I., Butler, L.K., Hayden, T.J., Romero, L.M. and Wikelski, M.C. 2009; (3) Bouton, S., Frederick, P.C., Rocha, C.D., Dos Santos, A.T.B. and Bouton, T.C. 2005; (4) Dooley, J.L., Sanders, T.A. and Doherty, P.F. 2010; (5) Ellenberg, U., Mattern, T. and Seddon, P.J. 2009; (6) Ellenberg, U., Mattern, T., Seddon, P.J. and Jorquera, G.L. 2006; (7) French, S.S., Gonzalez-Suarez, M., Young, J.K., Durham, S. and Gerber, L.R. 2011; (8) Goudie, R. Ian. 2006; (9) Guillemain, M., Blanc, R., Lucas, C. and Lepley, M. 2007; (10) Holm, T.E. and Laursen, K. 2009; (11) Hughes, K.A., Waluda, C. M., Stone, R.E., Ridout, M.S. and Shears, J.R. 2008; (12) Jayakody, S., Sibbald, A.M., Gordon, I.J. and Lambin, X. 2008; (13) Lafferty, K.D., Goodman, D. and Sandoval, C.P. 2006; (14) Margalida, A., Moreno-Opo, R., Arroyo, B.E. and Arredondo, A. 2011; (15) Martinez-Abraín, A., Oro, D., Conesa, D. and Jimenez, J. 2008; (16) Muehlenbein, M.P., Ancrenaz, M., Sakong, R., Ambu, L., Prall, S., Fuller, G. and Raghanti, M.A. 2012; (17) Pangle, W.M. and Holekamp, K.E. 2010; (18) Thiel, D., Jenni-Eiermann, S., Braunisch, V., Palme, R. and Jenni, L. 2008; (19) Viblanc, V.A., Smith, A.D., Gineste, B. and Groscolas, R. 2012; (20) Weston, M.A. and Elgar, M.A. 2005; (21) Zuberogoitia, I., Zabala, J., Martinez, J.A., Martinez, J.E. and Azkona, A. 2008; (22) Broseth, H. and Pedersen, H.C. 2010; (23) Neumann, W., Ericsson, G. and Dettki, H. 2010; (24) Rumble, M.A., Benkobi, L. and Gamo, R.S. 2005.

Results from Random Effects Models

Meta-analysis Model	μ	p-value	Z	n	SE	95% CI
Random Effects Model (REM)	0.411	0.228	1.206	21	0.341	-0.257 to 1.079
Unweighted REM	0.403	0.225	1.212	21	0.332	-0.248 to 1.054
Hunting REM	0.487	0.088	1.702	26	0.286	-0.073 to 1.048

Table 4. A comparison of statistical values from the three random effects models (μ represents overall effect size estimate for studies included in the model).

($p < 0.001$; $z = 10.93$) predictor of variation in fitness values. Longer study lengths found greater negative fitness effects from IHD. Again, a large range and variance in values (min= 2.5 days, max= 1460 days, SD= 353.85) reduced slope magnitude ($r = 0.0043$), although a biological pattern was clear. The diet of a species (herbivore, carnivore, or omnivore) was also an important predictor ($p = 0.04$; $z = -2.03$) of fitness differences. Carnivores ($n = 13$) were more negatively impacted by IHD than omnivores ($n = 5$). Herbivores were not statistically different from either group, or perhaps because of their underrepresentation ($n = 3$) (Figure 2), the true effect was not apparent. High heterogeneity among effect sizes suggests other meaningful predictors were not considered in the overall mixed effect model ($I^2 = 87.87\%$, $QM = 139.98$, $p < 0.0001$, $df = 3$).

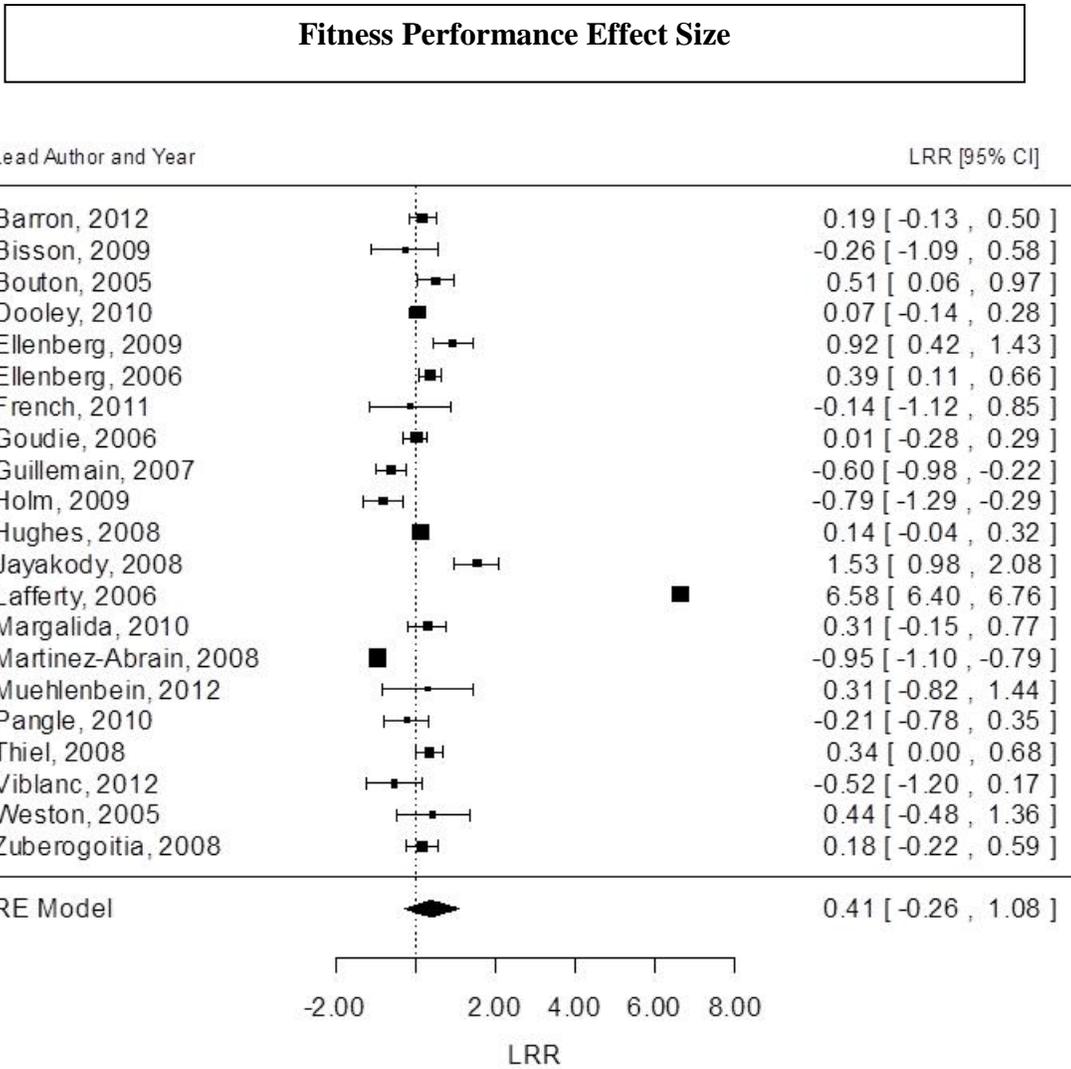


Figure 1. Forest plot depicting effect sizes for individual studies of behavior in response to IHD. Boxes represent log response ratios (LRR), with greater box width signifying a larger sample size. Whiskers represent 95% confidence intervals. Increasingly positive values represent better fitness outcomes when undisturbed.

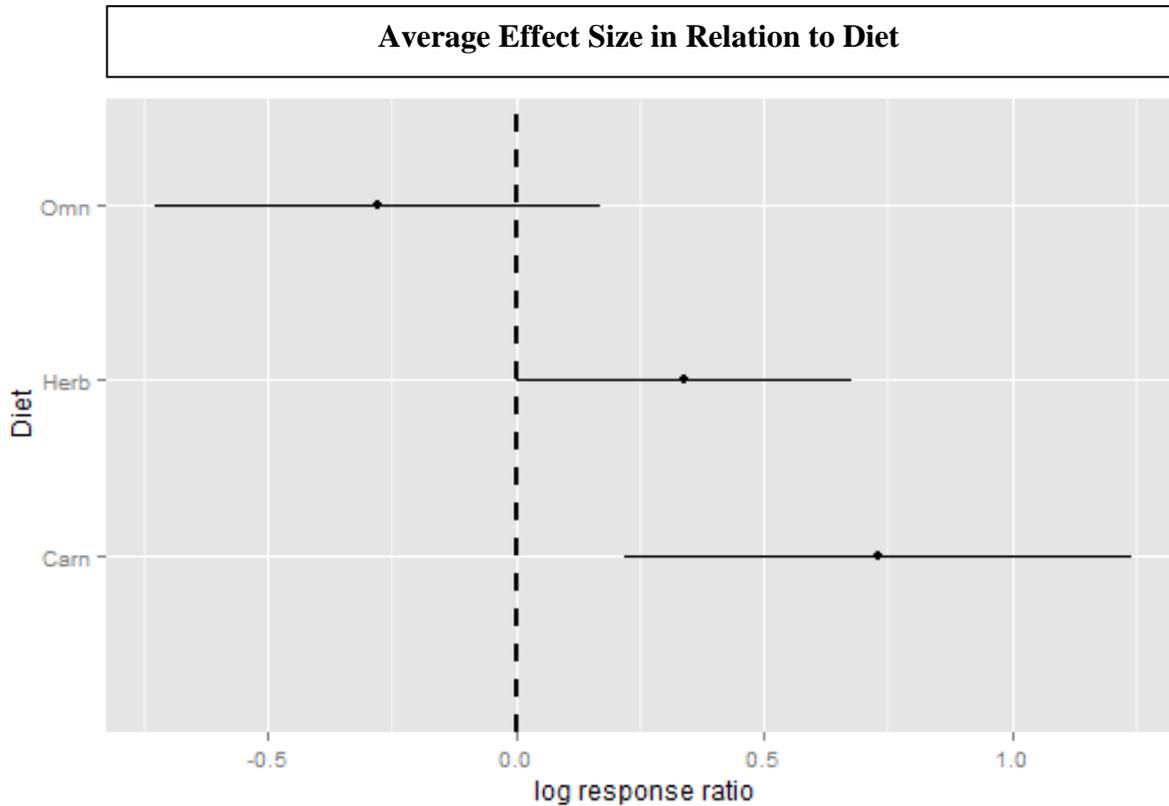


Figure 2. Forest plot showing influence of diet on effect size for omnivores (n= 5), herbivores (n= 3), and carnivores (n= 13) with 95% confidence intervals. Positive values represent better fitness outcomes when undisturbed.

A comparison of the twenty-four best (lowest AIC scores) mixed effect models (one, two, and three predictors) revealed a trend in explanatory power. If the number of times each variable was present in low-AIC models is used as a measure of value, their order of importance is: Length of study, generation time, diet, sociality, mass, habitat and season (equivalent), and local disturbance history and fitness measure (equivalent) (Table 5).

Akaike Information Criterion Scores of Best Models

Mixed Effect Model	AIC Score
Diet, Mass, Study Length	31.49
Generation Time, Sociality	31.5
Mass, Sociality, Study Length,	32.37
Generation Time, Season, Sociality	32.37
Generation Time, Season	33.66
Generation time, Mass, Study Length	33.66
Mass, Study Length	33.95
Habitat, Study Length	35.11
Sociality, Study Length	35.26
Diet, Generation Time, Study Length	35.47
Diet, Sociality, Study Length	35.58
Fitness Measure, Study Length	35.72
Diet, Fitness Measure, Study Length	35.86
Habitat, History of Disturbance, Study Length	35.9
Diet, Habitat, Study Length	35.9
Generation Time, Habitat, Study Length	36.01
Generation Time, Sociality, Study Length	36.04
Diet, Study Length	36.16
Diet, History of Disturbance, Study Length	36.48
Study Length	36.5
Fitness Measure, Generation Time, Study Length	36.57
Diet, Season, Study Length	36.62
Generation Time, History of Disturbance, Study Length	37.66
Generation Time, Season, Study Length	37.68

Table 5. Comparison of the 24 best (lowest) AIC scores for all mixed effect models. Only AIC scores affected model order, each may include one, two, or three predictors. After these first 24, other models nearly doubled in AIC values.

Discussion

Random effects model

I found a high degree of heterogeneity among studies, similar to other conservation meta-analyses (Ibanez-Alamo et al. 2012; Stankowich 2008). While high heterogeneity makes identifying trends difficult (Higgins & Thompson 2002), the random effects model still revealed a biological pattern suggesting that IHD negatively impacts fitness in wild populations ($\mu = 0.411$) (Figure 1). This trend, however, was not significant and the Null Hypothesis cannot be rejected. Four variables can explain the observed heterogeneity in fitness between studies, and the interactive effects from direct anthropogenic disturbance may augment fitness consequences for wildlife.

Generation time and mass

In contrast to previous studies (Rytwinski & Fahrig 2012; Rytwinski & Fahrig 2011; Blumstein 2006), I found that larger species with longer generation times are less affected by human disturbance. Rytwinski and Fahrig (2012; 2011) reported reduced abundance of larger species in close proximity to disturbed habitat. Because they used measures of abundance rather than fitness, however, it is unclear whether individual survival and reproduction were negatively impacted. Blumstein (2006) also found greater intolerance of disturbance for large species when using flight initiation distance (FID) in response to IHD as a fitness proxy. He suggests that conspicuousness to predators and reduced agility associated with large size may explain flushing at greater distances. I suggest two possible explanations for my contrary findings. First, using more concrete measures of fitness may have resulted in a better representation of the true effects of human disturbance. Just as mating success does not necessarily measure paternity (Leftwich et

al. 2012), overt behavioral responses to IHD may not result in reductions of fitness. The early flight responses of larger species found by Blumstein (2006) could function to reduce IHD exposure duration and prevent the accumulation of harmful stress-hormones. The second possible explanation for diminished fitness consequences in larger species with longer generation times is habituation. These traits are associated with longevity, which may provide increased learning opportunities for individuals through experience. Brain size positively correlates with mass and generation time across species (Rushton 2004), which could indicate an aptitude for learning adaptive responses to IHD cues. Alternatively, previous conclusions of a lower effect of disturbance on the fitness of larger species may reflect a difficulty in assessing it in species that reproduce at relatively slow rates. Longer-lived species are difficult (e.g. time and cost) to study for substantial portions of their existence (Austad 2001). Increasing study length could result in findings more consistent with those of my meta-analysis.

Study length

Study length explained the most variation ($p < 0.001$; $r = 0.0043$) in effect size between studies, with longer studies reporting more harmful effects of IHD on wildlife. In general, fundamental changes in the data that are gathered occur with variations in study length (Kapfer et al. 2011). Longer study times may more accurately reflect true values because fitness can change radically across a lifetime (DuVal 2012). Longer study times, however, may not always yield more relevant data. The costs and benefits of responses to IHD may change at different times of the year (e.g. higher cost of fleeing when defending a territory during the reproductive season). A shorter study spanning a period of greater vulnerability may better measure the impact of IHD than a relatively longer study during different times of the year. The majority of studies I used in the random effects model included data collected during the study species' breeding season. If

including periods of the year when individuals may be most vulnerable (e.g. breeding season) (most of the current studies included this), it seems probable that the negative correlation between study length and fitness effects in response to IHD reflects greater validity of data from longer studies.

Diet

I found diet to be an important predictor of behavioral responses to IHD. The biological pattern suggests that carnivores are most negatively affected by IHD, followed by herbivores.

Omnivores actually had marginally higher fitness in disturbed environments (Figure 2). Diet has been reported as a potential predictor of response to IHD (Heil et al. 2007; Geist et al. 2005; Blumstein 2006); however, no clear pattern exists in the literature. Blumstein (2006) reported species that capture live prey were more intolerant of disturbance. He suggested that these species might have greater sensory perception devoted to identifying movement, making them more responsive to IHD. Most predators do have extraordinary mechanisms for processing visual information (Thery & Gomez 2010). Additionally, the foraging habits of predators may be disrupted more than other life history strategies for two reasons. First, active hunting requires higher energetic expenditure than most foraging strategies (Gorman et al. 1998). Human disturbance might alter prey behavior and reduce hunting efficiency, or elicit costly flight responses in predators that are already burdened energetically. A second explanation involves increased kleptoparasitism from intra and interspecific predators. The high energetic costs of hunting impose selective pressures that favor stealing food from sympatric predators (or killing them directly), and predators have adapted to separate (spatially and temporally) foraging activities to reduce competition (Schuette et al. 2013). Human disturbance may disrupt optimal niche partitioning, and increase competition between carnivores.

I suggest three reasons why herbivores may also be vulnerable to harm from IHD. First, their diet is more difficult to digest. Because of the low rates of plant cell wall degradation, herbivores must consume large quantities of food and process it for long periods to extract nutrients (Steuer et al. 2011). In addition, as herbivore body size increases, average food quality decreases due to higher absolute nutrient requirements limiting picky grazing (Muller et al. 2013). Secondly, a low rate of energy return requires longer foraging durations; if IHD disrupts foraging, herbivores may suffer high fitness costs. Lastly, herbivores may face competition from domesticated ungulates (Acebes et al. 2012; but see Iranzo et al. 2013). This could limit food availability, and would compound the negative effects of IHD that reduce foraging time. In contrast to carnivores and herbivores, I found omnivores to be more tolerant of IHD. This reduced effect on fitness might exist because of a relatively wider spectrum of dietary options. For example, some omnivore populations have distinct foraging strategies that differ in food composition (McLellan 2011). If IHD disrupts a facultative foraging strategy, some omnivores may not suffer fitness reductions by utilizing alternative resources. It is important to remember, however, that herbivore and omnivore sample sizes were low and more information is needed to confirm the observed biological pattern.

Hunting influence

When I included studies involving hunting or hunting-like disturbances in the random effects model, the reduction in fitness of disturbed populations was greater (Table 4). Given that only five new data points were added in this analysis, the true effect of hunting may differ. The added influence of hunting may reduce the perceived reliability of informational cues, resulting in more harmful responses to IHD. For example, predator recognition and avoidance strategies can be costly to an individual (Fortin et al. 2004). When animals experience hunting, they may associate

predation with all types of human activities. When all humans are perceived to be predators, anti-predator behaviors are more costly due to over-stimulation. Although it is advantageous to flee from a hunting human, also fleeing from IHD may deplete vital energy reserves and increase opportunity costs by changing behavior.

All types of hunting, however, may not exacerbate negative fitness outcomes resulting from IHD. For example, humans often hunt artiodactyls from a stationary platform attached to a tree (tree stand). Because shots can be taken from great distances, conspecifics in close proximity probably only hear gunfire and flee before identifying human presence. Individuals exposed to this kind of hunting should not be more likely to associate IHD with predation than non-hunted populations. In addition, other species exposed to human hunting but not directly targeted should not be expected to readily react to humans as predators because their populations have not been experiencing selective pressure favoring that response.

Additive effects

I have identified at least five variables that are important in assessing behavioral responses of wildlife to indirect (IHD) disturbance. Wild populations, however, are not subject to indirect human influence alone. Direct anthropogenic harm to wildlife (i.e. habitat destruction, pollution, hunting, and introducing exotic species) interacts with indirect disturbance, and the effect may result in additive harm to individual fitness. For example, Thick-billed Murre (*Uria lomvia*) populations in eastern Canada are exposed to human harvest and oil pollution, which may threaten population stability (Wiese et al. 2004). Because of a carnivorous diet, small mass, and short generation time, these populations could be highly vulnerable to fitness reductions from IHD. The interaction of these indirect disturbances with direct anthropogenic harm is likely to

further reduce Murre populations. Another example of the possible additive effects of indirect and direct anthropogenic disturbance can be seen on the Pacific Island of Guam. Habitat destruction and the introduction of the non-native Brown Tree Snake (*Boiga irregularis*) have driven multiple species of birds, mammals, and reptiles to extinction (Mortensen et al. 2008). Reductions in fitness caused by IHD could force vulnerable species into extinction on the island. The results of this meta-analysis suggest that smaller species with shorter generation times, along with carnivores, would be most susceptible to further population declines from the additive effects of human disturbance.

Conclusion

I found that inadvertent human disturbance has no common harmful effect on the fitness of all types of wildlife. Small species with short generation times, and carnivores, in particular, seem to be more likely to suffer from IHD. However, our ability to detect reductions in fitness due to disturbance depended on study length. When human hunting-like disturbances occurred along with IHD, the overall effect on fitness was greater. High heterogeneity among studies made pattern identification difficult, and suggests that additional variables are influential in explaining variation. Sih's (2013) framework for understanding which factors influence behavioral responses to HIREC can benefit future study methodologies. Because indirect and direct sources of human disturbance to wildlife may have additive influences on fitness, considering the interactive effects of multiple variables will better inform conservation decisions.

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Chapter 3

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APPENDIX

APPENDIX I. FECAL PARASITE IDENTIFICATION

Parasite Name	Presumed Phyla	Descriptor	Distinguishing features	Image
Ramus	Nematoda	Thin, sinuous ends that gradually increase in girth near the center of worm-like body. Dark-yellow to brown body cavity, typically lighter near each end. Occasional branching structure originating from near the center of the organism totaling no more than 1/5 of total length- resembles “budding” of some asexual invertebrates.	Thin, winding ends and “budding” structure	16, 18, 22
Calix	Nematoda	Long, thin worm-like body gradually tapers near distal end. “Cephalized” region protrudes ventrally into a “cup-like” shape, with wider side facing downward. Color	“Cup-like” proximal end and long, thin body shape	10

		refractive		
Crescent Worm	Nematoda	Relatively shorter thin, worm-like body. Usually, entirety of body curved to form a crescent shape. Near proximal end, body slightly narrows, abruptly, before again widening to give the appearance of a small head.	Crescent shape and thin, tapering body	3, 4, 5
Mushroom-headed Worm	Nematoda	Relatively wider, worm-like body of uniformly similar width. Proximal end widened and rounded to give the appearance of a “mushroom cap.” Color dark yellow and refractive.	“Mushroom” head	6, 7
Robustus	Nematoda	Short, plump worm-like body that is usually curved at an angle of approximately 120°. Proximal end slightly widened and flattened at terminus.	Short, stout body with flattened proximal end	8, 9

		Color dark-yellow and refractive.		
Falx Worm	Nematoda	Short, curving worm-like body of similar uniform width. Proximal end is flattened. Distal end curves strongly, proximally to form a hooked shape. Color dark-yellow and refractive.	“hooked” distal end	15, 20
Cellula	Nematoda	Short, corpulent worm-like body that tapers to a point abruptly at distal end. Proximal end abruptly flattens. Body cavity appears compartmentalized, with different sections having varying colors from yellow to dark-brown and/or refractive.	Short, compartmentalized body	34
Egg	Nematoda	Oval-shaped egg approximately 1.5 times the length of its width. Distinctive narrow ring around the outer		17, 35

		<p>most portion, with the inner section appearing a slightly different (lighter or darker) shade of dark-yellow/brown as compared to the outer section.</p> <p>Inner section also contains folds of non-refractive material.</p>		
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Descriptions of common parasites (other than Coccidia) found in Ocellated Turkey fecal samples. Image numbers refer to microscope photos located at <http://otparasitepics.shutterfly.com/>.

VITA

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Education

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May 2007 Mississippi State University, Starkville, MS
B.S. Biology

Teaching and Work Experience

Graduate Assistantship (August 2010 – May 2013) **University of Mississippi Biological Sciences Department**

- Mastered material commensurate with teaching responsibilities for three curricula: BISC 160, BISC 161, BISC 163
- Helped devise assignments and class projects appropriate for assessing student performance
- Responsible for managing concerns and grades of approximately 90 students each semester

AmeriCorps Program (October 2009 - July 2010) **Environmental Educator: Department of Environmental Protection in Maine**

- Headed the WaterShed Protection Grant Program for the Maine Department of Environmental Protection:
- Traveled throughout the state of Maine to high schools and middle schools teaching the ecology of freshwater systems
- Researched Low-Impact-Development legislation to bolster efforts to change Maine law for the amelioration of water quality in the state.

Publications

Buchholz, R. & Hanlon, E. (2011). Ecotourism, Wildlife Management, and Behavioral Biologists: Changing Minds for Conservation. Chapter 17: Behavioral Responses to a Changing World, Oxford University Press.

O.A. Gutierrez, M.J. Wubben, M. Howard, B. Roberts, **E. Hanlon**, & J.R. Wilkinson. (2009). The Role of Phytohormones Ethylene and Auxin in Plant-Nematode Interactions. *Russian Journal of Plant Physiology* 56(1), 1-5.

Awards and Scholarships

- RJ Young Company Employee of the Month for August 2008
- Charles Sivelle Scholarship (2012)
- Reginald Ott Fellowship for Graduate Research in Biological Studies (2012)
- Sigma Xi Grants-in-Aid of research (2011)
- University of Mississippi Graduate Student Council Research Grant (2011)
- Charles Sivelle Scholarship (2011)
- Reginald Ott Fellowship for Graduate Research in Biological Studies (2011)
- National Scholars Honor Society
- Tri Beta Biological Honors Society
- National Dean's List
- Mississippi State University Dean's List