

VISUAL THRESHOLDS OF WHITE-TAILED DEER AS DETERMINED
BY BEHAVIORAL ASSAY

by

BRADLEY STEPHEN COHEN

(Under the Direction of Karl V. Miller and Robert J. Warren)

ABSTRACT

Despite the important role vision plays in a deer's (*Odocoileus virginianus*) perception of its environment and its consequent behavior, there has been little study of deer vision. Much of what is understood about deer vision is based on the anatomical structure of the eye, characteristics of photoreceptors in the retina, and electrophysiological measurements of photoreceptoric cells. However, similar inferences in other species were not validated in subsequent behavioral assays. Thus, assumptions about visual capabilities of animals require direct behavioral substantiation. Therefore, I used a behavioral measure to examine the spectral sensitivity of deer. I created a deer-training-apparatus (DTA) to train deer to associate a stimulus light with a food reward. After successfully training deer by utilizing the DTA, I tested their responsiveness to monochromatic lights in the ultraviolet and infrared spectrum and compared it with previous studies examining their photoreceptive sensitivity. I confirmed that deer's relative sensitivity to wavelengths of light in the infrared and ultraviolet spectrum was similar to that of their previously measured photoreceptor sensitivity.

INDEX WORDS: Behavior, Conditioning, *Odocoileus virginianus*, Perception, Vision, White-tailed deer

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by

Bradley Stephen Cohen
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BRADLEY STEPHEN COHEN

Major Professor: Karl V. Miller
 Robert J. Warren

Committee: John C. Maerz
 Adam S. Goodie

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
May 2011

TABLE OF CONTENTS

	Page
LIST OF FIGURES	vi
CHAPTER	
1 INTRODUCTION AND LITERATURE REVIEW	1
Introduction.....	1
Literature Review.....	3
Objectives	6
References.....	7
2 AN AUTOMATED DEVICE FOR TRAINING DEER TO VISUAL STIMULI....	12
Abstract.....	13
Introduction.....	13
Materials and Methods.....	14
Results and Discussion	17
Acknowledgements.....	18
References.....	19
3 SENSITIVITY OF WHITE-TAILED DEER TO ULTRAVIOLET AND INFRARED LIGHT: A BEHAVIORAL ASSAY	28
Abstract.....	29
Introduction.....	29
Methods.....	31
Results and Discussion	33

Acknowledgements.....	36
References.....	37
4 SUMMARY AND CONCLUSIONS	49
APPENDIX A: WIRING SCHEMATIC OF DEER-TRAINING-APPARATUS	51

LIST OF FIGURES

Figure 2.1: Deer-training-apparatus (DTA) showing the (1) programmable relay and (2) food dispenser (A), the side-by-side orientation of the two trough-boxes (B), and the device from inside the barn stall with (3) trough lids open and (4) lights above the lids (C).....	22
Figure 2.2: Functional block diagram of the program for “deer-training- apparatus” (DTA). After recording the data from the previous day’s session, the program is restarted and the light to be illuminated is assigned randomly. Performance, checked by correct (Y) or incorrect (N) decisions, is registered by the computer and verified by observers on randomly chosen intervals	24
Figure 2.3: Mean behavioral performance of the six adult, female white-tailed deer. The dotted line represents 75% correct. The vertical bars represent the 95% confidence interval	26
Figure 3.1: Deer-training-apparatus (DTA) showing the (1) programmable relay and (2) food dispenser (A), the side-by-side orientation of the two trough-boxes (B), and the device from inside the barn stall with (3) trough lids open and (4) lights above the lids (C).....	39
Figure 3.2: Functional block diagram of the program for “deer-training- apparatus” (DTA). After recording the data from the previous day’s session, the program is restarted and the light to be illuminated is assigned randomly. Performance, checked by correct (Y) or incorrect	

(N) decisions, is registered by the computer and verified by observers on randomly chosen intervals	41
Figure 3.3: Performance of one deer at one wavelength (650 nm) in an increment-threshold discrimination task. At each wavelength, the intensity of the monochromatic light was varied in steps of 0.3 log unit, with a range of intensities pre-selected so as to produce discrimination performance that varied from approximately 90% correct down to chance performance. The data was fit to a best fit line and the sensitivity threshold of each deer was determined at the intensity in which the deer performed at 70%	43
Figure 3.4: Mean (+/- standard error) behavioral performance of the seven adult, female white-tailed deer tested at a supra-threshold white-light. Deer were tested at this light for eight days before switching to other test lights to ensure they had retained their learned behavior. The dotted line represents 75% correct.....	45
Figure 3.5: Mean (+/- 95% C.I.) behavioral spectral sensitivity of seven female white-tailed deer obtained in an increment-threshold discrimination task. The solid lines represent the photoreceptive sensitivity function reported by Jacobs et al. (1994), showing the reported sensitivity of both the short-wavelength and medium-wavelength sensitive cone. The points represent sensitivity measurements which have been fitted by determining the best additive fit of the cone template functions.....	47

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Abundant white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780), populations can result in significant societal conflicts when they overlap with dense human populations. Annually on U.S. roadways, deer-vehicle collisions (DVCs) result in \$1.1 billion in damages and the loss of 200 human lives (Sullivan and Messmer 2003). Approximately 1.5 million drivers are involved in DVCs each year, many of which go unreported (State Farm Insurance Company 2006). Various techniques have been employed to mitigate DVCs, most of which have proven ineffective and costly (D'Angelo et al. 2004).

Mitigation techniques aimed at reducing DVCs typically rely on important aspects of deer physiology, such as hearing and vision. Deterrent devices based on deer vision or hearing, such as roadside reflectors and deer whistles, are ineffective at altering deer behavior and reducing DVCs (D'Angelo et al. 2006, Valitzski et al. 2009). Although recent studies have investigated the visual physiology of deer (D'Angelo et al. 2008) and despite a wealth of knowledge about white-tailed deer, little is known about deer vision and its role in deer behavior (VerCauteren and Pipas 2003) which may confound production of effective DVC deterrents.

Wildlife warning reflectors have been commonly employed along highways in attempts to reduce DVCs by “provid[ing] an optical warning fence to deer” (Strieter Corp., unpublished instruction manual:3). These reflectors are mounted on posts along roadsides and contain two reflective mirrors with plastic elements that redirect light from car-lights into the roadside

corridors. However, these systems are designed without a full understanding of deer visual capabilities and echo a significant problem with DVC deterrent devices – these systems are designed without exploiting the senses of the white-tailed deer (D'Angelo 2004). The color most commonly reflected from these devices is red, a wavelength well above the peak sensitivity of a deer's retinal photoreceptors (Zacks 1985, Jacobs et al. 1994). Therefore, it is not surprising that numerous studies have shown these reflectors and other devices reliant on deer vision are ineffective at reducing DVCs (Boyd 1966, Gilbert 1982, Zacks 1986, Waring et al. 1991, Armstrong 1992, Reeve and Anderson 1993, Sielecki 2001, D'Angelo et al. 2006, Blackwell and Seamans 2008) or altering deer behavior (Waring et al. 1991; Ujvári et al. 1998; VerCauteren et al. 2003, 2006; D'Angelo et al. 2006). A better understanding of the visual capability of white-tailed deer would provide the basis for developing efficient and physiologically relevant strategies to reduce DVCs (D'Angelo et al. 2004, 2006; Blackwell and Seamans 2008).

Most of what is known about deer vision is based on an understanding of the general physiological mechanisms underlying vision, even though similar assumptions have been found to be untrue in other species (Jacobs 1992). Understanding the visual capabilities of any animal requires coupling physiological studies with behavioral observation and substantiation (Jacobs 1992). To date, only three studies have been published that used a behavioral measure to examine the visual capabilities of white-tailed deer (Zacks and Budde 1983, Zacks 1985, Smith et al. 1989). However, each of these studies was limited by small sample size, as well as brightness, luminance and other variables that influence visual systems (VerCauteren and Pipas 2003).

Previously, D'Angelo (2007) examined morphological characteristics of the white-tailed deer eye. My research will use behavioral measures of deer visual thresholds, to delineate the differences between reported photoreceptive activity (Jacobs et al. 1994) and perceptive sensitivity particularly at the purported extreme ends of the deer's visual spectrum.

LITERATURE REVIEW

The eye of the white-tailed deer is typical of mammals in that light travels through the cornea, enters the eye via the pupil opening, and passes through the lens, aqueous humour, and vitreous humour before striking the retina (Walls, 1942). The retina contains photoreceptors responsible for converting the stimulus light into a neurological signal that is sent via the optic nerve to the brain where perception of the light occurs.

Deer eyes are well adapted to low light conditions, containing a tapetum lucidum that acts as a mirror, reflecting incident light that hasn't been absorbed by photoreceptors back to the retina (Duke-Elder 1958). The tapetum lucidum is a half-moon-shaped structure specialized for amplifying visual sensitivity and acuity of darker objects (D'Angelo et al. 2008). The tapetum lucidum of white-tailed deer is specialized to reflect short-wavelength blue colors and medium wavelength yellow colors (D'Angelo et al. 2008). Therefore, light that enters the eye of a white-tailed deer has multiple changes to be absorbed, and sensitivity to blue-yellowish wavelengths is enhanced. It is the tapetum lucidum that helps make the white-tailed deer's eye light-sensitive, providing an improved interpretation of visual images in low-light conditions (Ali and Klyne 1985).

The anatomical structure of the white-tailed deer eye is well adapted for their crepuscular activity (D'Angelo et al. 2008). Deer also possess a horizontal slit pupil that facilitates efficient eye function in a range of lighting conditions (D'Angelo et al. 2008). The horizontal slit pupil is

important for controlling the amount of light entering the eye and is capable of extreme vertical adjustments ranging from a narrow slit in bright light to a broad oval in low light situations (D'Angelo et al. 2008). The horizontal slit pupil allows the highly light-sensitive visual system of the white-tailed deer to function in full daylight without overwhelming the photoreceptors of the retina (Ali and Klyne 1985). At the same time this horizontal slit pupil helps enhance visual acuity by enabling all wavelengths of light to be focused on a strip of retinal cells that contain high densities of photoreceptors (Malmström and Kröger 2006).

Deer retinas contain both rod and cone photoreceptors (Witzel et al. 1978). Rod and cone photoreceptors respond differently to similar wavelengths of light. The photopigment in each type of cell is sensitive to different ranges of wavelengths and responds maximally to a specific wavelength, referred to as its peak sensitivity. Rod photoreceptors take little energy to activate and are responsible for vision in low-light conditions. In white-tailed deer, rod pigments have peak sensitivity at wavelengths of 497nm, which corresponds to blue-green light (Jacobs et al. 1994).

Cone photoreceptors contain highly specialized photopigments that require more energy to activate and are responsible for the perception of colors. Deer are dichromats—their eyes contain two types of cones with different spectral sensitivities (Jacobs et al. 1994, Jacobs et al. 1998). One cone photoreceptor contains a short-wavelength photopigment having peak sensitivity at 450–460 nm (Jacobs et al. 1994). The other cone photoreceptor contains a middle-wavelength photopigment having peak sensitivity at 537 nm (Jacobs et al. 1994). Cone photoreceptors are distributed throughout the deer's retina, but middle-wavelength cones occur at highest densities (~32,000/mm²) along a horizontal visual streak that aids in expanding the deer's field of view and visual acuity (Jacobs et al. 1994, D'Angelo et al. 2008).

Under low-light conditions, rod photoreceptors produce the majority of the electrical signals to the brain, aiding in the production of uncolored vision (Jacobs 1993). Under conditions with ample light, rod photoreceptors are over-stimulated and stop generating signals to the brain. In this situation, cone photoreceptors produce the majority of the signals, leading to the perception of both blue and yellow-green colors (Jacobs et al. 1994). This distinction of two different colors enables deer to perceive the difference between the land and the sky, helping them to better detect objects along the horizon (D'Angelo et al. 2008).

Despite the important role vision plays in a deer's perception of its environment and its consequent behavior (Sauer 1984, Birgersson et al. 2001), there has been little study in this area (Jacobs 1993, D'Angelo et al. 2004). Most of what is assumed about how deer perceive visual stimuli is based on the anatomical structure of the eye and the types of photoreceptors in the retina (VerCauteren and Pipas 2003). Similar inferences in other species, such as the pigeon (*Columba livia*) and the turtle (*Pseudemys scripta elegans*), have not been verified (Kreithen and Eisner 1978, Arnold and Neumeyer 1987). Thus, statements about visual capabilities require direct behavioral substantiation (Jacobs 1992).

Only three behavioral investigations of the visual capabilities of white-tailed deer have been published. Zacks and Budde (1983) used operant conditioning to demonstrate that white-tailed deer could discriminate between a long-wavelength stimulus and an achromatic stimulus. Utilizing a similar operant conditioning paradigm, Zacks (1985) further concluded deer were most sensitive to light at 545 nm. In a forced-choice feeding test, deer learned to discriminate between short-wavelength (500 nm) and long-wavelength (580-620 nm) stimuli, suggesting that deer could discriminate green from yellow and orange (Smith et al. 1989). However,

interpretation of these studies is difficult due to small sample size, brightness, hue, luminance and other variables that influence the visual systems of animals (VerCauteren and Pipas 2003).

Birgersson et al. (2001) attempted to address whether brightness was a possible confounding factor in the behavioral visual studies of cervids. They demonstrated that fallow deer (*Dama dama*) chose a color stimulus associated with a positive reward regardless of varied brightness and concluded that fallow deer use color to discriminate between visual stimuli. However, this study utilized a small sample and the colors painted onto stimulus plates expressed wavelengths across a large proportion of the visible light spectrum. Consequently, delineating what specific wavelength elicited the response is impossible. Because animals may solve discrimination problems in multiple ways, interpretation of studies employing complicating variables is open to bias (Jacobs 1981). Thus, a well-designed, operant-conditioning experiment that eliminates confounding variables is necessary to determine the sensitivity of white-tailed deer to various wavelengths.

OBJECTIVES

The goal of this research was to delineate the relative sensitivity of deer to wavelengths in the ultraviolet and infrared spectrum. My specific objectives were:

1. Design an automated device to train deer to associate a stimulus light with a food reward.
2. Examine if multiple devices could be used to train different deer at the same time.
3. Use this device to examine visual thresholds of deer to light at 360 nm, 405 nm, 430 nm, 590 nm and 650 nm.

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CHAPTER 2

AN AUTOMATED DEVICE FOR TRAINING DEER TO VISUAL STIMULI¹

¹Cohen, B.S., D.A. Osborn, G.R. Gallagher, R.J. Warren, K.V. Miller. 2011. To be submitted. .

ABSTRACT

Although many aspects of white-tailed deer (*Odocoileus virginianus*) biology and physiology have been studied thoroughly, few studies have confirmed deer cognitive perception, partly because of the difficulty of efficiently training sufficient numbers of deer to respond behaviorally in controlled experiments. We present a system that trains white-tailed deer to associate a supra-threshold, white-light stimulus with a food reward through operant conditioning techniques. The "deer-training-apparatus" (DTA) automatically dispenses food, rings a start buzzer, randomly assigns a stimulus light over one of two troughs, and registers a deer's choice. If a deer goes to a trough with the light illuminated, then a correct choice is registered and it is allowed to feed. All six deer tested met successful training criteria by Day 19, and a performance of $88.2 \pm 3.9\%$ correct choices by Day 25. We conclude that the DTA presents an effective and efficient way of training white-tailed deer, and provides an experimental platform for future research on behavior, perception, and preference. Thus, the DTA should be useful to researchers evaluating behavioral response of deer, and possibly other wild and domestic species, to various visual and auditory stimuli.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) likely provide more benefits to human society than any other North American wildlife species, with a net annual monetary value of >\$12 billion (Conover, 1997). Unfortunately, when deer become locally overabundant, conflicts with human interests often develop, resulting in economic, ecological and personal impacts. Various scientific studies have focused on strategies to minimize deer vehicle collisions and to reduce damage to cultivated plants (e.g., Blackwell and Seamans, 2008; VerCauteren et al., 2003, 2006). However, despite some understanding about white-tailed deer visual and auditory physiology

(D'Angelo et al., 2007, 2008; Heffner and Heffner 2010), little research has focused on deer perception of their environment, which may confound the efficacy of damage control strategies.

An understanding of deer perception requires direct behavioral validation to substantiate physiologically based suppositions (Coren et al., 1999). Without behavior-based research, we might not recognize possible disconnects between deer physiology and perception. However, training individual deer to respond in behavior-based trials is time consuming and difficult (Zacks and Budde, 1983; Zacks, 1985; Birgersson et al., 2001). Although technology has greatly enhanced the training efficiency of laboratory animals (e.g., Bhatt and Wright, 1992; Cook, 1992; Cook et al., 2004), training devices are not often suited or available for large animals, like deer.

We designed and tested an automated device ("deer-training-apparatus", DTA) for training deer to respond to perceptual stimuli. The device facilitates operant conditioning by forcing a deer to choose between two unique stimuli, providing a positive reward with a correct choice or removal of the reward with an incorrect choice. Herein, we describe the configuration and function of the DTA, and we present behavioral data on deer performance during training.

MATERIALS AND METHODS

Our research was conducted at the Daniel B. Warnell School of Forestry and Natural Resources' Whitehall Deer Research Facility at the University of Georgia (UGA), Athens, Georgia, USA. All procedures were approved by the UGA Institutional Animal Care and Use Committee (IACUC# A2010 1-010). About 50 white-tailed deer were maintained at the facility during the study. We randomly selected six semi-tame adult females, ages 2-6 years, and housed them individually in 2.7 m x 4.9 m barn stalls. Each stall was retrofitted with a DTA (Fig. 1). All stalls were located in the same barn, but visually separated by wooden walls. To familiarize each

deer with its new environment, we programmed each DTA to dispense food and provide deer with *ad libitum* access to food (Meadow's Edge Deer Feed, Meadow's Edge, Millen, GA, USA) for 48 h before training began. Afterwards, we programmed each DTA to dispense food and provide deer with limited access to food, with feeding frequency based on each deer's voluntary participation during training. Food was dispensed in increments of 57 g based on recommendations commonly used for white-tailed deer (French et al., 1956). This rate provided about 1.6 kg of food (100% of the recommended daily allotment) each day that a deer's performance rate equaled $\geq 75\%$ correct choices. Operation of each DTA was monitored daily to ensure it was functioning properly. All deer had access to water *ad libitum* and remained in the same stalls for the duration of the experiment.

We worked with the UGA Instrument Shop (Athens, GA, USA) to construct a DTA to facilitate automated operant conditioning of deer to a broad-spectrum, white-light stimulus generated by three light-emitting diodes ($\lambda_{\text{max}} = 543 \text{ nm}$, half-band width = 20.6 nm, color temperature = 6174 K, intensity = 41 lms) and a food reward. For the stimulus light, we selected a frequency and intensity that should have been highly visible to deer (Jacobs et al., 1994).

Each DTA consisted of a pair of wooden boxes (L, W, H = 25 cm x 45 cm x 61 cm), each with its own food bin (L, W, H = 25 cm x 45 cm x 23 cm) covered by a pneumatically controlled lid (Fig. 1). Each box contained a logic relay (TECO Genie II, Model SG2-20HR-12D, Teco Electric & Machinery Co., Taipei City, Taiwan), which we controlled with a program developed by the authors based on logic ladder software (SG2 Client v.3.2, Teco Electric & Machinery Co., LTD., 2010). The program defined the timing of training sessions, dispensed food to both bins, activated the start buzzer, randomly illuminated the stimulus light over one of the food bins,

activated infrared sensors in front of both food bins, and recorded (via an internal data logger) when a deer tripped either infrared sensor when attempting to feed (Fig. 2).

Three vertical wooden posts and three horizontal wooden braces separated each half of the DTA and assured that a deer could only access food from the bin that it had chosen. The two outward-most posts each housed an infrared sensor (AECO Sensors, Inzago, Italy) which projected a beam to a reflector on each side of the center post at 50 cm above the stall floor and 30 cm forward of each food bin. We mounted an electronic buzzer (ICC Intervox, Bohemia, NY, USA) above and central to both food bins to help capture the deer's attention at the beginning of each trial.

During 1-25 July 2010, we programmed each of six DTAs (i.e., one per deer) to conduct six daily training sessions, each of 20-min duration, between 00:00 and 20:00 hours. At the start of each trial, the buzzer sounded (2.9 kHz and 90 dB) for 0.1 s. Immediately afterwards, a stimulus light over one food bin was illuminated, and after 8 s, both food bin lids opened (Fig. 2). When a deer approached the food bin under the illuminated light, a correct response was recorded and the deer was allowed to eat for 60 s, before both lids closed. Immediately after both lids closed, 28 g of pelleted food was dispensed into each bin, followed by a 3-min delay before the start of the next trial. Dispensing food into both bins before their lids opened ensured that deer did not become conditioned to an auditory or aural stimulus. When a deer approached the food bin without the illuminated light, an incorrect response was recorded and both lids immediately shut to deny access to food. Then, there was a 3-min delay before the start of the next trial .

Experimental results were expressed as the percentage of correct responses. Deer were considered trained when they tripped the sensor associated with the illuminated stimulus light during $\geq 75\%$ of the trials for 5 consecutive days. Data are presented as mean \pm 95% C.I.

RESULTS AND DISCUSSION

Training deer to respond to an environmental stimulus requires a degree of repetition beyond the reasonable ability of human trainers. On the first day of the experiment, deer correctly selected the food bin under the stimulus light $54.6 \pm 4.7\%$ of the time (Fig. 3). By Day 14, their average daily performance exceeded 75% correct. By Day 19, all deer met our successful training criteria with a daily average performance of $85.5 \pm 6.9\%$ correct. As time progressed, variance in percentage of correct responses among deer generally decreased and overall correct performance increased to about 87%. When compared to studies in which human trainers used manual techniques to train deer to visual stimuli (Zacks and Budde, 1983; Zacks, 1985; Birgersson et al., 2001), the DTA was more efficient in terms of both time and effort. In addition, it offered other advantages over traditional manual-training techniques, such as absence of experimenter bias, reduction in the experimenter's time and effort, logging of inter-trial intervals and delays, and direct downloading of data to computer spreadsheets (Meier et al., 1998; Franz et al., 2002; Langbein et al., 2003). When considering the complex scheduling of trials, delays, food rewards, etc. needed to reinforce operant conditioning of animals, this automated training device greatly increased our research abilities.

Although vision plays an important role in a deer's perception of its environment and its consequent behavior (Sauer, 1984; Birgersson et al., 2001), there has been little study in this area (Jacobs, 1993). Most of what has been assumed about deer perception of visual stimuli was based on anatomical structure of the eye (VerCauteren and Pipas, 2003). Similar inferences

about the visual abilities of other species, such as the pigeon (*Columba livia*) and the turtle (*Pseudemys scripta elegans*), were unverified by direct behavioral substantiation (Kreithen and Eisner, 1978; Arnold and Neumeyer, 1987; Jacobs, 1992). We demonstrated that white-tailed deer could be easily trained to associate a supra-threshold white-light with a positive reinforcement food reward.

In conclusion, because the DTA and its accompanying software are malleable to research-specific programming, it will assist researchers in better understanding vision, as well as other complex biological processes such as auditory and olfactory senses. The DTA will bridge the gap between physiological interpretations and behavioral measures of sensory perception in white-tailed deer. Understanding an animal's perception is critical for better manipulation of its behaviors. Thus, research utilizing the DTA can be applied to mitigating human-deer conflicts such as deer-vehicle-collisions and crop damage. Besides serving as a training tool, in our opinion, the interactive design of the DTA provided captive deer in our study with important environmental enrichment, possibly facilitating improved animal welfare (Newberry, 1995).

ACKNOWLEDGEMENTS

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Figure 2.1. Deer-training-apparatus (DTA) showing the (1) programmable relay and (2) food dispenser (A), the side-by-side orientation of the two trough-boxes (B), and the device from inside the barn stall with (3) trough lids open and (4) lights above the lids (C).

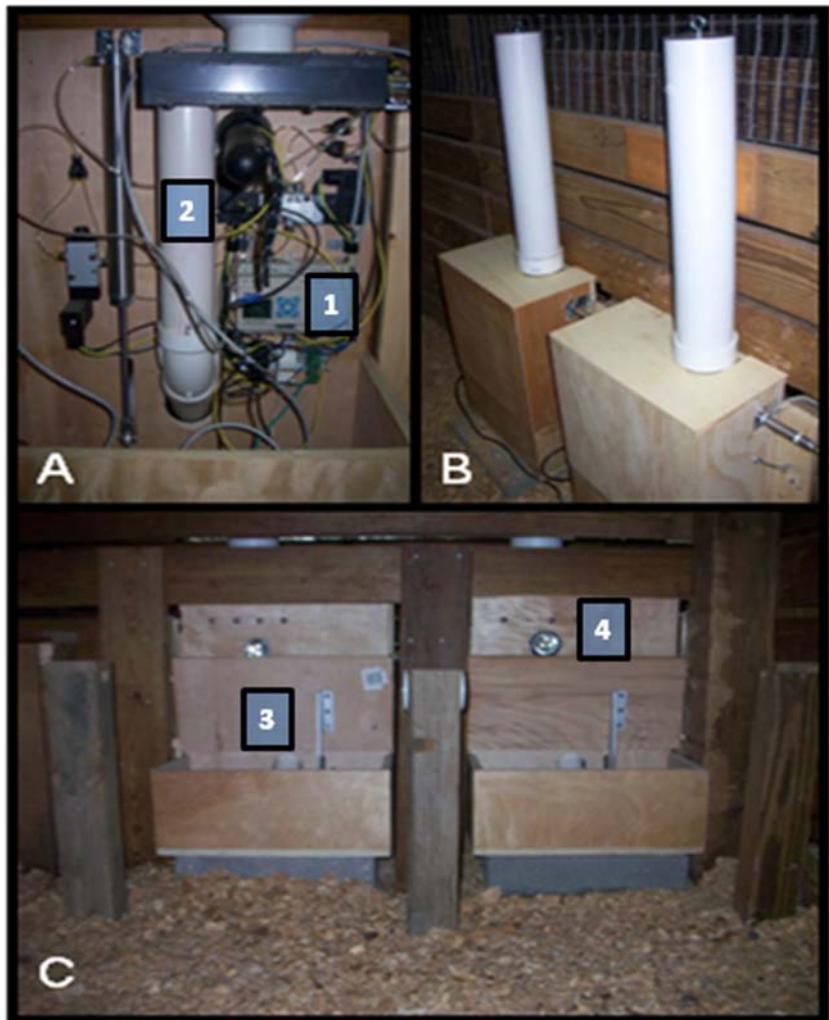


Figure 2.2. Functional block diagram of the program for “deer-training-apparatus” (DTA).

After recording the data from the previous day’s session, the program is restarted and the light to be illuminated is assigned randomly. Performance, checked by correct (Y) or incorrect (N) decisions, is registered by the computer and verified by observers on randomly chosen intervals.

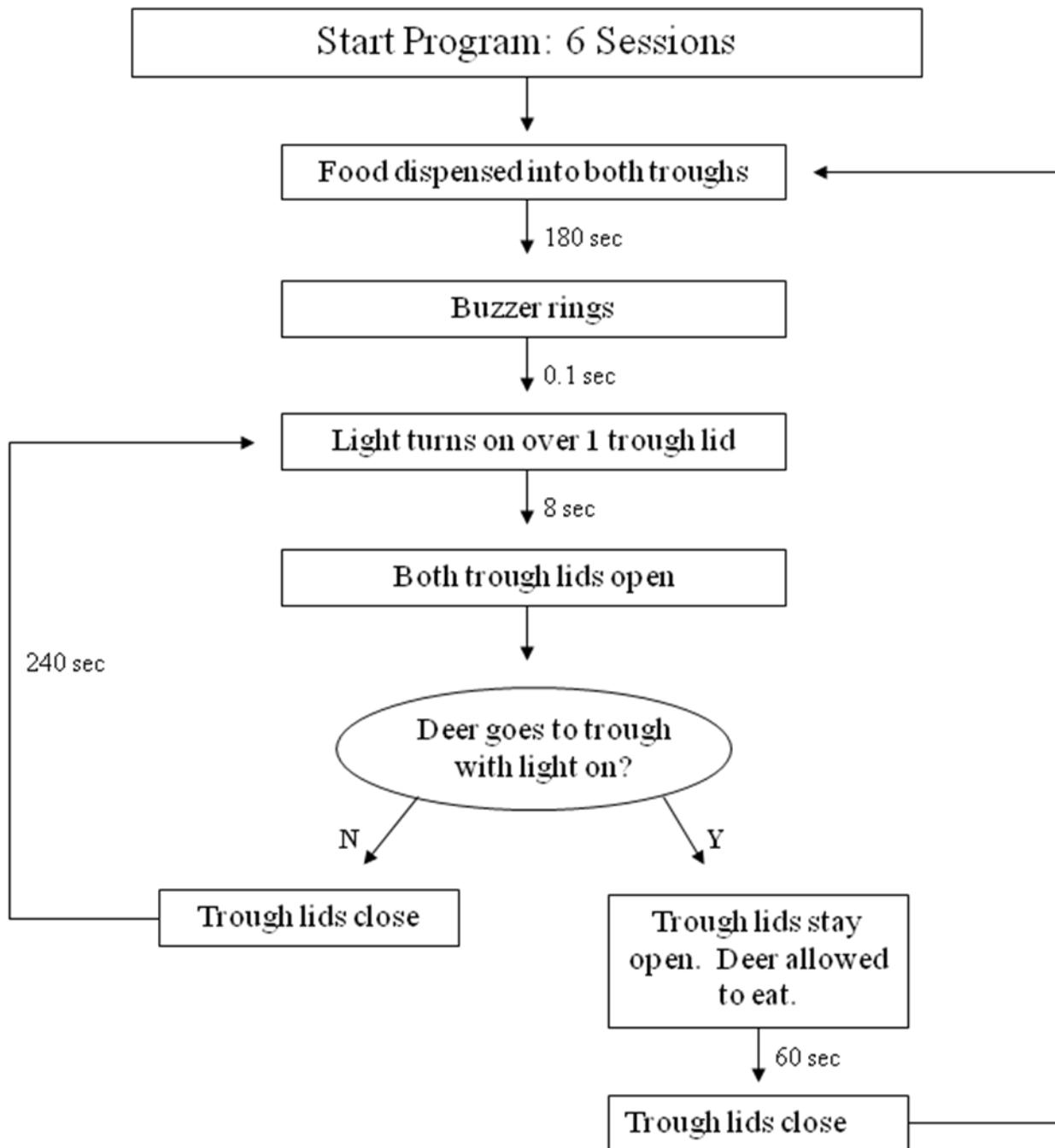
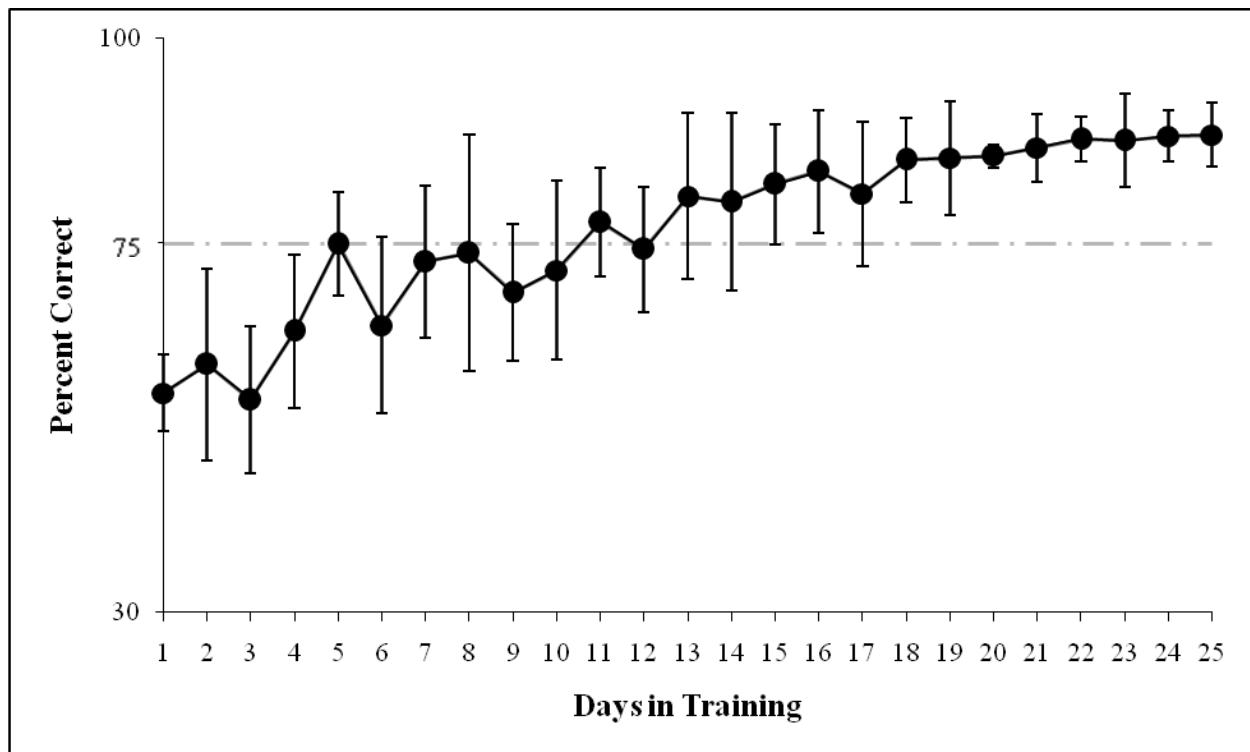


Figure 2.3. Mean behavioral performance of the six adult, female white-tailed deer. The dotted line represents 75% correct. The vertical bars represent the 95% confidence interval.



CHAPTER 3

SENSITIVITY OF WHITE-TAILED DEER TO ULTRAVIOLET AND INFRARED LIGHT: A BEHAVIORAL ASSAY¹

¹Cohen, B.S., D.A. Osborn, G.R. Gallagher, R.J. Warren, K.V. Miller. 2011. To be submitted.

ABSTRACT

Although many aspects of white-tailed deer (*Odocoileus virginianus*) biology and physiology have been studied thoroughly, few studies have confirmed deer cognitive perception, partly because of the difficulty of training deer to respond behaviorally in controlled experiments. We obtained a behavioral measure of relative visual sensitivity by comparing intensity thresholds based on performance of deer in forced-choice discrimination tests conducted at the short and long wavelengths of their purported visual spectrum. By using an automated training device, we taught deer to associate a food reward with a light stimulus. We recorded deer responses across a series of decreasing intensities for each wavelength until deer could no longer discriminate the stimulus light from an unlit light. When deer performed at chance percentages we assumed they could no longer perceive the light. We regressed a best fit line to each deer's performance as intensity decreased at a single wavelength, which was used to demarcate the sensitivity threshold to that wavelength. We compared thresholds across wavelengths and delineated sensitivity measurements best fitting previous cone template functions. Our results confirm white-tailed deer's relative spectral sensitivity, which agreed with previously measured cellular sensitivity and deer's visual perception. Deer are dichromats with a greater sensitivity to shorter wavelengths and less sensitivity to longer wavelengths. Additional behavioral studies are necessary to confirm previous anatomical and physiological investigations of deer sensory perception.

INTRODUCTION

The white-tailed deer eye is well adapted for function at a wide range of ambient lighting conditions, which is important considering their crepuscular movement patterns (D'Angelo et al. 2008). For example, a horizontal slit pupil allows the deer eye to function properly in full

daylight, without overwhelming the photoreceptors of the retina (Ali and Klyne 1985). In addition, the horizontal slit pupil enhances their visual acuity by directing light onto a strip of retinal cells containing a relatively high density of photoreceptors (Malmström and Kröger 2006).

Deer retinas contain rod and cone photoreceptors, with each being sensitive to different wavelengths of light because of differences in their photopigments (Witzel et al. 1978). Each photoreceptor responds maximally to a specific wavelength, referred to as its peak sensitivity. Cone photoreceptors are responsible for color perception and require more energy to activate than do rod photoreceptors, which are responsible for vision in low ambient light. Deer eyes contain two types of cones, one with photopigments having a peak spectral sensitivity of 450–460 nm and another with peak spectral sensitivity of 537 nm (Jacobs et al. 1994, 1998), providing the requisite basis for dichromatic vision. Cone photoreceptors are distributed throughout the deer's retina, but middle-wavelength cones occur at highest densities ($\sim 32,000/\text{mm}^2$) along a horizontal retinal streak that aids in expanding the deer's field of view and visual acuity (Jacobs et al. 1994, D'Angelo et al. 2008).

Limits of mammalian vision depend on several factors including the optical properties of the eye (i.e., size of eye, size of pupil, the refractive power of the eye's optical elements), the properties of the light-absorbing filters through which light must pass before reaching the photoreceptors, the light-absorbing properties of the photoreceptors, and the reflectivity of the tissues that lie behind the photoreceptors. For example, deer have a high density of medium-wavelength sensitive cones compared to short wavelength cones and a tapetum lucidum responsible for reflecting light inside the eye (D'Angelo et al. 2008), both of which may produce a difference between inferences based on photoreceptor sensitivity and actual perception.

Despite the important role vision plays in a deer's perception of its environment and its consequent behavior (Sauer 1984), most research has consisted of physiological studies or limited behavioral assays (Zacks and Budde 1983, Zacks 1985, Witzel et al 1978, Smith et al. 1989, Birgersson et al. 2001). Much of what is assumed about deer vision is based on the anatomical structure of the eye, characteristics of photoreceptors in the retina, and electrophysiological measurements of photoreceptoric cells (Jacobs et al. 1994, VerCauteren and Pipas 2003). However, similar inferences in other species, such as the pigeon (*Columba livia*) and the turtle (*Pseudemys scripta elegans*) were not validated in subsequent behavioral assays (Kreithen and Eisner 1978, Arnold and Neumeyer 1987). Differences between cellular response and visual perception could result from opponent neural interactions between photoreceptors, or from spectral filtering of light waves by the lens or other ocular structures (Jacobs 1992). Thus, assumptions about visual capabilities of animals require direct behavioral substantiation (Jacobs 1992).

To our knowledge, only three behavioral investigations of white-tailed deer vision have been published (Zacks & Budde 1983, Zacks 1985, Birgersson et al. 2001). However, small sample size and lack of experimental control of possible confounding variables (i.e., brightness, hue, luminance, etc.) make interpretation of these results difficult (Jacobs 1981, VerCauteren and Pipas 2003). Our objective was to obtain a behavioral confirmation of the spectral sensitivity of the white-tailed deer at the short and long wavelengths of their purported visual spectrum.

METHODS

Our research was approved by the University of Georgia Institutional Animal Care and Use Committee (AUP# A2010 1-010). We conducted the research at the Daniel B. Warnell School of Forestry and Natural Resources Whitehall Deer Research Facility at the University of

Georgia. Deer were housed separately in barn stalls, which were modified for purposes of this research. Each stall was equipped with an interactive deer-training-apparatus (Figure 1, 2; Chapter 2) and were allowed *ad libitum* access to water. We controlled ambient light conditions by placing shade cloth around the stalls and using ceiling-mounted fluorescent lights (75W, color temperature = 5973 K) to illuminate the test chamber in a 12:12 (light:dark) cycle.

We used standard conditioning techniques to train seven, semi-tame, singly penned adult (ages 2.5-5.5 years) female deer in a forced-choice test using a food-reward-based apparatus (Cohen 2011). Deer were trained to associate a supra-threshold white-light ($\lambda_{\text{max}} = 543 \text{ nm}$, half-band width = 20.6 nm, color temperature = 6174 K, intensity = 41 lms) with a food reward. During behavioral trials, each deer viewed two monochromatic lights, consisting of three narrow-bandwidth LEDs and each associated with its own interactive food trough. Test animals gained access to 57g of pelleted deer feed (Meadow's Edge Deer Feed, Millen, GA, USA) each time it attempted to feed from the trough below the illuminated light (i.e., the correct choice). When the deer attempted to feed from the trough below the non-illuminated light, it was denied access to feed. We randomly assigned illumination of each of the two lights and access to feed in each of the two troughs. Test trials began by sounding a bell to attract the deer's attention and terminated when the deer responded by attempting to feed from one of the troughs. We varied the intensity and spectral content of the test light to permit the determination of threshold performance. The deer were free to move about the test chamber and, depending on the position of the animal at the point where visual discriminations were made, the stimulus light subtended visual angles that fell in the range from 20-60°. Trained animals completed 20-40 test trials each day.

Upon successful training of seven deer to the supra-threshold white-light (Cohen 2011; Figure 4), we measured increment-threshold spectral at 360 nm, 380 nm, 405 nm, 430 nm, 590 nm and 650 nm. At each wavelength, we varied light intensity in increments of 0.3 log units. We pre-selected intensities to produce discrimination performance that varied from approximately 90% correct to chance performance ($50 \pm 10\%$ correct; Figure 3). We considered a choice to be correct when the deer attempted to eat from the illuminated trough, and we measured performance as the percentage of correct choices (number correct/number of total trials). We tested wavelengths in random order but evaluated various intensities sequentially. Each test continued over 48 hrs until >30 trials had accumulated at each intensity/wavelength combination. An internal data logger interfaced with the testing apparatus collected all data. We determined the sensitivity threshold for each deer when she responded at 70% performance. To obtain relative sensitivity values, the threshold intensity was standardized by first converting to quantum units (photons), then the largest intensity threshold value was assigned a value of one, and all other values were based on a ratio to this largest value. Values were converted logarithmically, and these mean threshold values between deer were plotted against those photoreceptive relative sensitivity values previously determined by electroretinography (Jacobs et al. 1994). Confidence intervals at $p = 0.05$ were determined for the relative threshold at each wavelength.

RESULTS AND DISCUSSION

Deer remained trained to a supra-threshold white-light, achieving performance levels of about 90% before they were tested at monochromatic wavelengths (Figure 3). At each wavelength tested, a best fit line was regressed to each deer's performance as intensity was

lowered. Our values corresponded well with the previous electroretinography (ERG), with only 590 nm having a lower relative sensitivity than previously reported (Figure 5).

Based on ERG data, it has been suggested that deer are dichromats, with photopigments having a high sensitivity to shorter wavelengths, and the two cone types having a peak spectral sensitivities of 450–460 nm and 537 nm (Jacobs et al. 1994). Previous studies with other animals have found discrepancies between cellular sensitivity and sensitivity determined by behavioral assays, likely being attributed to opposing neural interactions and the filtering of light by ocular media (Kreithen and Eisner 1978, Arnold and Neumeyer 1987, Jacobs 1992, Jacobs et al. 2004). Our results confirm the findings of Jacobs et al. (1994), with the wavelengths we tested falling within the values of the ERG. The only wavelength to not fall within its expected value was 590 nm, likely attributed to a poorer best fit line (with lower r-squared values) than that of the other wavelengths tested because deer's peak performance at this wavelength was lower and dropped off quickly as intensity was decreased. The lack of differences between cellular and perceptual sensitivity suggest filtering by ocular media and opposition of neural interactions do not occur. In fact, deer seem to lack any notable filtering pigment in their lens (such as the yellow pigment in humans which filters UV light), making it likely that these wavelengths strike the retina.

A better understanding of the color vision abilities of white-tailed deer is necessary to understand how they perceive their environment (VerCauteren and Pipas 2003). Employing discrimination tests allow inferences on deer perception because they closely approximate behaviors involved in visual perception (Jacobs 1981). Former studies using behavioral assessments to examine deer vision have been difficult to interpret because of small sample sizes and lack of experimental control of possible confounding variables (VerCauteren and Pipas

2003). Our study is the first to control for these variables by using tractable animals, equipment capable of eliminating experimenter bias, and objective measurements of deer's perception to lights with very narrow bandwidths.

Color vision in deer is also important for determining how deer interpret their environment and how this affects their interactions with humans (VerCauteren and Pipas 2003). For example, a better understanding of the visual capability of white-tailed deer provides the basis for developing efficient and physiologically relevant strategies to reduce deer-vehicle collisions (D'Angelo et al. 2006, Blackwell and Seamans 2008). Future strategies based on deer's visual perception to manipulate deer behavior and reduce deer-vehicle collisions should focus on utilizing wavelengths of light that deer are highly sensitive to such as the blue color spectrum.

The anatomical structure of the white-tailed deer eye is well adapted for predator detection (D'Angelo et al. 2008). Their visual streak allows enhanced surveillance of a broad area, and its spatial association with the tapetum lucidum improves contrast of visual scenes (D'Angelo et al. 2008). Our data suggests deer are highly sensitive to short wavelengths and no spectral filtering by ocular media. Deer movement is greatest during sunrise and sunset. At these times shorter wavelengths dominate the available light, as these wavelengths are more easily reflected from the atmosphere and back to earth. It seems that when deer are most active, even though less light is available for visual perception, deer's sensitivity to shorter wavelengths (ie., blues) allows them to better detect the horizon and movement across it. Thus, our data lends further support to the visual system of a white-tailed deer being well adapted for a prey species.

VerCauteren and Pipas (2003) argued that additional operant conditioning studies are needed to determine the sensitivity of deer to colors of various wavelengths. Our study helps to

fill this void and agrees with previous assertions that deer are dichromats and that they perceive their world in colors of blue to yellow-green, with a higher sensitivity to shorter wavelengths than humans. Vision provides confirmation of what other senses detect, plays an important part in behavior, and is important in predator detection, movement ecology and social communication (Sauer 1984, Birgersson et al. 2001, D'Angelo et al. 2008). Further research utilizing behavioral measurements of other aspects of deer vision, such as visual acuity, pattern discrimination, and brightness discrimination will provide additional understanding about how deer perceive their world and how these perceptions influence behavior.

ACKNOWLEDGEMENTS

This study was funded by the Georgia Department of Transportation through the Governor's Office of Highway Safety and the National Highway Traffic Safety Administration. This study was supported in part by resources and technical expertise from the University of Georgia Instrument Shop, a unit of the Office of Research Services in the Office of the Vice President for Research. We thank S. Cash for his help with data collection. We thank J. Neitz, J.C. Maerz and A.S. Goodie for their improvements to the design of the study and earlier drafts of this manuscript.

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Figure 3.1. Deer-training-apparatus (DTA) showing the (1) programmable relay and (2) food dispenser (A), the side-by-side orientation of the two trough-boxes (B), and the device from inside the barn stall with (3) trough lids open and (4) lights above the lids (C).

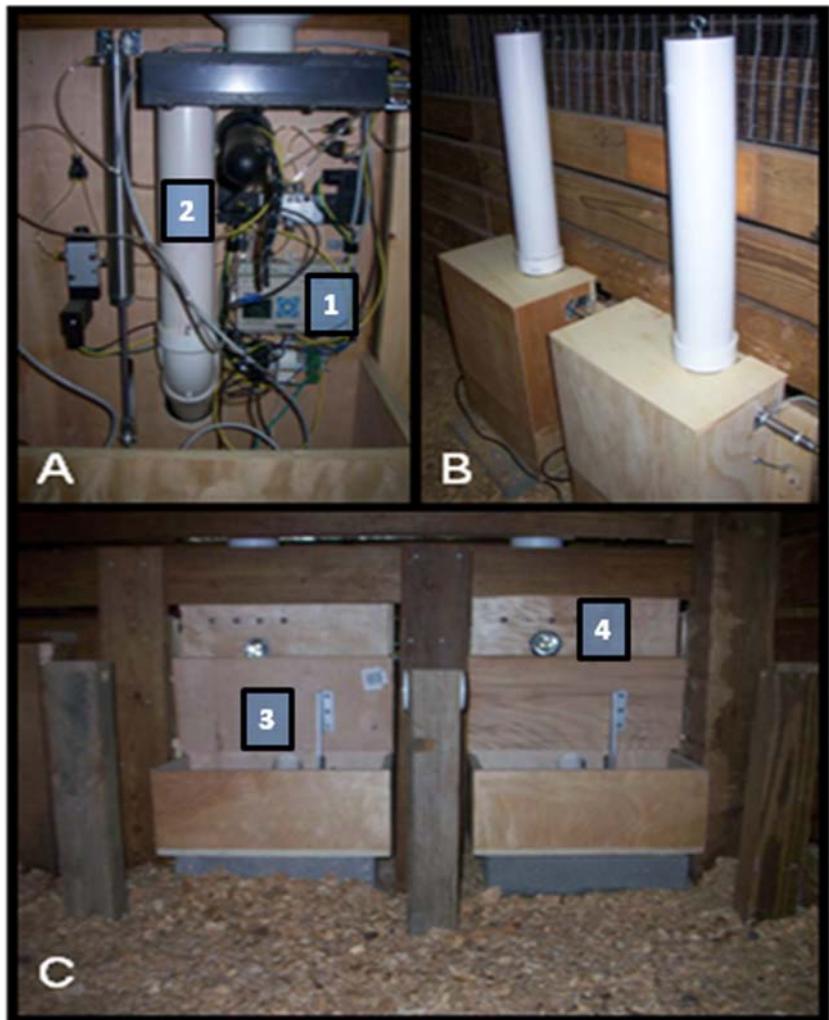


Figure 3.2. Functional block diagram of the program for “deer-training-apparatus” (DTA).

After recording the data from the previous day’s session, the program is restarted and the light to be illuminated is assigned randomly. Performance, checked by correct (Y) or incorrect (N) decisions, is registered by the computer and verified by observers on randomly chosen intervals.

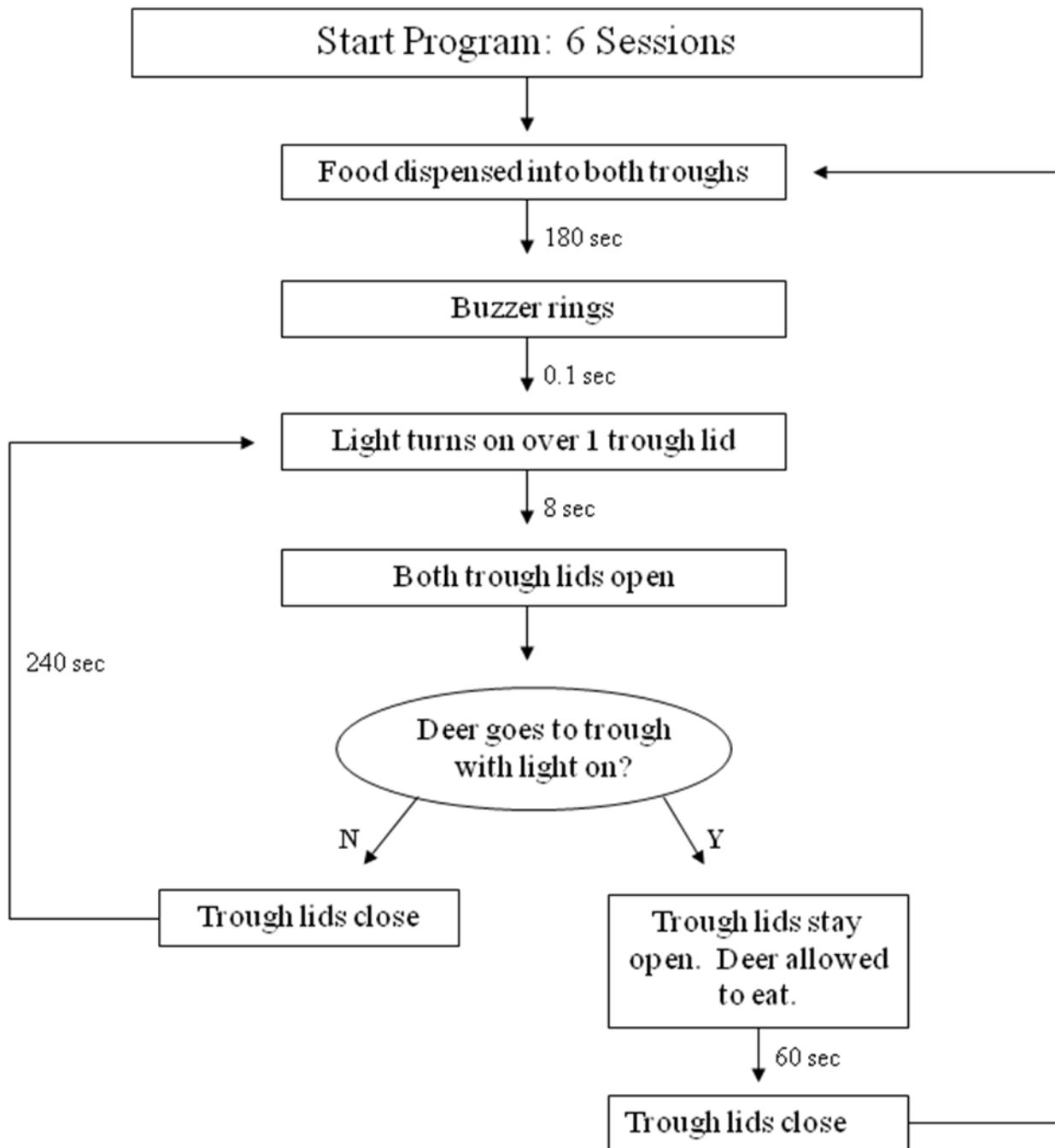


Figure 3.3. Performance of one deer at one wavelength (650 nm) in an increment-threshold discrimination task. At each wavelength, the intensity of the monochromatic light was varied in steps of 0.3 log unit, with a range of intensities pre-selected so as to produce discrimination performance that varied from approximately 90% correct down to chance performance. The data was fit to a best fit line and the sensitivity threshold of each deer was determined at the intensity in which the deer performed at 70%.

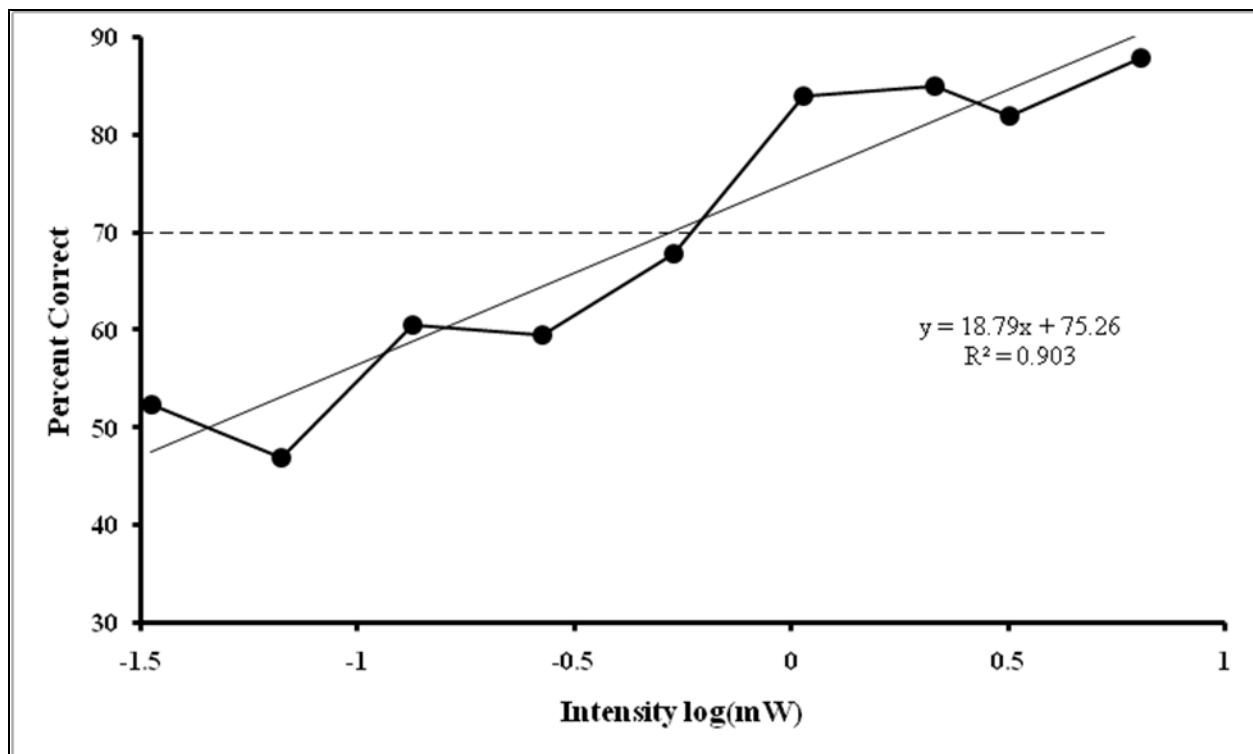


Figure 3.4. Mean (+/- standard error) behavioral performance of the seven adult, female white-tailed deer tested at a supra-threshold white-light. Deer were tested at this light for eight days before switching to other test lights to ensure they had retained their learned behavior. The dotted line represents 75% correct.

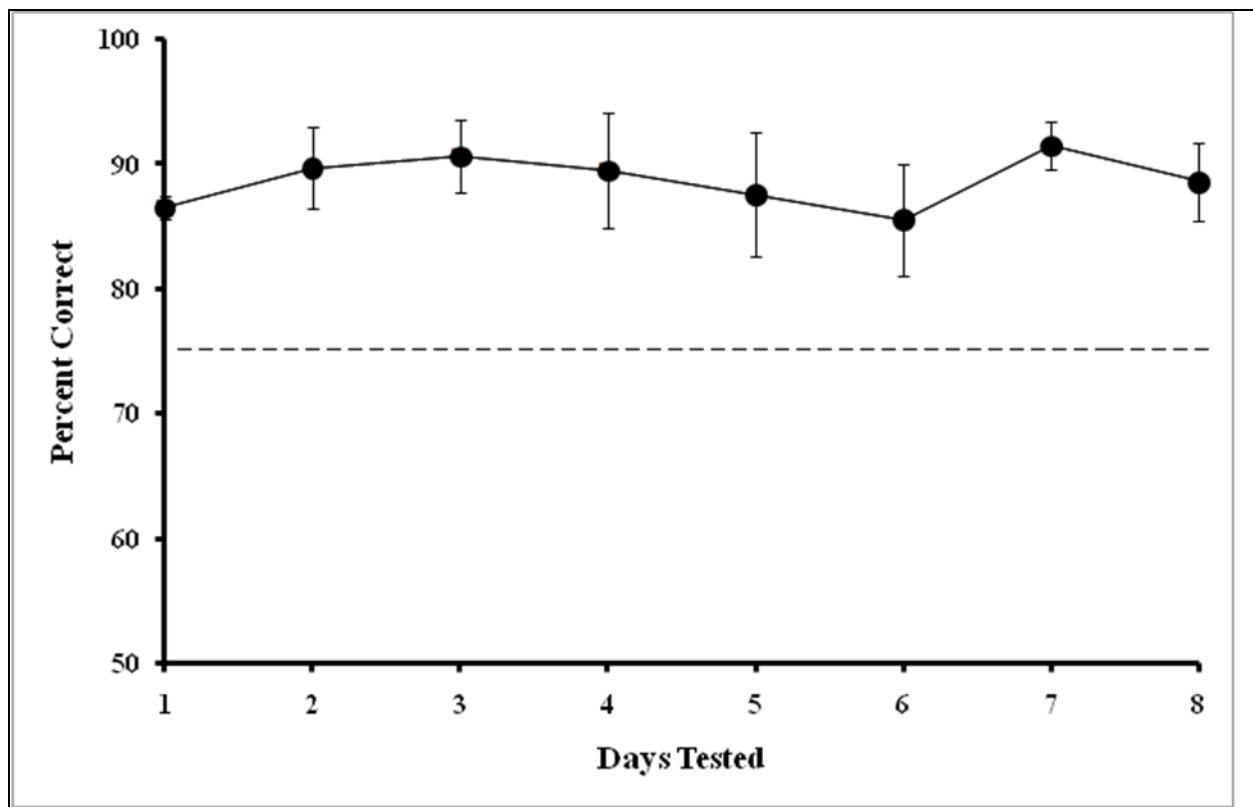
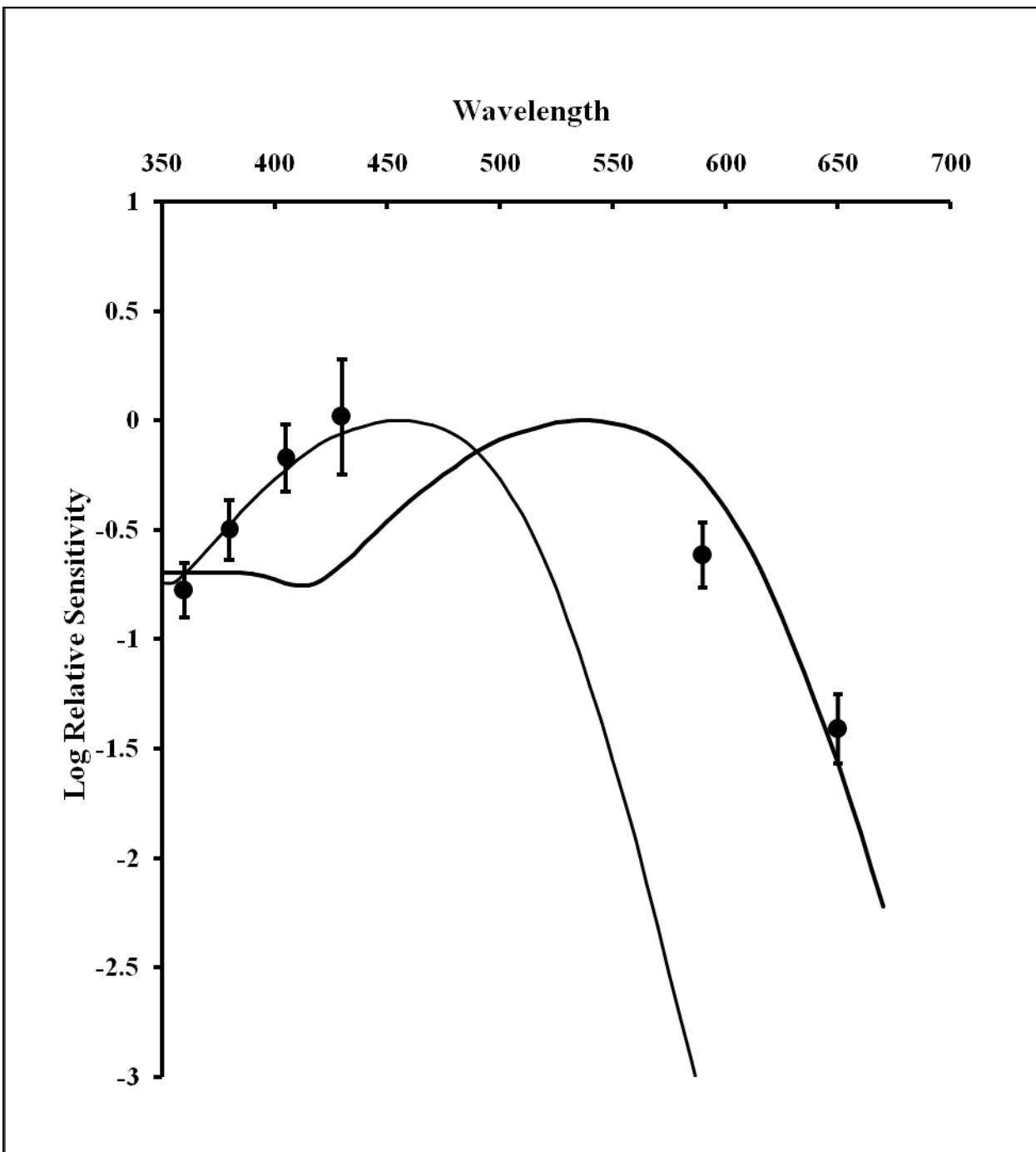


Figure 3.5. Mean (+/- 95% C.I.) behavioral spectral sensitivity of seven female white-tailed deer obtained in an increment-threshold discrimination task. The solid lines represent the photoreceptive sensitivity function reported by Jacobs et al. (1994), showing the reported sensitivity of both the short-wavelength and medium-wavelength sensitive cone. The points represent sensitivity measurements which have been fitted by determining the best additive fit of the cone template functions.



CHAPTER 4

SUMMARY AND CONCLUSIONS

Despite the important role vision plays in a deer's (*Odocoileus virginianus*) perception of its environment and its consequent behavior, there has been little study of deer vision, of which most were physiological studies or limited behavioral assays. Much of what is assumed about deer vision is based on the anatomical structure of the eye, characteristics of photoreceptors in the retina, and electrophysiological measurements of photoreceptoric cells. However, similar inferences in other species were not validated in subsequent behavioral assays. Thus, assumptions about visual capabilities of animals require direct behavioral substantiation. Therefore, I used a behavioral measure to examine the spectral sensitivity of deer.

During the study, I used seven female white-tailed deer, ranging in age from 1.5 to 5.5 years old. Deer were housed separately in barn stalls, which were modified for purposes of this research. Each stall was equipped with an interactive deer-training-apparatus (DTA). The DTA automatically dispenses food, rings a start buzzer, randomly assigns a stimulus light over one of two troughs, and registers a deer's choice. If a deer goes to a trough with the light illuminated, then a correct choice is registered. I found that six deer using the DTA met successful training criteria by Day 19, and a performance of $88.2 \pm 3.9\%$ correct choices by Day 25. I concluded that the DTA presents an effective and efficient way of training white-tailed deer, and provides an experimental platform for research on behavior, perception, and preference.

I obtained a behavioral measure of photoreceptive sensitivity by comparing intensity thresholds based on performance of deer in forced-choice discrimination tests conducted at the short and long wavelengths of their purported visual spectrum. I recorded their responses

across a series of decreasing intensities for each wavelength until they could no longer discriminate the stimulus light from an unlit light. When deer performed at random probabilities, we assumed they could no longer see the light, thus providing a measure of their sensitivity threshold to that wavelength. I compared thresholds across wavelengths and delineated sensitivity measurements. My results confirmed that the white-tailed deer's relative spectral sensitivity is similar to their photoreceptive sensitivity. I believe additional behavioral studies are necessary to provide confirmation of previous anatomical and physiological investigations of deer sensory perception.

APPENDIX A

WIRING SCHEMATIC OF DEER-TRAINING-APPARATUS

I created a device that trains white-tailed deer to associate a supra-threshold, white-light stimulus with a food reward through operant conditioning techniques. The "deer-training-apparatus" (DTA) automatically dispenses food, rings a start buzzer, randomly assigns a stimulus light over one of two troughs, and registers a deer's choice. If a deer goes to a trough with the light illuminated, then a correct choice is registered and it is allowed to feed. The following diagram is the wiring schematic for the deer-training-apparatus.

DEER TRAINING DEVICE

