DEVELOPMENT AND EVALUATION OF DEVICES DESIGNED TO MINIMIZE DEER-VEHICLE COLLISIONS

by

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

ABSTRACT

Deer-vehicle collisions are an increasingly common occurrence throughout the range of white-tailed deer (*Odocoileus virginianus*), resulting in human injury and death, damage to vehicles, and waste of deer as a wildlife resource. Most states attempt to minimize deer-vehicle collisions through a variety of techniques. However, few research efforts have sufficiently examined the efficacy of such techniques, and a distinct paucity of information exists on deer behavior relative to these mitigation efforts. A more thorough understanding of the physiological processes driving deer behavior may aid in the development and implementation of strategies designed to minimize the incidence of deer-vehicle collisions. In this study, I evaluated the behavioral responses of white-tailed deer relative to a common commercial device for prevention of deer-vehicle collisions, wildlife warning reflectors. I also examined the anatomy and physiology of the hearing and visual systems of deer that may prove integral to the invention of economically effective strategies to minimize deer-vehicle collisions. I observed deer behaviors relative to roads before and after individual installations of 4 colors of wildlife warning reflectors (red, white, blue-green, and amber) during 90 observation nights. My data indicated that wildlife warning reflectors did not alter deer behavior such that deer–vehicle collisions might be prevented. Using auditory brainstem response testing, I determined that white-tailed deer hear within the range of frequencies we tested, from 0.25-30 kHz, with best sensitivity between 4-8 kHz. The upper limit of human hearing lies at about 20 kHz, whereas we demonstrated that deer detected frequencies to at least 30 kHz. This difference suggests that research on the use of ultrasonic (frequencies >20 kHz) auditory deterrents is justified as a possible means of reducing deer-human conflicts. To gain knowledge of visual specializations influencing the behavior of white-tailed deer, we examined gross eye characteristics, structural organization of the retina, and the density and distribution of cone photoreceptors. White-tailed deer possess a horizontal slit pupil, reflective tapetum lucidum, cone photoreceptors concentrated in a horizontal visual streak, and typical retinal structure. The visual system of white-tailed deer is similar to other ungulates and is specialized for sensitivity in low light conditions and detection of predators.

INDEX WORDS: Deer, Deer-vehicle collisions, Deterrents, Hearing, Vision, White-tailed deer, Wildlife warning reflectors

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Deer (*Odocoileus* spp.)-vehicle collisions result in human injury and death, damage to vehicles, and waste of deer as a wildlife resource (Romin and Bissonette 1996). Sullivan and Messmer (2003) estimated that 1.5 million deer-vehicle collisions occur annually in the United States at a cost of nearly $1 billion in damages and resulting in over 200 human fatalities. Within the state of Georgia alone, approximately 51,000 deer-vehicle collisions occur annually (Georgia Department of Natural Resources, personal communication). Most states attempt to minimize deer-vehicle collisions through a variety of techniques including vehicle-mounted devices, installation of deterrents along roads, alteration of roadside habitats, and driver education campaigns (Romin and Bissonette 1996). However, few research efforts have sufficiently examined the efficacy of such techniques, and a distinct paucity of information exists on deer behavior relative to these mitigation efforts.

Many deer deterrent devices were designed with little reference to the sensory capabilities of deer, as evidenced by a lack of published information on the subjects. A more thorough understanding of the physiological processes driving deer behavior may aid in the successful development and implementation of strategies designed to minimize the incidence of deer-vehicle collisions. Despite an abundance of scientific research focusing on the senses of domestic species, relatively little is known about the visual and auditory capabilities of white-tailed deer (*Odocoileus virginianus*). Designers of livestock facilities routinely use knowledge of anatomical and physiological components that influence animal behavior to achieve effective handling and containment (Rehkämper and Görlach 1997). Yet, mechanisms intended to alter deer movements in relation to roadways continue to be engineered without consideration for standard deer sensory processes. In this study, I evaluated the behavioral responses of white-tailed deer relative to one of the most common commercially sold devices for prevention of deer-vehicle collisions, wildlife warning reflectors. I also sought to develop a clear understanding of the anatomy and physiology related to the hearing and visual capabilities of deer that may prove integral to the invention of economically effective strategies to minimize deer-vehicle collisions.

LITERATURE REVIEW

Strategies for Reducing Deer-vehicle Collisions

Wildlife warning reflectors.–Studies of wildlife warning reflectors have used a diversity of testing methods of various levels of scientific validity, ultimately resulting in a limited understanding of reflector efficacy. Most reflector evaluations were based on counts of deer carcasses within test sections, either pre- and post-installation of reflectors (Ingebrigtsen and Ludwig 1986, Pafko and Kovach 1996); when reflectors were covered versus uncovered (Schafer and Penland 1985, Armstrong 1992, Reeve and Anderson 1993); or within reflectorized sections as compared to adjacent control sections (Reeve and Anderson 1993). Such methods failed to consider changes in deer densities, seasonal movements, or traffic patterns. Beyond differences in experimental design, comparison of results among different reflector studies was confounded further by the variety of reflector models tested and the distinct spectral properties of those devices.

Little is known about how deer react to reflector activation along roadways or if individual animals become habituated to the devices over time. Ujvári et al. (1998) demonstrated that in the absence of vehicles and their associated noise and light, free-ranging fallow deer (*Dama dama*) visiting a bait site became increasingly habituated to light reflections from WEGU wildlife-warning reflectors (Walter Dräbing KG, Kassel, Germany) over a period of 17 nights. Additionally, electrophysical measurements of the spectral mechanisms of white-tailed deer (*Odocoileus virginianus*) showed that peak sensitivity of deer color vision was well below the long wavelength of red (Jacobs et al. 1994), which was the most commonly marketed color of wildlife-warning reflectors. The developers of wildlife warning reflectors may have lacked the underlying physiological and behavioral information necessary for developing devices from the perspective of deer.

Fences and wildlife crossing structures.–Roadside fencing has been the most studied device implemented to reduce the incidence of deer-vehicle collisions. Most research indicated that fences were not an absolute barrier to deer, and only served to reduce the number of animals entering the roadway (Bellis and Graves 1978, Falk et al. 1978). Conventional wire fencing must be at least 2.4 m high to limit the ability of deer to jump over it. Construction of fencing is prohibitively expensive for many applications. Alternative low-in-height fence designs, such as solid barrier fencing (Gallagher et al. 2003) and non-traditional configurations of electric fence (Palmer et al. 1985, Seamans et al. 2003, Fenster and Knight 2006) and barbed-wire (Knight et al. 1997), may provide a less-expensive fencing option to exclude deer from roadways and other areas.

Regular maintenance of fences is both costly and necessary for effectiveness (McKnight 1969). Gaps created by weather events, humans, and animals are quickly exploited by deer, and may create "hotspots" for deer-vehicle collisions when deer enter the roadway corridor and are unable to locate an escape point. Although fencing is not a complete barrier to deer, its presence may severely limit the natural movements and gene flow of deer populations and other wildlife. Fencing coupled with a variety of underpasses (Reed et al. 1975, Clevenger and Waltho 2000, Brudin 2003, Gordon and Anderson 2003, Quinn and Smith 2003, Servheen et al. 2003), overpasses (Reed et al. 1979), road-level crosswalks (Lehnert et al. 1996, Lehnert et al. 1997), one-way gates (Reed et al. 1974, Ford 1980, Ludwig and Bremicker 1983), and other strategies were tested to allow animals to cross roadways at controlled areas along fenced highways. Crossing structures were most successful when used where traditional migratory routes of mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and other migratory species intersect highways. An intimate understanding of the proper physical design, location, and integration into the habitat of crossing structures at a particular location is necessary to encourage utilization by the targeted wildlife species.

Motorist warning devices.–Active and passive driver warning devices were largely ineffective at reducing vehicle speeds and preventing deer-vehicle collisions. Drivers ignored the common "deer crossing" sign, perhaps because of its overuse (Pojar et al. 1975). Reduced vehicle speed was the most common method used for assessing the effectiveness of warning devices, even though this response was not the primary desired effect of warning drivers about site-specific dangers associated with wildlife crossings (Pojar et al. 1971, Pojar et al. 1972, Pojar et al. 1975, Reed et al. 1979). No studies to date have assessed driver alertness or other changes in driver behavior relative to warning devices through surveys directed at motorists actually exposed to such strategies.

The effectiveness of recently developed active warning systems, which only alert drivers when animals are present near the roadway, was unclear despite the high cost of such devices (Huijser and McGowen 2003, Newhouse 2003, Gordon et al. 2004). Researchers indicated that non-redundant command type messages impact driver behavior more than notification style messages (Lee et al. 1999), which suggests that educating drivers during periods when they are most likely to encounter roadway dangers (i.e., during the fall and spring when deer-vehicle collisions are most common) may be most effective. Such techniques should be evaluated through direct communication with drivers.

Time and location of deer-vehicle collisions.–Most research indicated that peaks in deer-vehicle collision rates occurred late in the evening, at night, and in the early morning on a diurnal basis, and seasonally in the spring and fall (Bellis and Graves 1971, Bellis et al. 1971, Carbaugh et al. 1975, Allen and McCullough 1976, Case 1978). Modern analyses of deer-vehicle collision sites typically involved Global Information Systems (GIS) technology combined with regression modeling to identify areas likely to experience an elevated deer-vehicle collision rate. GIS modeling also was used to select areas for implementation of mitigation strategies based on landscape features, economic feasibility, and other criteria. However, models designed to predict hotspots for deer-vehicle collisions may not be applicable among different regions. For example, in a Pennsylvania study, a model developed by Bashore et al. (1985) suggested that increased line of sight for motorists (i.e., open habitats) in an area increased the probability of the occurrence of deer-vehicle collisions. Contrasting this finding, a model developed by Finder et al. (1999) for roads in Illinois predicted that a reduction in distance to forest edge along a road segment increased deer-vehicle collisions.

Many predictive models show corresponding results relative to the influence of humans on ecosystems. Models including increased landscape fragmentation, number of buildings, bridges, and human population density, which are all indicative of development by humans, showed positive correlation with the number of deer-vehicle collisions across the range of white-tailed deer (Finder et al. 1999, Hubbard et al. 2000, Farrell and Tappe 2003, Nielson et al. 2003). Likewise, drivers experienced higher rates of deer-vehicle collisions on road segments in and near areas closed to hunting, such as public parks and recreation areas (Finder et al. 1999, Nielson et al. 2003). Premo and Rogers (2001) used data from deer-vehicle collision sites to formulate an adaptive strategy for averting deer-vehicle collisions in an urbanized area, including modification of driver behavior at times of greatest risk, and periodic control of deer populations.

Human dimensions associated with deer-vehicle collisions.–The general public greatly values deer as a public resource. Surveys showed, however, that public opinion about deer management and deer-vehicle collision mitigation was affected significantly by human perception of personal risk and cost of implementation (Stout et al. 1993). Conover (1997) hypothesized that as deer populations increase, the negative monetary values of deer will increase at a faster rate than the deer population. Correspondingly, Conover (1997) recommended that the goal of modern deer management should be to maintain deer populations at levels where the net positive benefit of deer is highest.

Human dimensions researchers suggested that professionals involved with wildlife management and roadway management should combine public risk-assessment data with biological data to make decisions about alternative management strategies (Stout et al. 1993, Johnson 2003). Their rationale seems justified as Drake et al. (2003) noted that although the majority of citizens from suburban New Jersey felt that deer control measures were necessary, most were unaware of options for management. Professionals from wildlife management and transportation agencies are charged with the responsibility to institute measures to reduce the risk of deer-vehicle collisions. Future research should focus on methods to effectively communicate with the public regarding strategies for reduction of deer-vehicle collisions.

Alternative mitigation strategies.–Although no "alternative strategy" has proven effective in reducing vehicle collisions with white-tailed deer, the high incidence of deer-vehicle collisions warrants research in new areas. Intercept feeding for migratory mule deer proved marginally effective in reducing the incidence of deer-vehicle collisions in Utah, however successful adaptation of this technique to white-tailed deer in the eastern U.S. is unlikely (Wood and Wolfe 1988). Other alternative approaches included variations of highway lighting (Reed 1981) and even placing imitations of deer with raised tails along roadways (Graves and Bellis 1978). Although not successful in reducing deer-vehicle collisions, such approaches provide evidence that future research on strategies for reduction of deer-vehicle collisions may require a departure from typical study designs.

Deer Hearing and Sound Deterrents

Despite the popular use of sound deterrents for the attempted resolution of deer-human conflicts, information on the hearing abilities of white-tailed deer is limited in the scientific literature. Research on deer hearing was mainly preliminary in nature. However, separate unpublished studies by Stattelman (A. Stattelman, University of Georgia, unpublished data) and Risenhoover et al. (K. Risenhoover, Texas A&M University, unpublished data) demonstrated similar results regarding deer hearing. Both studies suggested that hearing by white-tailed deer was best in the 1-8 kHz range with a marked peak at 4 kHz, well below the sounds produced by wildlife-warning whistles. Likewise, in a behavioral study of reindeer (*Rangifer tarandus*), frequency range of hearing was relatively flat from 1 kHz to 16 kHz, with best sensitivity at 8 kHz (Flydal et al. 2001). The aforementioned studies suggested that the range of deer hearing is similar to humans and does not extend into ultrasonic frequencies. The upper limit of human hearing lies at about 20 kHz (Durrant and Lovrinic 1995), and ultrasonic frequencies are those >20 kHz. Yet, vehicle-mounted sound deterrents (Shu Roo, Ermington, Australia; International Resources Inc., Altoona, Indiana, USA) were advertised by their manufacturers as being effective at dispersing deer from roadways by producing ultrasonic sounds in the 16-22 kHz range, which they claimed were audible to deer, but not to humans.

Contrary to claims by manufacturers, behavioral responses by deer to sound deterrents may be unpredictable or nonexistent. Warning whistles were reported to be ineffective in eliciting any response in free-ranging mule deer (Romin and Dalton 1992). Belant et al. (1998) concluded that motion-activated, acoustic frightening systems operating at 1.4 kHz and in the 20-35 kHz range were ineffective in deterring white-tailed deer from preferred feeding areas. Gilsdorf et al. (2004) developed a device with an infrared system to detect the presence of deer entering the edge of a cornfield, which activated an audio alarm system designed to broadcast deer distress calls. They noted that the device elicited a flight response in deer. However deer were observed to both run away from or into the fields that the device was intended to protect. Unpredictable behavioral responses by deer to sound deterrents in roadway situations may have adverse consequences, including human injury and death.

Bomford and O’Brien (1990) reviewed literature on sonic devices used as animal deterrents. They concluded that although numerous devices had been developed and assessed, many reported tests were inconclusive because of inadequate experimental design. Further research on the hearing physiology of deer and behavioral responses by deer to sound are necessary. Deterrent strategies should be designed to produce sounds within the hearing range of deer and should be implemented to elicit known and repeatable behavioral responses by deer in the actual conditions in which conflicts occur.

Deer Vision

White-tailed deer possess eyes of the basic mammalian form (Ali and Klyne 1985). However, the specific anatomical structures and function of the white-tailed deer eye have not been studied. The mostly crepuscular and nocturnal habitats of deer (Marchinton and Hirth 1984) lead many to surmise that the deer retina contained only rod photoreceptors for vision in low-light conditions. The lack of cone photoreceptors would likely render deer incapable of color vision as suggested by Dalrymple (1975). However, Witzel et al. (1978) established that the retina of white-tailed contained cones. Jacobs et al. (1994) used electroretinogram flicker photometry to study the spectral mechanisms in the retinas of white-tailed deer and fallow deer (*Dama dama*). Both species appeared to possess a maximum rod pigment sensitivity of about 497 nm and two classes of photopic receptors. Both species also shared a common short-wavelength-sensitive cone mechanism in the region of 450-460 nm (blue). The white-tailed deer peak medium wavelength cone sensitivity was about 537 nm (yellow-green), and the fallow deer peak medium wavelength cone sensitivity was about 542 nm. They concluded that deer resemble other ungulates and many other types of mammals in having two classes of cone pigment, and, thus, the retinal basis for dichromatic color vision. Subsequent to the findings of Jacobs et al. (1994), Yokoyama and Radlwimmer (1998, 1999) identified the molecular genetics of photopigments necessary for color perception in white-tailed deer.

Although the retina of deer contains cones, the density and distribution of cones throughout the retina were not studied. Müller-Schwarze (1994) speculated that all species of deer have a visual streak corresponding to a horizontal band of increased cone density in the central retina, because of which, “day or night, a deer’s acuity is excellent” (Müller-Schwarze 1994:60). Regardless of the possible distribution of cones, white-tailed deer acuity may be limited by the overall density of their cones. Visual acuity increases directly with density of cones by enhancing the fineness of the retinal grain (Walls 1942). Witzel et al. (1978) estimated that cones were present at densities of about 10,000 cones/mm^2 at the locations they sampled in the deer retina. In contrast, Curcio et al. (1990) found cones in the human optic fovea at densities much greater than deer between 100,000-324,000 cones/mm^2. This difference among cone densities in deer and humans suggests that deer visual acuity may be limited.

Developing an understanding of the density and distribution of cones in the white-tailed deer would provide insight into the role their vision plays in intraspecific communication, avoidance of predators, and deer-human interactions. The presence of a visual streak would afford white-tailed deer with enhanced ability to monitor a broad area and to detect movement. Information on other ocular components (e.g., cornea, pupil, lens) of the deer eye would demonstrate the treatment of light in preparation for absorption by the deer retina (Walls 1942). Together, these data would enable comparison among the visual abilities of deer and other species. More comprehensive knowledge of the visual system of deer may enable the exploitation of their visual differences (versus humans) for the development of effective visual deterrent strategies.

OBJECTIVES

Based on our review of the literature, I designed a series of research projects to accomplish the following objectives, which were examined in individual chapters:

1. Determine the effect of Strieter-Lite (Strieter Corp., Rock Island, Illinois) wildlife warning reflectors in altering the behavior of white-tailed deer along roadways in the presence vehicles–Chapter 2.
2. Investigate the visual physiology of white-tailed deer, including mapping the density and distribution of cones, and describing the anatomical features of the deer eye–Chapter 3.
3. Investigate the hearing range of white-tailed deer–Chapter 4.

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CHAPTER 2

EVALUATION OF WILDLIFE WARNING REFLECTORS FOR ALTERING WHITE-TAILED DEER BEHAVIOR ALONG ROADWAYS[1]

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[1] D'Angelo, G. J., J. G. D'Angelo, G. R. Gallagher, D. A. Osborn, K. V. Miller, and R. J. Warren. 2006. Evaluation of wildlife warning reflectors for altering white-tailed deer behavior along roadways. Wildlife Society Bulletin 34:1175-1183.

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ABSTRACT

We evaluated the behavioral responses of white-tailed deer (*Odocoileus virginianus*) to 4 colors of wildlife warning reflectors (red, white, blue-green, and amber) that are purported to reduce the incidence of deer–vehicle collisions. We observed deer behaviors relative to roads before and after installation of wildlife warning reflectors using a forward-looking infrared camera during 90 observation nights. Our data indicate that wildlife warning reflectors did not alter deer behavior such that deer–vehicle collisions might be prevented.

Key words: behavior, deer–vehicle collision, forward-looking infrared camera, *Odocoileus virginianus*, road kill, white-tailed deer, wildlife warning reflectors.

INTRODUCTION

Deer (*Odocoileus* spp.)–vehicle collisions are a major concern throughout much of the United States, accounting for human injury and death, damage to vehicles, and waste of deer as a wildlife resource (Romin and Bissonette 1996). Most states attempt to minimize deer–vehicle collisions through a variety of techniques, including signage, modified speed limits, highway lighting, roadside fencing, over- or underpasses, warning whistles, habitat alteration, deer hazing, driver awareness programs, and reflective devices (Romin and Bissonette 1996). However, few studies have examined the efficacy of such techniques, and a distinct lack of information exists concerning deer behavior relative to mitigation efforts.

Strieter-Lite® (Strieter Corp., Rock Island, Ill.) wildlife warning reflectors are marketed as a proven and humane technique for reducing wildlife–vehicle collisions (www.strieter-lite.com). These reflectors are mounted on posts along roadsides and consist of a plastic housing with 2 reflective mirrors with plastic elements, which redirect light through colored lenses (Fig. 2.1). The manufacturer claims that the reflectors deter deer from attempting road-crossings by altering and distributing light from oncoming vehicle headlights across the road and into roadside corridors to “provide an optical warning fence to deer” (Strieter Corp., unpublished instruction manual:3).

Investigations of the effectiveness of wildlife warning reflectors have produced variable results for a variety of reflector models (Gilbert 1982, Armstrong 1992, Reeve and Anderson 1993, Pafko and Kovach 1996). However, these earlier studies often were limited by sample size and insufficient experimental design. Most studies used counts of deer carcasses along roadways to assess reflector effectiveness, and rarely used quality controls such as video surveillance of test sections or driver surveys to account for collisions that resulted in injured deer wandering from the roadside. Further, previous reflector studies provided little data on the behavioral reactions of free-ranging deer to reflector activation by the headlights of oncoming vehicles. This is a significant omission, given that these behavioral reactions constitute the very basis for the purported effectiveness of these reflectors.

Schafer and Penland (1985) documented a decrease in vehicle collisions with white-tailed deer (*O. virginianus*) and mule deer (*O. hemionus*) when Swareflex® reflectors (D. Swarovski & Co., Wattens, Austria) were used in an experiment that alternated covering and uncovering the devices. Alternatively, Reeve and Anderson (1993) used a similar study design and concluded that Swareflex reflectors were ineffective at reducing mule deer road kills in a migratory corridor. Waring et al. (1991) reported that Swareflex reflectors did not alter white-tailed deer crossing behavior; however, this conclusion was based on observations of only 14 attempted road crossings by deer in the presence of vehicles at night. Our objective was to determine the effect of 4 colors (red, white, blue-green, and amber) of Strieter-Lite reflectors in altering white-tailed deer roadway behavior in the presence of vehicles at night.

STUDY AREA

We conducted our study at the Berry College Wildlife Refuge (BCWR) within the 11,340-ha Berry College Campus in northwestern Georgia, USA. The 1,215-ha BCWR, located in Floyd County, lies within the Ridge and Valley physiographic province (Hodler and Schretter 1986) with elevations ranging from 172–518 m. The BCWR was characterized by campus-related buildings and facilities interspersed with pastures, woodlots, and larger forested tracts. Forested areas were dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), and pines (*Pinus* spp.). Hunting was prohibited on BCWR and deer were abundant with an approximate density of 40 deer/km^2 (J. Beardon, Georgia Department of Natural Resources, personal communication). The BCWR contained approximately 24 km of 2-lane paved roads (M. Hopkins, Berry College Physical Plant, personal communication). In the past decade, 12–24 deer–vehicle collisions were reported annually on these roads (Berry College Police Department, unpublished data). The BCWR was open to public traffic during daylight hours. After dark, only vehicles with Berry College permits were allowed access through a gate staffed by campus police. Vehicle traffic at night was still a regular occurrence with approximately 1,600 students and staff residing on campus. Average traffic volume on BCWR roads was 28.8 (SE = 9.1) vehicles/hour for the 5-hour period after sunset during our study.

We selected 2 test areas on BCWR separated by >5 km. The main campus test area was characterized as a campus-to-farm transition area. The test section of roadway separated a <2.5-cm-high groomed lawn of orchard grass (*Dactylis glomerata*), fescue (*Lolium arundinaceum*), and white clover (*Trifolium repens*) from a 6-m-wide mowed roadside area of white clover, which transitioned into a Bermuda grass (*Cynodon dactylon*) field used for hay production. The mountain campus test area was composed of a groomed lawn similar in plant composition to that on the main campus test area and was interspersed with <20 hardwood and conifer trees. The mountain campus test area was bordered by several campus buildings, parking lots, and ponds.

METHODS

Test Area Establishment

The Strieter-Lite instruction manual indicates that the reflectors should emit light to linear distances of ≥38.1 m. Based on this information, physical characteristics of our study area, and equipment limitations, we defined an "area of influence" (Taylor and Knight 2003), centered on the sections of roadway we selected for reflector testing (Fig. 2.2). The area of influence extended 27.4 m perpendicular from the paved edges of the roadway and was 182.9 m in length centered on the mid-line of each test area. According to the manufacturer's claims, all deer within the area of influence should have detected light transmitted by reflectors. Within this area we also were able to accurately record specific deer behaviors and estimate deer movement distances.

We installed a 3-m-high elevated observation platform located 6 m from the roadway edge near the mid-line of each test area. We constructed 1.2-m-high plywood walls around the seating area of the observation platform to conceal the observer and equipment from the deer. We mounted a forward-looking infrared (FLIR) ThermaCAM B1 camera with a 12° lens (FLIR Systems, Inc., Boston, Mass.) to the safety rail of the observation platform. The observer was able to manipulate the FLIR in 360° rotation and ≥90° of vertical tilt. We connected the FLIR to a 33-cm black and white monitor to ease viewing, and placed the monitor on the floor of the observation platform in front of the observer. We powered the monitor with a 12-V, deep-cycle marine battery and a 750-W direct current to alternating-current electrical power inverter.

We developed distance markers to aid our estimation of distances and to delineate the area of influence within test areas. We designed the distance markers to collect heat during the day, store and subsequently radiate more heat than the surrounding environment at night, thus making the markers detectable in the FLIR. To create the distance markers, we filled 591-ml plastic drink bottles with automobile windshield washer fluid and coated the filled bottles with black rubberized automobile undercoating (Bondo Corp., Atlanta, Ga.). We used rot-resistant braided nylon twine (Wallace Cordage Co., Covington, Tenn.) to attach the bottles to 102-cm-long plastic fence posts with a steel shaft for step-in installation. On both sides of the road, we established 5 transects on each side of the mid-line of the test area at a spacing of 18.3-m. The transect length was perpendicular to the roadway with a starting point 9.1 m from the road edge. Along transects, we installed 5 distance markers spaced 4.6 m apart. We determined our distance estimation error under normal observation conditions at night by estimating distances to random locations (n = 60) of co-workers standing within test areas. We pooled estimates from both test areas and calculated mean estimation errors for perpendicular distances from the road as 1.57 m (SE =1.64 m) and 1.83 m (SE = 1.58 m) for lateral distances from the mid-line of the test areas.

At each test area, we installed 15 steel U-posts (Midwest Air Technologies Inc., Lincolnshire, Ill.) on each side of the roadway according to installation instructions for the Strieter-Lite Wild Animal Highway Warning Reflector System. Spacing between posts on the same side of the road was 15.2 m with a 15.2-m perpendicular distance between lines of posts on opposite sides of the road. We evenly staggered posts on opposite sides of the roadway in a diagonal fashion. This configuration ensured total reflector coverage of the area of influence because we installed reflectors 19 m beyond its endpoints. To facilitate deer accommodation to study-related objects in the test areas other than the reflectors, we installed the observation platforms, steel U-posts, and distance markers >2 weeks prior to the start of pretreatment observations. During pretreatment phases, no reflectors were present on the posts. We installed reflectors in daylight >8 hours prior to collecting the first observations for respective treatment phases. On each post, we directed an upper reflector toward the roadway and directed a lower reflector 180° opposite the roadway with the bottom of each reflector 61.0–76.2 cm above the crown of the road. We cleaned reflectors once per week using water and lens paper. A representative from Strieter Corporation inspected and approved our placement of reflectors on both test areas. Animal use procedures were approved by the Institutional Animal Care and Use Committees of the University of Georgia (IACUC # A2004-10102-0) and Berry College (IACUC # 2003/04-06).

Behavioral Observations

We observed deer–vehicle interactions for 4 hours per night beginning 30 minutes after sunset. The observer entered the observation platform >30 minutes prior to the start of recording observations to reduce disturbance to deer in the area. We cancelled observation nights during times of precipitation and heavy fog to reduce possible interference of light transmission by water particles in the air or on reflector lenses.

We conducted 15 nights of pretreatment observations in both test areas from 18 November 2004–25 January 2005. On the main campus test area, we installed the red reflectors on 26 January 2005 and conducted observations on 15 nights from 26 January–10 March 2005.

We removed the red reflectors on 11 March 2005. We installed the white reflectors on 24 March 2005 on the main campus test area and conducted observations on 15 nights from 24 March–18 April 2005. On the mountain campus test area, we installed the blue-green reflectors on 8 February 2005 and conducted observations on 15 nights from 8 February–18 March 2005. We removed the blue-green reflectors on 19 March 2005, installed the amber reflectors on 8 April 2005, and conducted observations on 15 nights from 8 April–1 May 2005. Whereas seasonal variations in deer behavior related to breeding occur, this source of error likely would have had minimal effect on this experiment because we observed behavioral reactions of deer along our test sections of roadway after peak rutting season and before fawning season occurred.

For each deer–vehicle interaction observation, the observer selected a focal animal within the area of influence but outside of a 9-m buffer on both sides of the midline of the test area. We established this buffer to exclude animals from observation, which, because of their proximity, were most likely to be influenced by the presence of the observer. We chose focal animals to examine responses of individuals at different perpendicular and lateral distances within the area of influence and in different positions within groups of deer. We observed deer–vehicle interactions during normal traffic, which included small- to medium-sized passenger vehicles. We excluded observations, which included tractor trailers, buses, and other nonpassenger vehicles because travel by these types of vehicles was rare during the night on BCWR. When traffic was not available and deer were present in the area of influence, the observer used a 2-way radio to instruct a co-worker in a waiting vehicle to drive through the test area. We instructed the driver to maintain a continuous speed of about 48 km/hour and to use the vehicle's high-beam headlights unless other vehicles were in the test section of road. We set these conditions to simulate a typical vehicle traveling on BCWR (J. Baggett, Berry College Police Department, personal communication).

We grouped specific deer behaviors into 5 general categories, which were integral for assessment of deer–vehicle collision risk: 1) passive, 2) active toward the road, 3) active away from the road, 4) active parallel to the road, and 5) within the road (all behaviors within the paved surface of the road). At 2 periods during each observation, the observer classified the behavior of the focal animal and estimated the focal animal's perpendicular distance from the road edge and lateral distance from the mid-line of the test area. The observer recorded information for period 1 as the vehicle reached a point 50-m from the beginning of the area of influence. We selected this vehicle location for period 1 because curvatures of the test sections of roadway ensured that the headlights of the moving vehicle did not shine on the areas of influence until after that point. The observer recorded information for period 2 as the vehicle passed the focal animal or as the focal animal and vehicle interacted in the roadway (Fig. 2.3). We separated individual observations by ≥3 minutes.

Data Analysis

We scored changes in general behavior categories (responses) from period 1 to period 2 for each focal animal observation. The scoring scale ranged from those responses that had a high likelihood of causing a deer–vehicle collision (negative responses) to those that lessened the risk of a deer–vehicle collision (positive responses; Table 2.1). We used Chi-square tests (Sokal and Rolf 1995) to make comparisons of behavior score categories among pretreatment and treatment phases within individual test areas. We calculated total distance moved and perpendicular distance moved from observation period 1 to observation period 2. We used paired *t*-tests (Sokal and Rohlf 1995) to determine differences in total and perpendicular distances moved within positive and negative response categories among pretreatment and treatment phases within individual test areas.

RESULTS

From 18 November 2004–1 May 2005, we recorded 1,370 deer responses to vehicles during 90 nights of observations (4 hrs each; Table 2.2). Irrespective of experimental phase or reflector color, we classified the largest proportion of behavioral responses as neutral. Changes in behavior were similar within the defined levels of positive and negative responses; thus, we present results as responses of the respective groups.

Main Campus Test Area

Behavioral responses.—Comparing the pretreatment to the red-reflector treatment, we observed a decrease in the proportion of positive behavioral responses and an increase in the proportion of negative responses (Table 2.2; $\chi_4^2 = 25.99$, $P \leq 0.001$). From pretreatment to the white reflector treatment, we observed a decrease in the proportion of neutral behavioral responses and an increase in the proportion of negative and positive responses ($\chi_4^2 = 42.65$, $P \leq 0.001$).

Distance moved.—The perpendicular distance of the focal animal from the roadway for period 1 was less during pretreatment than during the red reflector treatment (Table 2.3; $t = -5.77$, df = 341, $P \leq 0.001$). However, for deer demonstrating positive responses, we detected no differences in total distance moved ($t = -0.94$, df = 74, $P = 0.348$) or perpendicular distance moved from the roadway ($t = -1.31$, df = 74, $P = 0.193$). For deer demonstrating negative responses, total distance moved was greater during pretreatment than during the red reflector treatment ($t = 3.39$, df = 52, $P = 0.001$) and we detected no difference in perpendicular distance moved toward the roadway ($t = 1.90$, df = 52, $P = 0.063$).

The perpendicular distance of the focal animal from the roadway for period 1 was less during pretreatment than during the white reflector treatment (Table 2.3; $t = -2.12$, df = 454, $P = 0.035$). However, for deer demonstrating positive responses, we detected no difference in the total distance moved ($t = 0.180$, df = 81, $P = 0.858$) or perpendicular distance moved away from the roadway ($t = 0.055$, df = 79, $P = 0.956$). For negative responses, total distance moved ($t = 3.58$, df = 24, $P = 0.002$) and perpendicular distance moved toward the roadway ($t = 3.05$, df = 25, $P = 0.005$) were greater during pretreatment than during the white reflector treatment.

Mountain Campus Test Area

Behavioral responses.—From pretreatment to the blue-green reflector treatment, the proportion of behavioral responses increased in the neutral and negative behavior categories and correspondingly decreased in the positive response category (Table 2.2; $\chi_4^2 = 14.37$, $P = 0.006$). From pretreatment to the amber reflector treatment, we observed a decrease in the proportion of neutral behavioral responses and increases in the proportion of negative and positive responses (Table 2.2; $\chi_4^2 = 52.69$, $P \leq 0.001$).

Distance moved.—The perpendicular distance of the focal animal from the roadway for period 1 was similar ($t = 1.04$, df = 525, $P = 0.301$) during the pretreatment and blue-green reflector treatment (Table 2.3). For deer demonstrating positive responses, total distance moved ($t = 2.40$, df = 102, $P = 0.018$) and perpendicular distance moved from the roadway ($t = 1.66$, df = 100, $P \leq 0.001$) were greater during pretreatment than during the blue-green reflector treatment. For deer demonstrating negative responses, we detected no difference in total distance moved ($t = 1.48$, df = 80, $P = 0.143$) or perpendicular distance moved toward the roadway ($t = 0.417$, df = 80, $P = 0.678$) among the pretreatment and blue-green reflector treatment (Table 2.3). During the blue-green reflector treatment, we observed a deer–vehicle collision within the area of influence. The deer initially moved at a trot toward the roadway and stopped at a perpendicular distance of 10 m from the roadway before running into the path of the vehicle. The deer was struck in the hindquarters and moved >150 m from the roadway out of sight of the observer. The vehicle stopped immediately after the collision and then continued driving.

The perpendicular distance of the focal animal from the roadway for period 1 was less ($t = 2.23$, df = 500, $P = 0.026$) during the amber reflector treatment than during the pretreatment (Table 2.3). However, for deer demonstrating positive responses, the total distance moved ($t = 3.98$, df = 108, $P \leq 0.001$) and perpendicular distance moved from the roadway ($t = 4.29$, df = 98, $P \leq 0.001$) were greater during the pretreatment. For deer demonstrating negative responses, there was no difference in the total distance moved ($t = 1.28$, df = 107, $P = 0.203$) among the pretreatment and the amber reflector treatment. However, deer demonstrating negative responses during the pretreatment moved a greater perpendicular distance toward the roadway ($t = 2.21$, df = 107, $P = 0.029$).

Effect on Animals Moving Toward the Road

To further assess the potential of wildlife warning reflectors to reduce deer–vehicle collisions, we separately analyzed a subset of 221 observations where the focal animals were actively moving (i.e., walking or running) toward the road before the vehicle entered the test area. These observations represent those most likely to have resulted in a deer-vehicle collision. During the pretreatment phase when no reflectors were in place, the focal animal reacted in a positive manner and stopped moving toward the road in 64% of the observations ($n = 36$, pooled for both test areas). In comparison, the proportion of positive behavioral responses was lower for all reflector treatments than for the pretreatments (red reflector treatment = 13%, $n = 24$, χ_1^2

= 25.60, $P \leq 0.001$; white reflector treatment = 55%, $n = 92$, $\chi_1^2 = 3.02$, $P = 0.082$; blue-green reflector treatment = 14%, $n = 21$, $\chi_1^2 = 12.50$, $P \leq 0.001$; amber reflector treatment = 50%, $n = 48$, $\chi_1^2 = 4.46$, $P = 0.035$).

DISCUSSION

Descriptions of deer behavior relative to roadways are limited in the literature. Our pretreatment observations of deer responses to vehicles indicated that deer tend to avoid crossing roads in the presence of vehicles. Our data were consistent with observations by Waring et al. (1991) of white-tailed deer road-crossing behavior in Crab Orchard National Wildlife Refuge, Illinois. Before Swareflex reflectors were installed, Waring et al. (1991) observed that 71.4% (*n* = 89) of crossings by white-tailed deer were completed without a deer–vehicle interaction on a 2-lane highway, which experienced heavy traffic. Although deer–vehicle collisions are common and problematic (Sullivan and Messmer 2003), when considering the abundance of deer and the density of roads throughout their range (Federal Highway Administration 1998), deer–vehicle collisions likely are rare compared to the frequency of crossings attempted by deer. However, the road-crossing success of deer in localized areas may be impacted by factors including vehicle speed, traffic volume and patterns, vehicle types, motorist awareness of deer, weather conditions, ambient and vehicle-produced light levels, characteristics of the habitat–roadway interface, and mitigation strategies.

Our study questions claims that wildlife warning reflectors “deter deer from crossing the highway when reflecting vehicle headlights” (Strieter Corp., unpublished instruction manual:27). Our results demonstrated that deer exposed to each of the 4 colors of reflectors we tested were more likely to be involved in negative deer–vehicle interactions than without the devices present. Further, any increase in the proportion of positive behavioral responses was coincident with an equal or greater increase in the proportion of negative responses within a given treatment phase. Likewise, when we observed an increase in neutral responses, similar decreases in positive and negative responses were evident. Our analysis focusing only on deer moving toward the roadway indicated that the wildlife warning reflectors appeared to provide no reduction in the potential of a negative deer–vehicle interaction.

Although group size may affect flight response in deer (LaGory 1987) and road-crossing behavior, we chose not to evaluate its effect on deer in our study because highway departments that use reflectors have no control over whether deer attempt road crossings singly or as a member of a group. Determining age and sex of focal animals was not always possible using FLIR, so we did not consider the effects of these variables in our analyses. However, >90% of the deer we observed probably were does.

In the only previous study of deer behavior near roads, Waring et al. (1991) also reported that roadside reflectors (Swareflex) had no impact on the crossing behavior of white-tailed deer or the incidence of road kills. Ujvári et al. (1998) examined the habituation of fallow deer (*Dama dama*) to repeatedly occurring light reflections from a red WEGU reflector (Walter Dräbing KG, Kassel, Germany) placed directly in front of a bait site. During the first experimental night, fallow deer fled from the stimulus in 99% of cases, but over the remaining 16 experimental nights, deer exhibited increasing indifference to reflections, which was explained by habituation to the stimulus. To examine for possible acclimatization, we made comparisons of behavior score categories among entire pretreatment phases and successive 5-night blocks of each treatment phase (i.e., nights 1–5, 5–10, and 10–15) within individual test areas (G. J. D'Angelo, unpublished data). Generally, during our treatment phases, we observed the greatest differences in behavioral responses from pretreatment to treatment nights 1–5, but these differences were not indicative of flight and alarm as in Ujvári et al. (1998). Rather, we observed similar changes in positive and negative responses, which corresponded to an opposite shift in neutral responses. We detected the greatest shifts in behavioral responses from pretreatment levels during the white and amber reflector treatments. Since we tested these reflector treatments during spring versus autumn and winter when the red and blue-green reflectors were tested, it is possible that deer responses to reflectors may be influenced by seasonal differences.

Electrophysical measurements of the spectral mechanisms in white-tailed deer have shown that peak sensitivity of deer color-vision is well below the long wavelength of red (Jacobs et al. 1994), which is the most commonly marketed color of wildlife warning reflectors. VerCauteren et al. (2003) concluded that deer were not frightened by 2 models of red laser beams because deer could not detect the red color or the intense brightness of the lasers. Based on characteristics of deer color-vision (Jacobs et al. 1994) and the assumption that reflectors would be effective, we hypothesized that the ranked order of effectiveness in deer–vehicle collision risk prevention would follow a gradient with short-wavelength reflector-lens colors being most effective and long-wavelength lens colors being least effective: 1) blue-green reflectors (short wavelengths), 2) white reflectors (short, medium, and long wavelengths), 3) amber reflectors (medium and long wavelengths), and 4) red reflectors (long wavelengths), and 5) pretreatment (no wavelengths reflected). Our experiments demonstrated nearly opposite results with individual reflector treatments apparently increasing deer–vehicle collision risk from pre treatment levels. We observed the highest level of deer–vehicle collision risk during the blue-green reflector treatment phase with slightly lower levels of risk during the amber, red, and white reflector phases in respective order of decreased risk. This suggests that negative responses by deer may directly increase with greater perception of light from the reflectors.

Evidence for nocturnal mammals with visual systems comparable to white-tailed deer (i.e., tapetum lucidum, retina dominated by rod photoreceptors, and oval-shaped pupil with a large opening) suggests that the rapidity of their visual adaptation from darkness to abrupt increases in light (e.g., vehicle headlights) may be considerably slower than that of diurnal species like humans (Ali and Klyne 1985). A possible explanation for the increase in negative deer-vehicle interactions from pretreatment levels during each of the reflector treatments in our study may be that light from reflectors in combination with vehicle headlights overwhelmed the deer visual system. However, Sielecki (2001) reported that the primary reflected light intensity of Swareflex and Strieter-Lite reflectors was minimal. Sielecki (2001) found that all models, regardless of lens color, reflected <0.1 lux at a distance of 2 m, which is an illumination level less than that of a full Moon on a clear night (0.1 lux). Alternatively, Sielecki (2001) also observed a more intense white surface reflection from the external lens surface of the Swareflex and Strieter-Lite reflectors, which had a luminance value "several times to several hundred times higher than that of coloured light from the coloured lenses" (Sielecki 2001:484). During our trials, we also observed the white surface reflection described by Sielecki (2001). However, this reflection occurred as the vehicle passed an individual reflector, which logically is too late to prevent deer from entering the path of an oncoming vehicle. In our observations the white surface reflection transmitted no detectable light to diagonally or laterally adjacent reflectors.

MANAGEMENT IMPLICATIONS

We concluded that the wildlife warning reflectors we tested did not alter deer behavior such that deer–vehicle collisions might be prevented. Our data indicated that deer exhibit an increase in negative behavioral responses toward vehicles in the presence of reflectors. We suggest that until further research on deer–vehicle collision reduction strategies becomes available, management efforts should focus on 1) implementing proper deer-herd management programs, 2) controlling roadside vegetation to minimize its attraction to deer and maximize visibility for motorists, 3) increasing motorist awareness of the danger associated with deer–vehicle collisions, 4) thoroughly monitoring deer–vehicle collision rates, and 5) encouraging communication and cooperation among governments, wildlife researchers, highway managers, motorists, and others involved in issues of deer–human conflict.

Although many aspects of deer biology are well studied, we lack basic knowledge of anatomy and physiology related to the sensory capabilities of deer. Advancing this information may prove integral to the development of effective and economically feasible strategies to minimize deer–vehicle collisions. Further, our understanding of deer behavior related to most mitigation strategies is inadequate. Future development of deer-deterrent devices and strategies should be guided by knowledge of deer senses and behavior. Prior to extensive deployment of mitigation strategies in the field, researchers should empirically test their effectiveness in altering deer road-crossing behavior and ultimately the potential of such techniques for preventing deer–vehicle collisions.

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Figure 2.1. Wildlife warning reflectors mounted on a steel U-post within the area of influence, Berry College Campus and Wildlife Refuge, Mount Berry, Georgia, during 2004–2005.

Figure 2.2. Experimental section of roadway established for evaluating the effect of wildlife warning reflectors on the behavior of white-tailed deer along roadways on Berry College Campus and Wildlife Refuge, Mount Berry, Georgia, during 2004–2005.

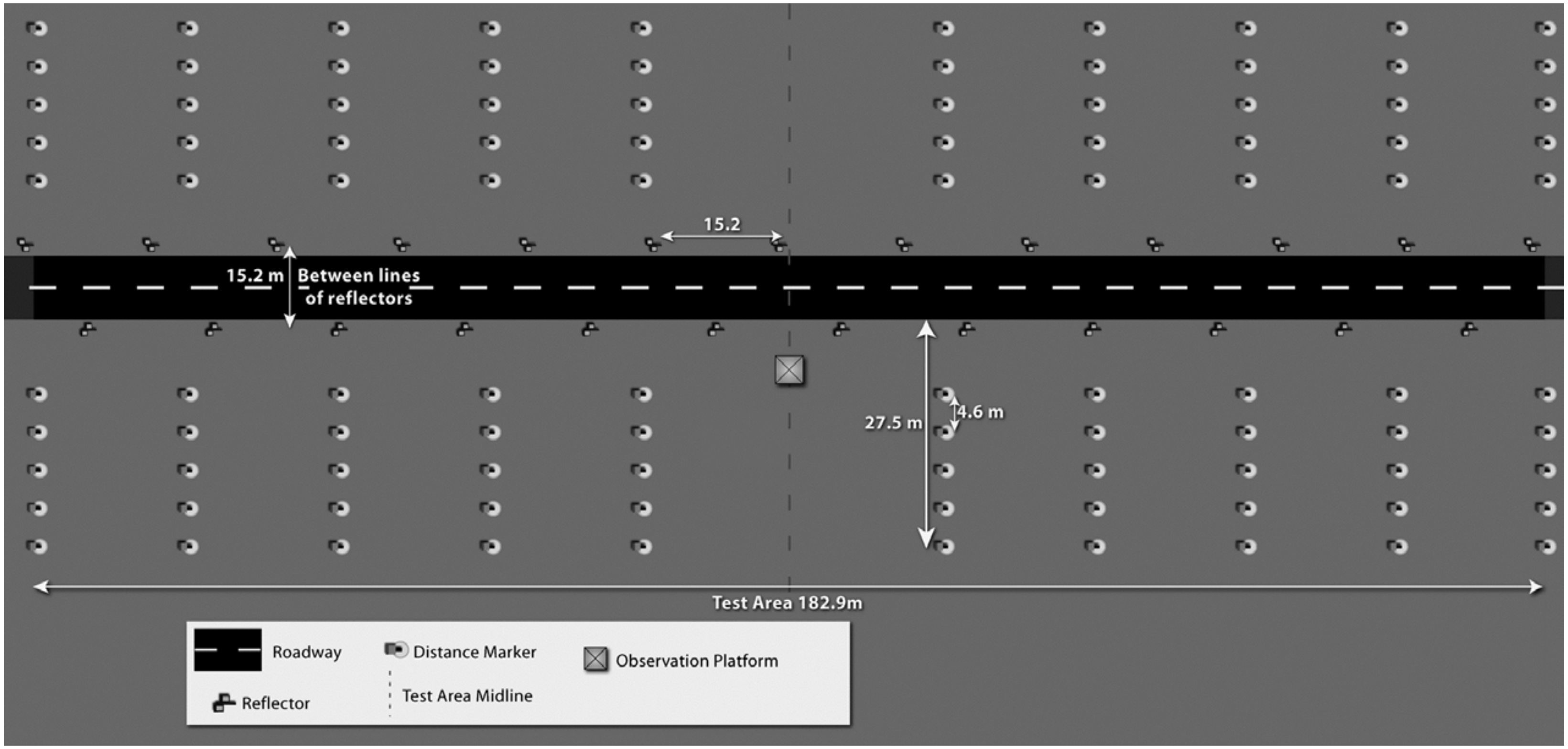
15.2
15.2 m Between lines of reflectors
27.5 m
4.6 m
Test Area 182.9m
Roadway
Distance Marker
Observation Platform
Reflector
Test Area Midline

Figure 2.3. Deer–vehicle interaction as captured using a forward-looking infrared camera on 19 April 2005 during the amber-colored wildlife warning reflector treatment phase on Berry College Campus and Wildlife Refuge, Mount Berry, Georgia.


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Table 2.1. White-tailed deer behavior scores for wildlife warning reflector testing based on changes in deer behavior near roads from before a vehicle entered the test area (period 1) to as the vehicle passed the deer or interacted with the deer in the roadway (period 2) on the Berry College Campus and Wildlife Refuge, Mount Berry, Georgia, during 2004–2005. Negative scores indicated increased risk of a deer–vehicle collision (DVC), neutral scores indicated no change in DVC risk, and positive scores indicated decreased DVC risk.

Behavior score	Period 1	Period 2
−2	Passive	Within road
−2	Active toward road	Within road
−2	Active away from road	Within road
−2	Active parallel to road	Within road
−2	Within road	Within road
−1	Passive	Active toward road
−1	Active toward road	Active toward road
−1	Active away from road	Active toward road
−1	Active away from road	Active parallel to road
−1	Active parallel to road	Active toward road
0	Passive	Passive
0	Passive	Active parallel to road
0	Active away from road	Passive
0	Active parallel to road	Active parallel to road

Behavior score	Period 1	Period 2
+1	Passive	Active away from road
+1	Active toward road	Passive
+1	Active toward road	Active parallel to road
+1	Active away from road	Active away from road
+1	Active parallel to road	Passive
+1	Active parallel to road	Active away from road
+2	Active toward road	Active away from road
+2	Within road	Passive
+2	Within road	Active away from road
+2	Within road	Active parallel to road
+2	Within road	Active toward road

Table 2.2. Proportions (%) of white-tailed deer behavioral response scores exhibited during each of the experimental phases of wildlife warning reflector testing on Berry College Campus and Wildlife Refuge, Mount Berry, Georgia, during 2004–2005.

			Behavior score				
			<u>Negative responses</u>		<u>Neutral</u>	<u>Positive responses</u>	
Test area	**Experimental phase**	***n***	**−2**	**−1**	**0**	**+1**	**+2**
Main campus	Pretreatment	161	3.73	2.48	70.81	18.01	4.97
	Red reflectors	182	6.04*	7.14*	69.78	16.48*	0.55*
	White reflectors	295	7.12*	10.50*	51.10*	21.02*	10.20*
Mountain campus	Pretreatment	307	2.61	3.58	72.96	16.94	3.91
	Blue-green reflectors	226	3.09**	6.63**	80.00**	8.85**	1.33**
	Amber reflectors	199	9.04*	7.54*	54.77*	20.10*	8.54*

* $P \leq 0.001$ for differences observed in behavioral responses among pretreatment and treatment phases as determined by Chi-square analysis.

** $P \leq 0.01$ for differences observed in behavioral responses among pretreatment and treatment phases as determined by Chi-square analysis.

Table 2.3. Mean (SE) perpendicular distance of the focal animal from the road as the vehicle entered the test area (period 1), and mean (SE) perpendicular and total distances moved from period 1 to when the vehicle passed the deer or the deer and vehicle interacted in the roadway (period 2), for negative and positive behavioral responses of white-tailed deer during experimental phases of wildlife warning reflector testing on Berry College Campus and Wildlife Refuge, Mount Berry, Georgia, during 2004–2005.

			Perpendicular distance	Perpendicular distance moved		Total distance moved	
Test area	**Experimental phase**	***n***	**Period 1**	**Negative responses**	**Positive responses**	**Negative responses**	**Positive responses**
Main campus	Pretreatment	161	10.4 (7.8)	8.9 (7.1)	4.8 (4.2)	13.1 (10.4)	5.6 (4.9)
	Red reflectors	182	15.5 (8.6)*	5.9 (4.4)	6.0 (3.8)	6.0 (4.6)*	6.4 (3.9)
	White reflectors	295	12.1 (8.0)**	4.2 (3.7)**	4.8 (3.4)	5.2 (4.3)**	5.5 (4.1)
Mountain campus	Pretreatment	307	13.6 (7.9)	4.7 (3.7)	6.4 (5.0)	9.3 (8.3)	7.8 (6.3)
	Blue-green reflectors	226	12.9 (7.8)	4.4 (3.0)	3.6 (2.4)*	6.7 (6.7)	4.9 (3.1)**
	Amber reflectors	199	11.9 (8.2)**	3.3 (2.9)**	3.6 (1.9)*	6.8 (10.8)	4.4 (2.9)*

* $P \leq 0.001$ for differences observed in perpendicular distances for period 1 and perpendicular and total distances moved among pretreatment and treatment phases as determined by Chi-square analysis.

** $P \leq 0.05$ for differences observed in perpendicular distances for period 1and perpendicular and total distances moved among pretreatment and treatment phases as determined by Chi-square analysis.

CHAPTER 3

VISUAL SPECIALIZATION OF AN HERBIVORE PREY SPECIES, THE WHITE-TAILED DEER[2]

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[2] D'Angelo, G. J., G. A. Williams, M. T. Pardue, D. A. Osborn, G. R. Gallagher , R. J. Warren., and K. V. Miller. To be submitted to *Canadian Journal of Zoology*.

ABSTRACT

To gain knowledge of visual specializations influencing the behavior of white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)), we examined gross eye characteristics, structural organization of the retina, and the density and distribution of cone photoreceptors. White-tailed deer possess ocular features similar to other ungulates including a horizontal slit pupil, reflective tapetum lucidum, typical retinal structure, and cone photoreceptors concentrated in a horizontal visual streak. The tapetum improves sensitivity in low-light conditions. The visual streak provides deer with enhanced surveillance of a broad area. In daylight, the spatial association of the visual streak and tapetum likely improves the contrast of visual scenes and perception of color. The horizontal slit pupil protects the retina of deer in bright light conditions and concentrates light on the visual streak for improved acuity. As expected for a crepuscularly active prey species, the visual system of white-tailed deer is specialized for sensitivity in low light conditions and detection of predators.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) are widely extant from the tropics to the arctic in a variety of habitats ranging from densely vegetated coastal wetlands to open prairies (Geist 1998). Their circadian activity patterns are typically described as arrhythmic with peaks in activity near dawn and dusk (Marchinton and Hirth 1984). In diverse habitats and lighting conditions, whitetails must rely on vision for avoidance of predators, foraging, intraspecific communication, and general negotiation of their home ranges. Although many aspects of their biology have been studied thoroughly, the visual abilities of white-tailed deer continue to be the subject of much discussion and conjecture within the scientific and deer hunting communities. Knowledge of deer vision may provide a foundation toward understanding deer behavior and anti-predation strategies, and may be useful for developing physiologically based strategies to reduce deer-human conflicts.

The basic structure of the eye of white-tailed deer is of the typical mammalian form (Walls 1942). An image in its most basic composition, photons of light, enters the mammalian eye through the cornea, passes through the aqueous humor into the pupil opening of the iris and into the lens. Light from the lens passes through the vitreous body, and strikes the retina. The cornea is the first mechanism to refract light. The pupil restricts the amount of light entering the rest of the eye, and the lens inverts and focuses the image on the retina (Ali and Klyne 1985). The retina is an extension of the optic brain, and is organized in layers of interconnected cells, the most prominent of which are the rod and cone photoreceptors. The rods are responsible for vision in low-light conditions, whereas the cones enable color vision and distinguish fine detail. Light forming the image is absorbed by the photoreceptors in the retina and is sent via the optic nerve to the brain for interpretation (Ali and Klyne 1985). The other cells composing the retina are designed to transmit information from and support the function of the photoreceptors. These include the ganglion cells, bipolar cells, horizontal cells, Müller glial cells, and amacrine cells (Cohen 1992).

There are 3 nuclear layers in the mammalian retina, including the ganglion cell layer, the inner nuclear layer, and the outer nuclear layer. The ganglion cells form the nerve layer closest to the vitreous chamber. The inner nuclear layer contains the nuclei of the horizontal, bipolar and amacrine cells. The outer nuclear layer, containing the nuclei of the rods and cones, is the outermost nerve layer, which light reaches as it passes through the eye. Between the inner nuclear layer and the ganglion cell layer is the inner plexiform layer. Within the inner plexiform layer, synaptic connections are made involving bipolar neurons, amacrine cells, and ganglion cells (Cohen 1992). Between the outer nuclear layer and the inner nuclear layer, lies the outer plexiform layer in which synaptic connections are made among the horizontal cells, bipolar neurons, and the photoreceptors (Cohen 1992). The photoreceptors transmit information to the ganglion cells via synaptic connections with bipolar cells (Ali and Klyne 1985). Ganglion cells can have extensively spreading dendrites, so each ganglion cell may receive information from many rods and cones (Cohen 1992). Further lateral transmissions are facilitated by the horizontal and amacrine cells (Ali and Klyne 1985). The axons of the ganglion cells form the optic nerve fibers, which are routed throughout the retina and leave the eye at the optic nerve head (Cohen 1992). The retinal structures are bound by the Müller glial cells, which extend in height the full thickness of the retina (Cohen 1992). Characteristics of the nuclear layers can reflect retinal adaptations among species.

Witzel et al. (1978) confirmed the presence of rods and cones in the white-tailed deer retina. They found cones at densities of about 10 000/mm^2 in the central retina, however their examination did not include systematic surveys across the entire retina or classification of different types of cones. With electroretinogram flicker photometry, Jacobs et al. (1994) detected the presence of 2 classes of cone photopigments in white-tailed deer. Staknis and Simmons (1990) failed to identify the presence of cones, but rods were readily visible at all locations they sampled with scanning and transmission electron microscopy. The discrepancies among the aforementioned studies suggest that cones may not be evenly distributed throughout the retina of white-tailed deer.

Based on data from other ungulates, Müller-Schwarze (1994) speculated that all species of deer have a visual streak corresponding to a horizontal band of increased cellular density in the retina, which affords them increased acuity. Recently, Ahnelt et al. (2006) found that 2 species of cervids, red deer (*Cervus elaphus* (Linnaeus 1758)) and roe deer (*Capreolus* capreolus (Linnaeus 1758)), have an arrangement of medium-wavelength cones characteristic of a horizontal visual streak. No data exist on the density and distribution of cones throughout the white-tailed deer retina. Our objectives were: 1) to describe the gross morphology of the white-tailed deer eye integral to understanding retinal function, 2) to examine the microscopic structure of the white-tailed deer retina, 3) to determine the density and distribution of cones in the white-tailed deer retina to identify whether they possess a visual streak.

MATERIALS AND METHODS

Study Area and Animals

White-tailed deer were collected on the Daniel B. Warnell School of Forestry and Natural Resources Whitehall Experimental Forest (WEF), an 337-ha property on the campus of the University of Georgia, Athens, Georgia. WEF was located in the Piedmont Uplands physiographic province, and was bordered on 3 sides by the Oconee River. The topography of WEF was characterized by rolling hills separated by small creek drainages. Dominant cover types included pine (*Pinus* spp.) plantations of various ages, and mixed pine and deciduous forests. Forested areas were interspersed with hay fields, small ponds, roads and buildings.

Dissection and Gross Measurements

All animal procedures were performed following the *Canadian Journal of Zoology* guidelines, with prior approval from the University of Georgia Institutional Animal Care and Use Committee (#A2004-10102-0), and under the authorization of a Georgia Department of Natural Resources Wildlife Resources Division scientific collection permit (#29-WSF-05-115).

Free-ranging white-tailed deer were euthanized by sharpshooting with a high-powered rifle. Gross eye measurements were made with digital vernier calipers (Mitutoyo Corporation, Japan) accurate to ±0.2 mm. Immediately post-mortem, interocular distance was measured, a dorsal orientation mark was created in the cornea with a heated dissecting needle, and the eyes were enucleated. The external gross eye measurements included: axial length, vertical and horizontal equatorial diameters, vertical and horizontal corneal diameters, depth of the anterior chamber, and depth of the vitreous chamber.

One eye of each deer was used for gross external measurements and then dissected to obtain measurements of corneal thickness (central and peripheral), and lens diameter and thickness. The remaining eyecups were post-fixed in 4% paraformaldehyde for 24 hours. The retina was then dissected from the eyecup and the tapetum lucidum, and radial incisions were made to flatten the retina in preparation for subsequent mounting on slides. Following processing of the eyes, we aged deer by tooth wear and replacement criteria (Severinghaus 1949).

Histology

For the opposite eye of each deer, gross external measurements were made and then a solution of 2% paraformaldehyde/2.5% glutaraldehyde was injected into the anterior and vitreous chambers with a syringe and small gauge needle. The whole eye was immersed in a solution of 2% paraformaldehyde/2.5% glutaraldehyde for >24 hours. Subsequently, each eye was equatorially bisected. Orientation of all tissue samples were noted throughout processing.

From the posterior segment of the eye, a 4-5 mm wide vertical band centered on the optic nerve head was dissected. From this band, 5 2-mm^2 tissue samples were excised from sites centered: 1) 4 mm superior of the optic nerve head, 2) centered on the optic nerve head, 3) 2 mm inferior of the optic nerve head, 4) 2 mm temporal of the optic nerve head, and 5) 4 mm temporal of the optic nerve head. Tissue samples were dehydrated through a graded series of alcohols, embedded in plastic, and serially sectioned (thickness = 0.5 μm) on an ultramicrotome using a diamond knife. All tissue sections were stained with toluidine blue.

Using a light microscope (Leica Microsystems Inc., Bannockburn, USA) and CCD camera (Leica Microsystems Inc., Bannockburn, USA) tissue sections were photographed. Micrographs were imported into Image-Pro Plus software (Media Cybernetics, Bethesda, USA), and the thickness of each individual retinal layer measured.

Immunohistochemistry

All immunohistochemical steps were performed at 4 C° on a rotator. Retinas were immersed in phosphate buffered saline (PBS) for 3 5-minute rinses followed by a 1-hour rinse. Retinas were immersed for 12 hours in 10% normal goat serum diluted in a solution of PBS, bovine serum albumin, Triton X, and sodium azide (PBTA). Primary antibodies diluted in PBTA were applied to retinas for 72 hours. Primary antibodies consisted of either antisera JH455 (1:5000 dilution) to label the short wavelength cone (S cone) opsin or antisera JH492 (1:5000 dilution) to label the medium wavelength cone (M cone) opsin. Following incubation in the primary antibody, retinas were again rinsed in PBTA, followed by incubated in goat anti-rabbit biotinylated secondary antibody diluted in PBTA for 24 hours. Before mounting, retinas were rinsed and then flat-mounted in mounting medium (Vectashield Laboratories, Inc., Burlingame, USA). A coverslip was applied and nail polish was used to seal the coverslip. Shrinkage of retinal tissue was considered to be negligible.

To count cones, 1-mm intervals were surveyed across the retina in 0.0024-mm^2 sampling windows using a fluorescent light microscope (Nikon, Melville, USA) and a CCD camera

(Princeton Scientific Instruments, Monmouth Junction, USA). Cone distribution maps were developed for densities of S cones and M cones of individual retinas.

Data Analyses

Mean gross eye measurements were calculated for fawns (0.5 years old) and adults (>1.0 years old). We calculated lens thickness ratio by dividing lens thickness by axial length. Gross eye measurements were compared between fawns and adults with a Student's *t* test.

Measurements were pooled from all sample locations to calculate mean retinal layer thickness. To examine age effects on the thickness of retinal layers, a linear regression was conducted using Statistix Version 8.0 software (Analytical Software, Tallahassee, USA) with age specified as the independent variable and layer thickness specified as the dependent variable.

The mean photoreceptor density/mm^2 for each retina labeled in immunohistochemical experiments was calculated and the photoreceptor density/mm^2 was averaged for all retinas labeled with either S cone opsin or M cone opsin.

RESULTS

From 22-28 November 2006, eyes from 6 free-ranging female white-tailed deer were obtained, including 3 fawns (approximately 0.5 years old) and 3 adults (2.5-years old, $n = 1$; 3.5-years old, $n = 1$; 6.5-years old, $n = 1$). All deer included in our sample appeared healthy with no signs of ocular disease. The eyes of deer we examined were approximately spherical (Table 3.1, Figure 3.1). The corneas were oval with the length of the horizontal corneal diameter exceeding the length of the vertical corneal diameter ($t_{[22]} = -4.20$, $P = 0.0002$, $n = 12$). With the exception of central and peripheral corneal thicknesses, all gross measurements of the eyes of adult deer exceeded those of fawns. However, lens thickness ratio did not differ among fawns and adults (pooled mean = 0.3, SE = 0.01, $t_{[4]} = -1.76$, $P = 0.08$, $n = 6$). The pupil was a horizontal slit.

The tapetum lucidum was a prominent half moon shape radiating from a point on its inferior border centered approximately 1 mm superior of the optic nerve head, and extending about two-thirds into the superior retina (Figure 3.2). The inferior border of the tapetum was nearly horizontal. The tapetum was iridescent, and reflected an azure blue color centrally transitioning to blue-green and yellow in its periphery.

The thickness of the outer nuclear layer decreased with age ($r^2 = 0.686$, $P = 0.042$, $df = 5$)(Figures 3.3, 3.4). But, the thickness of other retinal layers was not related to age (ganglion cell layer: $r^2 = 0.081$, $P = 0.584$, $df = 5$; inner plexiform layer: $r^2 = 0.113$, $P = 0.514$, $df = 5$; inner nuclear layer: $r^2 = 0.539$, $P = 0.096$, $df = 5$; outer plexiform layer: $r^2 = 0.008$, $P = 0.865$, $df = 5$; outer and inner segments of photoreceptors: $r^2 = 0.202$, $P = 0.371$, $df = 5$). Mean total retinal thickness for all deer was 227.1 micrometers (SE = 48.9, $n = 6$).

The density of M cones averaged 16 414/mm^2 (range = 4717, $n = 3$) ranging from an average minimum of 7322/mm^2 (range = 500, $n = 3$) to an average maximum of 35 700/mm^2 (range = 12 832, $n = 3$; Figure 3.5). The area of maximum density of M cones was characteristic of a horizontal visual streak approximately 2-3 mm superior of the optic nerve head.

We found S cones at densities lower than the density of M cones (Figure 3.6). The density of S cones averaged 1602/mm^2 (range = 317, $n = 2$) ranging from an average minimum of 442/mm^2 (range = 50, $n = 2$) to an average maximum of 4883/mm^2 (range = 1433, $n = 2$).

DISCUSSION

The size and spherical shape of the white-tailed deer eye was similar to the human eye (Markowitz and Morin 1985, Howland et al. 2004). In comparison to other vertebrates, white-tailed deer have a large eye relative to their body size and in absolute terms (Walls 1942, Ali and Klyne 1985, Howland et al. 2004). Larger eyes have increased distance between the cornea/lens and retina, which increases the size of the image projected on the retina (Walls 1942). Since the diameter of photoreceptors varies little among species, the number of photoreceptors that are available to absorb light is greater in larger eyes (Walls 1942). By maximizing image size and the number of photoreceptors in the retina, larger eyes enhance visual acuity. Although illumination of the image projected on the retina decreases with increasing image size, the tapetum of deer likely compensates for such loss of brightness (see below; Ali and Klyne 1985).

The thickness of the lens is another optical feature which impacts the size of the image projected on the retina. Species with strongly nocturnal visual systems tend to have large lenses within a large anterior chamber (e.g., mouse (*Mus musculus* (Linnaeus 1758)), lens thickness ratio = 0.6 (M.T. Pardue, Emory University, unpublished data)). The large lens causes the optical center of the eye to be closer to the retina, which decreases the size of the image projected onto the retina. The projection of a smaller image increases brightness at the expense of visual acuity because fewer photoreceptors are impacted to absorb light (Ali and Klyne 1985). Species active diurnally have low lens thickness ratios, such as humans (lens thickness ratio = 0.2, Markowitz and Morin 1985). An eye with a low lens thickness ratio projects a large image on the retina with reduced brightness. The larger image is intercepted by many cones for increased acuity. The moderate lens thickness and large eye of deer appears well suited for their mostly crepuscular activity patterns. Their eye likely produces an image of sufficient size and brightness for navigation and avoidance of predators when light is at moderate levels.

The deer pupil is highly versatile to function in a range of lighting conditions. Whereas the pupil of humans is round (Ali and Klyne 1985), white-tailed deer possess a horizontal slit pupil. Likewise, Malmström and Kröger (2006) observed a horizontal slit pupil in other cervids, including European elk (*Alces alces* (Linnaeus 1758)), red deer, and reindeer (*Rangifer tarandus*

(Linnaeus 1758)). The slit pupil of white-tailed deer extends nearly the entire horizontal width of the cornea and is capable of vertical adjustment from a narrow slot in bright light conditions dilating to a broad oval when light is limited (G.J. D'Angelo unpublished data). The eyes in our study likely demonstrated the maximum dilation of the white-tailed deer pupil since we obtained the measurements post-mortem. The slit pupil allows species like deer with highly light-sensitive visual systems to function in full daylight without overwhelming the retina (Ali and Klyne 1985).

The horizontal slit pupil may facilitate color vision during full daylight. In a sample of terrestrial vertebrates, Malmström and Kröger (2006) found that species with slit pupils also had multifocal lenses. Ocular media (e.g., cornea, lens, etc.) have different refractive indices for different wavelengths of color causing different wavelengths of color to focus at different distances within the eye (i.e., linear chromatic aberration; Walls 1942). Multifocal lenses have concentric zones of different refractive indices, with each zone designed to create a well-focused image on the retina for one of the spectral types of cones (Malmström and Kröger 2006). In conditions of bright light, the pupil constricts to protect the retina. When round pupils constrict, the periphery of the lens is obstructed. The slit pupil, even when constricted, enables the use of the full diameter of the lens such that all wavelengths of color may be focused on the retina (Malmström and Kröger 2006).

The tapetum lucidum is a membrane attached to the retina to enhance vision in low light. Reflections from the tapetum lucidum produce the characteristic eye shine of deer and other species with light-sensitive visual systems when they are alighted by bright sources of light (Walls 1942). Like most ungulates, the tapetum of white-tailed deer is composed of regularly arranged collagen fibers (Ollivier et al. 2004). The tapetum reflects light that has already passed through the eye back to the photoreceptors a second time to increase the absorption of light and improve interpretation of visual images (Ali and Klyne 1985).

Ollivier et al. (2004) concluded that the tapetum of herbivores was less evolved than carnivores, with tapetal variations in herbivores being more suited for maximal reflectance rather than use of specific wavelengths. However, we found that the coloration of the tapetum of white-tailed deer was of short-wavelength blues and medium-wavelength yellows, which is consistent with the photopigments shown to be most sensitive to deer (Jacobs et al. 1994). Since scattering of light during reflection may reduce the ability of the eye to resolve the details of an image (Walls 1942), the specialized coloration of the tapetum may preserve acuity by reducing the total amount of light reflected to include only the wavelengths most perceptible to deer.

We found that the tapetum of white-tailed deer was restricted to the superior retina. Miller and Murphy (1995) suggested that a superiorly oriented tapetum in dogs (*Canis familiaris* (Linnaeus 1758)) functioned during both night and day. They reasoned that the superior retina receives light mostly from the ground, and the inferior retina receives light from the sky, so the tapetum probably improves the ability of animals to decipher details of the darker ground by increasing the contrast of the entire scene. Tapetal function during daytime would enhance the visual acuity of deer, especially in dense vegetation and closed canopy forests where light infiltration is reduced and much of the visual scene is in shadow. In conditions of intense reflectivity from the ground (e.g., snow), the deer eye must adjust for tapetal function to avoid overwhelming the retina. Two such protective mechanisms are a reduction in pupil size and alteration of the sensitivity of photoreceptors in different regions of the retina (Ali and Klyne 1985).

The structural organization of the white-tailed deer retina was similar to other vertebrates (Ali and Klyne 1985). However, the deer retina appears to be thicker compared to many terrestrial mammals. For example, the total thickness of the white-tailed deer retina was greater than that of the horse (*Equus caballus* (Linnaeus 1758), total retinal thickness = 80 to 130 µm, Ehrenhofer et al. 2002), ferret (*Mustela putorius* (Linnaeus 1758), total retinal thickness = 138-160 µm, Wen et al.1985), dog (total retinal thickness = 151-184 µm, Wen et al.1985), and cat (*Felis catus* (Linnaeus 1758), total retinal thickness = 145-150 µm, Wen et al.1985). Yet, similar to the white-tailed deer in our study, Chan et al. (2006) estimated that the total thickness of the human retina was about 260 µm with the outer retinal complex (outer nuclear layer and inner and outer segments of the photoreceptors) occupying about 95 µm. This contradicts some comparisons of the retinas of diurnal (e.g. humans) versus arrhythmic species (e.g., deer)(Walls 1942, Ali and Klyne 1985). Cones are thicker than rods, so fewer rows of cones can be accommodated in a retinal area. Therefore, diurnal species generally possess a thinner outer nuclear layer because the preponderance of cones in their retina limits the number of cell layers. However, with the exception of the human optic fovea, the density of cones in the human retina is generally less than we observed in deer (Ahnelt et al. 2006). An evaluation of the number of photoreceptor cell layers in different regions of the retina may reveal differences among humans and deer.

Although our sample of deer was limited, we included a representation of ages typical of many wild populations. Our observation of a reduction in the thickness of the outer nuclear layer of deer with age was consistent with studies of other species. In human subjects from 6 to 79 years old, Alamouti and Funk (2003) observed a reduction in both the retinal nerve fiber layer and total retinal thickness. An age-related thinning of the outer nuclear layer of the mouse was shown by Li et al. (2001), but they concluded that the changes were not related to a reduction in the number or structural integrity of rod and cone photoreceptors. In contrast, DiLoreto et al. (1994) observed degeneration of photoreceptors and a concomitant decrease in outer nuclear layer thickness with age in rats (Fischer 344 strain) known previously to exhibit age-related retinal degeneration. Unknown are the cellular and molecular processes responsible for age-related neural loss (DiLoreto et al. 1994, Li et al. 2001).

Ahnelt et al. (2006) observed M cone patterns in red deer and roe deer similar to the visual streak in the retina of white-tailed deer. In contrast, Ahnelt et al. (2006) demonstrated that the human retina contains a fovea centralis, a small circular area with M cone density >150 000/mm^2. The visual streak of white-tailed deer likely has far less acuity than the fovea in humans because the density of cones is relatively limited in the deer retina. Humans have close set eyes that are active, moving regularly within the orbit. Human eyes scan in conjunction across visual scenes to maximize the visual acuity of the fovea and to use binocular vision for perception of three dimensions. In contrast, deer have laterally directed eyes that are relatively immobile within the orbit (Walls 1942). As a prey species, deer must constantly monitor their surroundings to avoid predation, but also must minimize movement to avoid detection by predators. The visual streak of deer in combination with their wide set eyes likely provides them with enhanced ability to monitor the horizon and to detect movement with a wide field of view while keeping their head and eyes stationary.

Advantages of the visual streak are not limited to motion detection by sedentary animals. Ahnelt et al. (2006) suggested that the visual streak of cheetahs (*Acinonyx jubatus* (Schreber 1775)) was an adaptation to optimize visual sampling during chases in the savannah. The contrast of vertical habitat features against the visual streak probably aids navigation of white-tailed deer through intricate habitats when fleeing danger. Likewise, the flagging motion of their characteristic white tail across the visual streak likely helps maintain herd cohesion of deer in flight.

The visual streak and the tapetum of deer occur in the superior retina. This spatial association supports the theory that the tapetum also functions to enhance vision in daylight. Within the visual streak cones are densely packed, therefore, rods are likely limited or absent within this region (Walls 1942). Cones do not function in low light conditions, thus the alignment of the tapetum and visual streak would only be useful when light is sufficient to stimulate function of the cones. Visual acuity and color perception of deer probably improves with increasing light intensity because the horizontal slit pupil is more constricted and concentrates the image on the central and most sensitive portion of the cone-rich visual streak. When light is limited, the reflectance of color is suppressed. Accordingly, the pupil of deer is dilated to project light onto a broad area of the retina for light absorption by many rods to enhance image interpretation without regard to color.

Although we found S cones at densities lower than M cones, the presence of S cones corroborates the basis for dichromatic color vision of white-tailed deer (Jacobs et al. 1994, Calderone et al. 2003). Spatial coincidence of the maximum areas of S cones and M cones did not occur in the white-tailed deer retina. The ventral bias of the distribution of S cones in deer may be a mechanism which enables their detection of predators silhouetted against the short-wavelength colors of the sky (Ahnelt et al. 2006). Such detection would be important to deer susceptible to ambushes by feline predators in trees or to bedded fawns, which are sought by ground-searching predators such as coyotes (*Canis latrans* (Say 1823)) and black bears (*Ursus americanus* (Pallas Year unknown)).

Eyes of white-tailed deer are specialized for function in a variety of habitats and lighting conditions. The visual streak of deer is similar to other cervids, and provides deer with enhanced surveillance of a broad area. The tapetum lucidum improves sensitivity in low-light conditions. The spatial association of the visual streak and tapetum and the color reflectance of the tapetum likely improves the contrast of visual scenes and perception of color in daylight. The horizontal slit pupil of deer serves to protect their light-sensitive retina in bright light conditions and concentrate light on the visual streak for improved acuity. The visual system of white-tailed deer is similar to other ungulates and is well suited for sensitivity in low light conditions and detection of predators.

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Table 3.1. Measurements of anatomical features of eyes of white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780), $n = 6$) collected at Daniel B. Warnell School of Forestry and Natural Resources Whitehall Experimental Forest, University of Georgia, Athens, Georgia during 22-28 November 2006.

	Fawns		Adults				
	Mean	SE	Mean	SE	*t*	df	*P*
Interocular distance	81.1	0.2	94.9	1.9	-3.521	4	0.012
Axial length	25.3	0.2	27.8	0.2	-7.082	10	<0.0001
Vertical equatorial diameter	26.5	0.2	28.7	0.2	-5.420	10	0.0001
Horizontal equatorial diameter	27.0	0.2	28.6	0.2	-4.159	10	0.0009
Anterior chamber depth	5.1	0.3	6.7	0.3	-2.963	10	0.007
Vitreous chamber depth	20.9	0.2	23.1	0.5	-2.761	10	0.010
Vertical corneal diameter	17.7	0.2	19.7	0.3	-3.729	10	0.002
Horizontal corneal diameter	19.9	0.2	22.0	0.2	-4.491	10	0.0006
Central corneal thickness	0.6	0.1	0.6	0.1	0.417	4	0.349
Peripheral corneal thickness	0.5	0.1	0.5	0.0	-0.277	4	0.398
Vertical pupil diameter	12.8	0.3	15.4	0.3	-4.307	10	0.0008
Horizontal pupil diameter	14.2	0.1	15.6	0.3	-2.908	10	0.008
Lens diameter	13.0	0.1	14.3	0.3	-2.697	4	0.027
Lens thickness	7.4	0.2	9.2	0.4	-2.659	4	0.028

Figure 3.1. Enucleated eye of white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) collected at Daniel B. Warnell School of Forestry and Natural Resources Whitehall Experimental Forest, University of Georgia, Athens, Georgia during 22-28 November 2006 (1 = cornea, 2 = lens, 3 = ciliary body, 4 = retina, 5 = optic nerve head). The eye was dissected bilaterally, and photographed in 4 parts at 0.8X magnification. In Adobe Photoshop CS3 (San Jose, United States), we merged the photographs of the 4 parts with no further alterations to the images. Reader should note that the eye was postfixed in a solution of 2% paraformaldehyde/2.5% glutaraldehyde postfixatives, which altered the coloration and opacity of the eye.

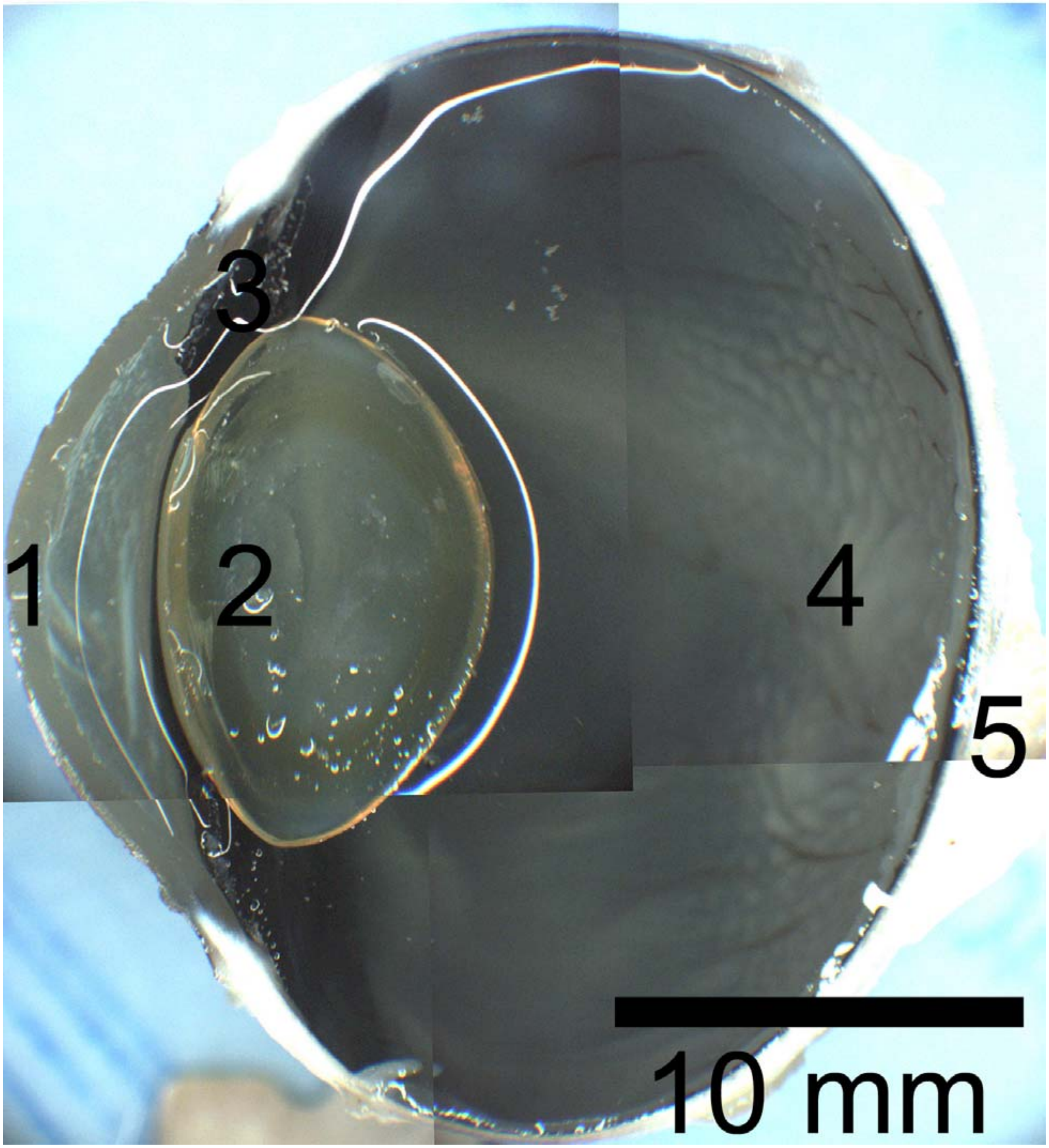

3
1
2
4
5
10 mm

Figure 3.2. Radially flattened ocular fundus of white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) collected at Daniel B. Warnell School of Forestry and Natural Resources Whitehall Experimental Forest, University of Georgia, Athens, Georgia during 22-28 November 2006. The eye was postfixed in 4% paraformaldehyde, which slightly altered the coloration of the ocular fundus. The white circle indicates the location of the optic nerve head.

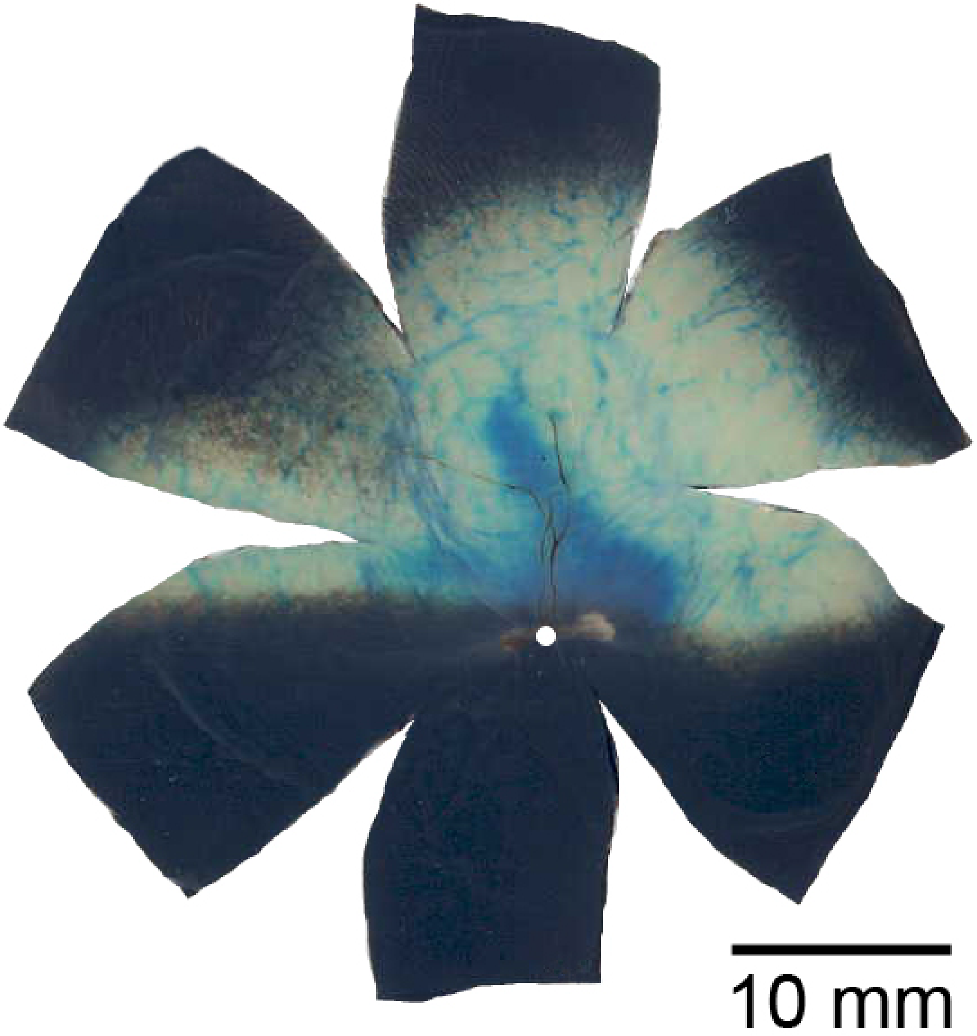

10 mm

Figure 3.3. Light micrograph of the retina of 0.5-year-old white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) collected at Daniel B. Warnell School of Forestry and Natural Resources Whitehall Experimental Forest, University of Georgia, Athens, Georgia on 22 November 2006. The layers shown include: ganglion cell layer (GCL), inner plexiform layer (IPL), inner nuclear layer (INL), outer plexiform layer (OPL), outer nuclear layer (ONL), and the outer and inner segments of photoreceptors (OIP). The structural organization of the retina of white-tailed deer was similar to other terrestrial mammals. The retina was artificially detached from the retinal pigment epithelium (RPE) during processing.

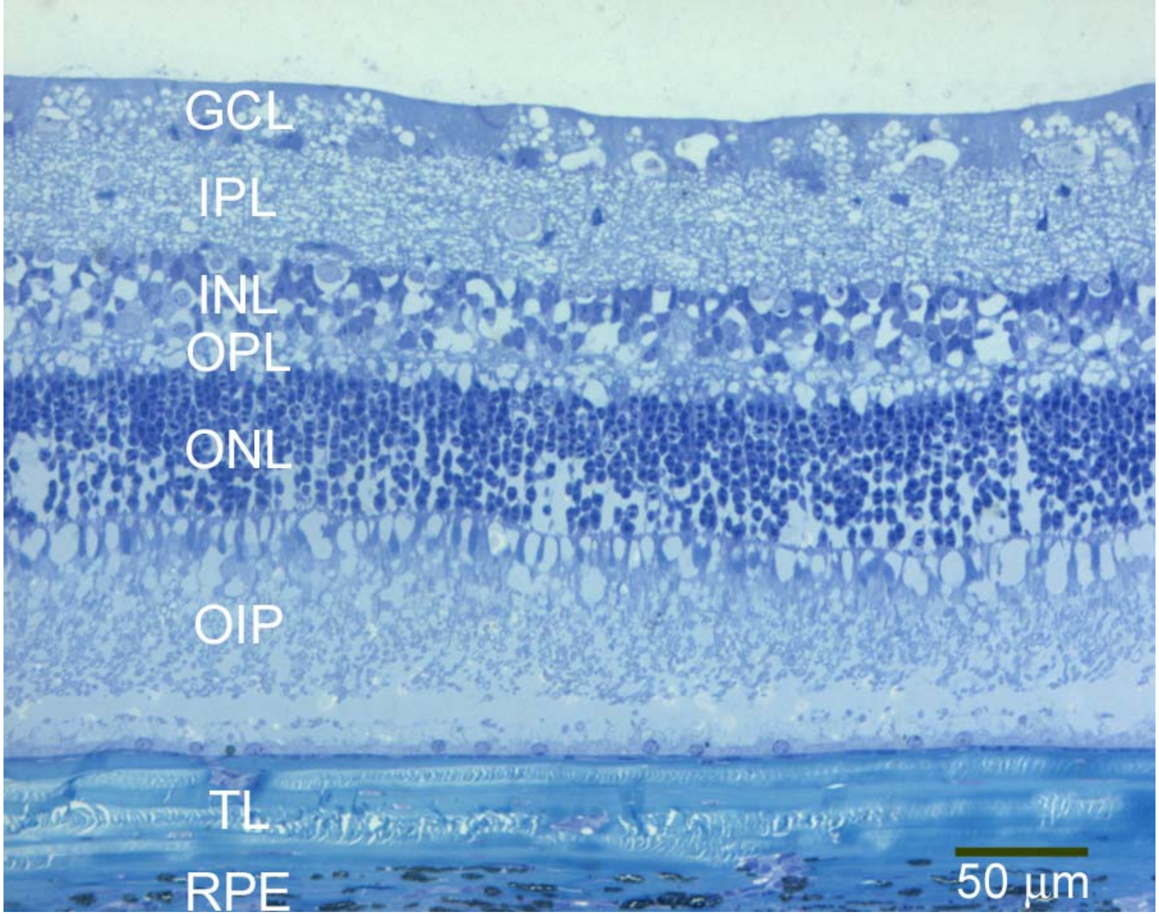

GCL
IPL
INL
OPL
ONL
OIP
TL
RPE
50 µm

Figure 3.4. Thickness of individual retinal layers of white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780), *n* = 6) collected at Daniel B. Warnell School of Forestry and Natural Resources Whitehall Experimental Forest, University of Georgia, Athens, Georgia during 22-28 November 2006. Thickness of the outer nuclear layer decreased with age, but the thickness of other retinal layers was not related to age.

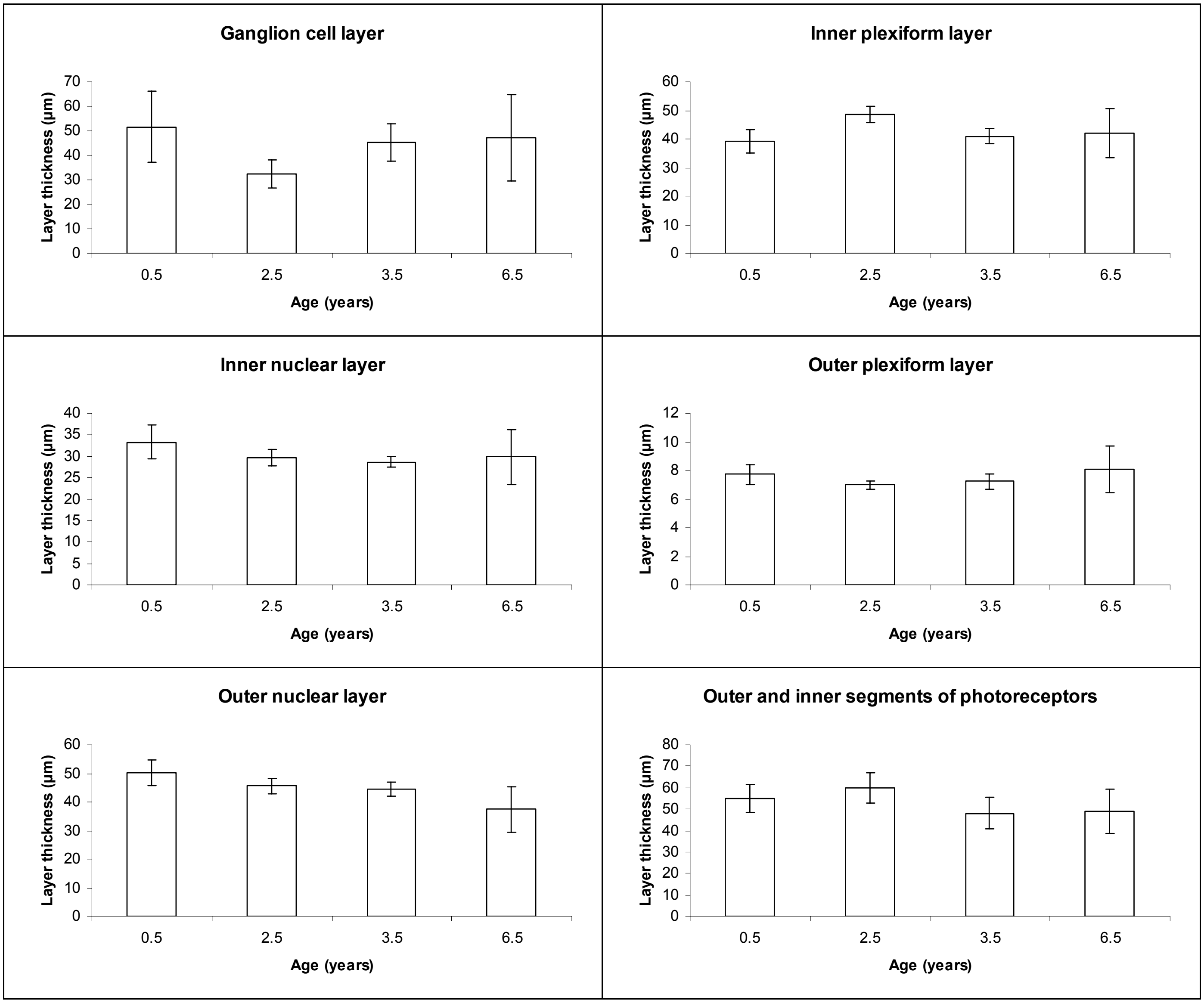

Ganglion cell layer
Layer thickness (µm)
0
10
20
30
40
50
60
70
0.5
2.5
3.5
6.5
Age (years)
Inner plexiform layer
Layer thickness (µm)
0
10
20
30
40
50
60
0.5
2.5
3.5
6.5
Age (years)
Inner nuclear layer
Layer thickness (µm)
0
5
10
15
20
25
30
35
40
0.5
2.5
3.5
6.5
Age (years)
Outer plexiform layer
Layer thickness (µm)
0
2
4
6
8
10
12
0.5
2.5
3.5
6.5
Age (years)
Outer nuclear layer
Layer thickness (µm)
0
10
20
30
40
50
60
0.5
2.5
3.5
6.5
Age (years)
Outer and inner segments of photoreceptors
Layer thickness (µm)
0
10
20
30
40
50
60
70
80
0.5
2.5
3.5
6.5
Age (years)

Figure 3.5. Density map of medium wavelength cones of white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) collected at Daniel B. Warnell School of Forestry and Natural Resources Whitehall Experimental Forest, University of Georgia, Athens, Georgia during 22-28 November 2006. Cones were labeled immunohistochemically using JH492 antisera. The density of M cones averaged 16 414/mm^2 (range = 4717, $n = 3$) ranging from an average minimum of 7322/mm^2 (range = 500, $n = 3$) to an average maximum of 35 700/mm^2 (range = 12 832, $n = 3$). The area of maximum density of M cones was characteristic of a horizontal visual streak approximately 2-3 mm superior of the optic nerve head. The location of the optic nerve head is indicated by a gray circle.

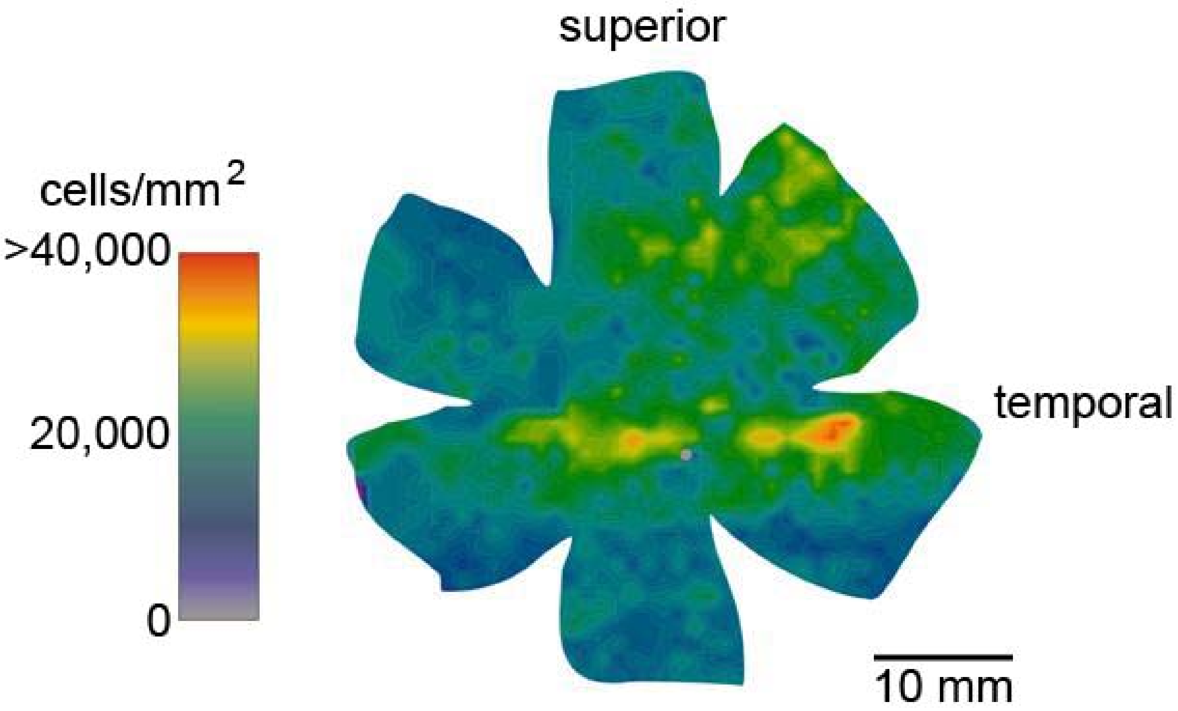
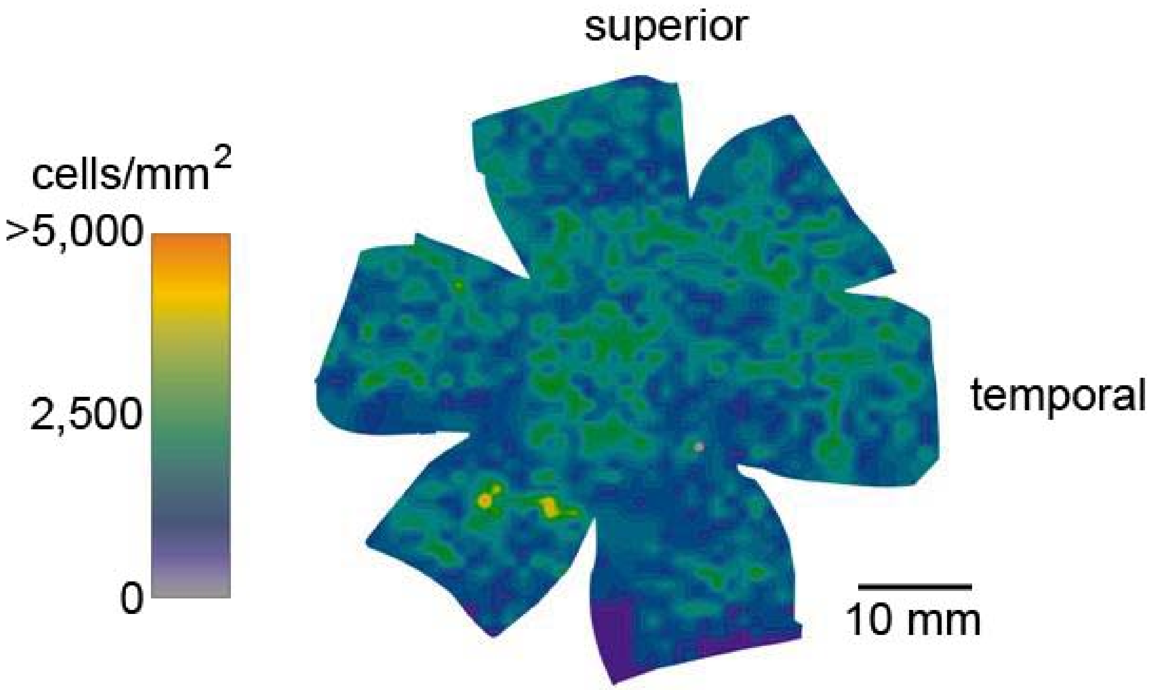

superior
cells/mm^2
>40,000
20,000
0
temporal
10 mm

Figure 3.6. Density map of short wavelength cones of white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) collected at Daniel B. Warnell School of Forestry and Natural Resources Whitehall Experimental Forest, University of Georgia, Athens, Georgia during 22-28 November 2006. Cones were labeled with JH455 antisera. We found S cones at densities lower than the density of M cones. The density of S cones averaged 1602/mm^2 (range = 317, *n* = 2) ranging from an average minimum of 442/mm^2 (range = 50, *n* = 2) to an average maximum of 4883/mm^2 (range = 1433, *n* = 2).


superior
cells/mm^2
>5,000
2,500
0
temporal
10 mm

CHAPTER 4

HEARING RANGE OF WHITE-TAILED DEER AS DETERMINED BY AUDITORY BRAINSTEM RESPONSE[3]

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[3] D'Angelo, G. J., A. R. De Chicchis, D. A. Osborn, G. R. Gallagher, R. J. Warren, and K. V. Miller. 2007. Hearing range of white-tailed deer as determined by auditory brainstem response. Journal of Wildlife Management:in press.

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ABSTRACT

Using Auditory Brainstem Response (ABR) testing, we determined that white-tailed deer (*Odocoileus virginianus*) hear within the range of frequencies we tested, from 0.25-30 kHz, with best sensitivity between 4-8 kHz. The upper limit of human hearing lies at about 20 kHz, whereas we demonstrated that white-tailed deer detected frequencies to at least 30 kHz. This difference suggests that research on the use of ultrasonic (frequencies >20 kHz) auditory deterrents is justified as a possible means of reducing deer-human conflicts.

Key words: auditory brainstem response, deterrent, hearing, *Odocoileus virginianus*, sound, white-tailed deer

Although the hearing abilities of white-tailed deer (*Odocoileus virginianus*) have been the subject of speculation and debate, especially related to the reduction of deer-human conflicts using auditory alarms, no scientific evidence has been published on the hearing range of the species. Several studies characterized the hearing abilities of other ungulates to examine the possible effects of human-produced noise on animal behavior. Flydal et al. (2001) used behavioral training experiments to determine the hearing range of captive reindeer (*Rangifer tarandus tarandus*), and DeYoung et al. (1993) generated baseline auditory brainstem response (ABR) data for desert mule deer (*O. hemionus eremicus*) and bighorn sheep (*Ovis canadensis*). Krausman et al. (2004) used ABR to assess the auditory characteristics of desert ungulates that were exposed to sound from military activities.

ABR testing is the accepted protocol for diagnosis of hearing for noncooperative subjects, including animals (Jacobson 1994). ABRs are electrophysiologic responses generated when sound stimulates the ear, auditory nerve, and regions of the auditory brainstem (Hall 1992). The differences in electrical potentials elicited by an auditory stimulus are recorded via electrodes placed strategically on the head. Acquisition of the neural response is time-locked to stimulus onset. The stimulus is presented repeatedly and the responses are averaged by computer to extract the auditory-related response from the background electrical activity. These auditory-evoked responses are then displayed on a monitor as a series of waves having distinct peaks and valleys. The amplitudes, latencies, and relationship of those waveforms are analyzed by an experienced clinician to determine the lowest threshold of hearing at that frequency. Proper ABR assessment requires that the subject remain immobile and in a state of quiet rest. ABR is not affected by many anesthetic drugs, and those used to induce muscle paralysis may actually enhance ABR readings by reducing muscle related artifact (Hall 1992, Hall and Harris 1994).

Basic knowledge of white-tailed deer hearing can improve understanding of deer behavior and may assist in the development of effective deterrent strategies. Our objective was to determine the hearing range of white-tailed deer using ABR.

STUDY AREA

We conducted our research at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, Athens. The facility was 2.4 ha in area and was encompassed by 3-m high woven-wire fencing. Deer were housed in outdoor paddocks (0.4-0.8 ha) and 3 x 6-m covered barn stalls with food and water provided ad libitum. The animals we used were raised in captivity, were in good general health, and had no known exposure to abnormally high levels of noise.

METHODS

We constructed a sound-testing booth (height = 2.3 m, width = 2.2 m, length = 4.7 m) with plywood, 2.5-cm thick insulating foam and 2 layers of indoor carpeting on all surfaces to minimize ambient noise. We moved deer from outside paddocks to individual stalls ≥12 hours before testing. We removed feed from the stall ≥12 hours before sedating deer with a xylazine hydrochloride (HCL) and ketamine HCL mixture of 1:7. We administered lesser doses of the 1:7 xylazine HCL to ketamine HCL mixture as necessary throughout each testing session to maintain adequate sedation and to reduce physiological interference in the evoked responses. Depending on the tameness of each deer, we delivered the initial sedative by hand-injecting deer intramuscularly or by remote delivery using a tranquilizer dart. Once immobilized, we carried deer into the sound-testing booth and placed them in a wooden cradle, which supported the deer on its sternum 90 cm above the floor. We applied ophthalmic ointment (Paralube® Vet Ointment, Pharmaderm, Melville, New York, USA) to prevent corneal desiccation and covered their eyes with an opaque cloth to avoid arousal by light. We placed sandbags and cloth towels under the head and neck of the deer to provide stability and to level the head along its lateral axis.

We used an Intelligent Hearing Systems Smart EP (Miami, Florida, USA) evoked-potential system to produce auditory stimuli and to assess hearing thresholds. We placed 3 sub-dermal electrodes at locations corresponding to points on the sinus, vertex and dorsal border of the left zygomatic arch in the skull of the deer. The auditory stimuli consisted of tone bursts (1.5 msec rise/fall; 3 msec duration) gated with Blackman filters and delivered at a rate of 29.9/second to 1 of 2 types of transducers. For frequencies 0.25-2 kHz, we delivered acoustic stimuli through a Hi-tex speaker (Hong Kong, China); we delivered frequencies 4-30 kHz via a

Radioshack super tweeter (Forth Worth, Texas, USA). We controlled intensity levels by a Yamaha model 2050 2-channel amplifier (Buena Park, California, USA). We mounted the speakers on tripods to provide tilt and height adjustments, and leveled and centered the speaker with the opening of the left ear canal of the deer at a distance of 15.2 cm from the tragus. We amplified the electroencephalogram activity 100,000 times and bandpass filtered from 0.1 to 3 kHz. We measured the ABRs from the averaged responses to 1,024 tone-burst stimuli of alternating phase. We employed an analysis time of 10.24 msec. At each frequency and intensity level, we measured ≥2 ABRs to ensure that the response replicated. Before testing, we measured stimulus output levels using a Quest model 1900 sound level meter having peak hold capability and a model QE4110 0.85-cm microphone (Oconomowoc, Wisconsin, USA). We measured ambient noise levels using a Quest model 1700 sound level meter with a 1/3 octave band OB-300 filter and a model 4936 1.3-cm prepolarized condenser microphone(Oconomowoc, Wisconsin, USA). We verified attenuation linearity for the range of intensities employed, until sound levels fell into the noise floor.

We obtained ABR thresholds for the frequencies 0.25, 0.5, 1, 2, 4, 8, 12, 16, 20 and 30 kHz. Initially, we presented auditory stimuli to deer at 70 decibels (dB) Sound Pressure Level (SPL) and gradually decreased auditory intensity in 10 dB SPL steps until we no longer detected a reliable response. Once we approximated the hearing threshold at an individual frequency, we tested at intensities ±5 dB SPL to refine our threshold estimate. If we obtained no response at 70 dB SPL, we gradually increased the stimulus level in 5 dB SPL steps up to 90 dB SPL, at which time we terminated testing for that frequency. We performed all animal use procedures in a humane manner, and received prior approval from the University of Georgia Institutional Animal Care and Use Committee (#A2004-10102-0).

RESULTS

From 29 October 2004 to 29 April 2005, we conducted ABR testing on 13 deer. Average testing time to determine minimum hearing thresholds at all frequencies for an individual deer was 178 min (SE = 8). Included in the experiments were 3 deer <1 yr old (2 female, 1 male), 3 deer 1.5 to 2.0 yr old (1 female, 2 male), 3 deer 2.5 to 3.0 yr old (2 female, 1 male), and 4 deer 3.5 to 4.0 yr old (3 female, 1 male). A typical ABR recording in our deer sample showed a series of four waves (Fig. 4.1). We determined the ABR threshold by tracking wave III in the complex because this wave was most consistently reproduced at the lowest intensity levels. The mean latencies for wave III at 70 dB SPL were 4.85 msec (SE = 0.07) and 4.86 msec (SE = 0.07) at 4 kHz and 8 kHz, respectively. All hearing thresholds were above the ambient noise levels we recorded (Fig. 4.2; Tables 4.1, 4.2). We were unable to collect frequency specific information on ambient noise for 20 to 30 kHz because of equipment limitations at the time of measurement.

DISCUSSION

Our results suggest that white-tailed deer hear within the range of frequencies we tested, from 0.25 to 30 kHz, with best sensitivity between 4 and 8 kHz. DeYoung et al. (1993) used ABR to determine mean hearing thresholds for bighorn sheep and desert mule deer for frequencies from 1 to 4 kHz and obtained similar results. Likewise, Krausman et al. (2004) observed similar hearing thresholds for pronghorn (*Antilocapra americana*) and desert mule deer for the frequencies they tested from 0.5 to 8 kHz.

Flydal et al. (2001) used behavioral training to determine that the hearing ability of 2 yearling reindeer ranged from 0.07 kHz to 38 kHz with best sensitivity at 8 kHz. They found that the reindeer detected sounds at lower thresholds than we recorded in white-tailed deer, and concluded that the hearing of reindeer was similar to that of cattle, horse, goat, pig, and sheep as determined by behavioral tests. It should be noted, however, that behavioral testing may be more sensitive at determining minimum hearing thresholds than ABR. For example, in an experiment with normally hearing human subjects, thresholds determined by behavioral experiments were lower than those determined by ABR (Gorga et al. 1988). This is not surprising given the ear's ability to integrate energy over time. Previous psychophysical research showed that as the duration of a tone increases up to about 200 msec, hearing threshold decreases in direct proportion to time (Garner and Miller 1947). Although, ABR can be in good agreement with behavioral threshold assessments of hearing at 0.5 kHz and 2 to 4 kHz (Stapells et al. 1995). Differences in hearing thresholds on the order of 10 dB SPL have been reported between the two procedures (Gorga et al. 1984, Gorga et al. 1988). Nevertheless, ABR can be used effectively to estimate relative sensitivity among frequencies, and can be used to compare sensitivity among species.

We found that best hearing sensitivity of deer from 4 to 8 kHz corresponds to the dominant features of their vocalizations. Atkeson et al. (1988) described 12 vocalizations of white-tailed deer using sonagraphic analysis. They demonstrated that most calls were composed of frequencies between 1 and 8 kHz with the strongest intensities of individual calls between 3 and 6.5 kHz. The relationship among hearing sensitivity and vocalizations of deer suggests that auditory deterrent devices may be heard most reliably by deer at frequencies similar to their vocalizations.

Our estimate of best hearing sensitivity of deer from 4 to 8 kHz overlaps with the range of frequencies which humans hear best, from 2 to 5 kHz (Durrant and Lovrinic 1995). The upper limit of human hearing lies at about 20 kHz (Durrant and Lovrinic 1995), whereas we demonstrated that white-tailed deer detected frequencies to at least 30 kHz. This difference suggests that research on the use of ultrasonic (frequencies >20 kHz) auditory deterrents is justified as a possible means of reducing deer-human conflicts such as deer-vehicle collisions and depredation of plants in residential areas without being intrusive to the human auditory system. Given our estimate of white-tailed deer hearing at 30 kHz and with consideration for the temporal integration factors discussed above, it appears that ultrasonic auditory deterrents would need to emit sounds at moderate intensities (45 to 60 dB SPL at the deer's ear) to be heard reliably by deer.

Auditory devices marketed to deter wildlife may not produce ultrasonic sounds at sufficient intensities as claimed by the manufacturers. Scheifele et al. (2003) evaluated the sound produced by 2 designs of vehicle-mounted deer whistles and determined that the primary frequency of operation was 3.3 kHz for closed-end whistles, and 12 kHz for open-end whistles. Bender (2003) analyzed sound produced by 2 models of the ROO-Guard®, a device marketed to deter kangaroos (*Macropus* spp.) and other wildlife, and found that sound outputs were composed mostly of audible frequencies and some ultrasonic frequencies. In field tests, the ROO-Guard® failed to alter the behavior of kangaroos.

The physical properties of sound waves and safety concerns relative to human hearing may limit the feasibility of generating sounds from a moving vehicle at intensities sufficient to provide adequate warning distance for deer to react and avoid a collision. The intensity of sound is governed in part by the inverse square law, which states that in an environment with no obstructions, sound intensity is inversely proportional to the distance squared from the sound source (Ratcliff 1999). Therefore, if an auditory device emitted sound stimuli at an intensity of 100 dB SPL at 1 m (based on maximum permissible noise exposure level for 2 hours/day for employees in the USA; Occupational Safety and Health Administration 2006), under ideal conditions and without consideration for the effects of vehicle speed, we would expect the sound intensity to be approximately 60 dB SPL at 100 m from the vehicle. Whether this hypothetical warning distance of 100 m would provide deer with adequate time to react to an approaching vehicle in a range of roadway conditions is unknown.

Although the possibility may exist to produce ultrasonic sounds at intensities to be heard reliably by deer, consideration must be given to white-tailed deer hearing physiology and practical field application in the development of such strategies. Further, controlled field experiments should be conducted to assess whether auditory deterrents alter white-tailed deer behavior as desired.

MANAGEMENT IMPLICATIONS

Our data provide a basis for the development of auditory deterrents throughout the hearing range of white-tailed deer. To be consistently audible to deer, however, auditory deterrents must be of adequate sound intensity at specific frequencies.

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. G. Ollick donated his time, advice and audio equipment. We acknowledge the technical support of J. G. D'Angelo, especially in the construction of the sound-testing booth. We thank S. J. Dahmes and Wildlife Artist Supply Company for use of their facilities and equipment. S. B. Castleberry and M. T. Mengak of the University of Georgia and 2 anonymous reviewers provided helpful comments on this manuscript. J. Hall III and N. Decker assisted with data interpretation.

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Associate editor: Mason

Figure 4.1. Sample auditory brainstem response waveform for one white-tailed deer at 4 kHz during a testing session on 01 Jan 2005 at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, Athens. "III" indicates Wave III as it was tracked to hearing threshold at 35 dB Sound Pressure Level.

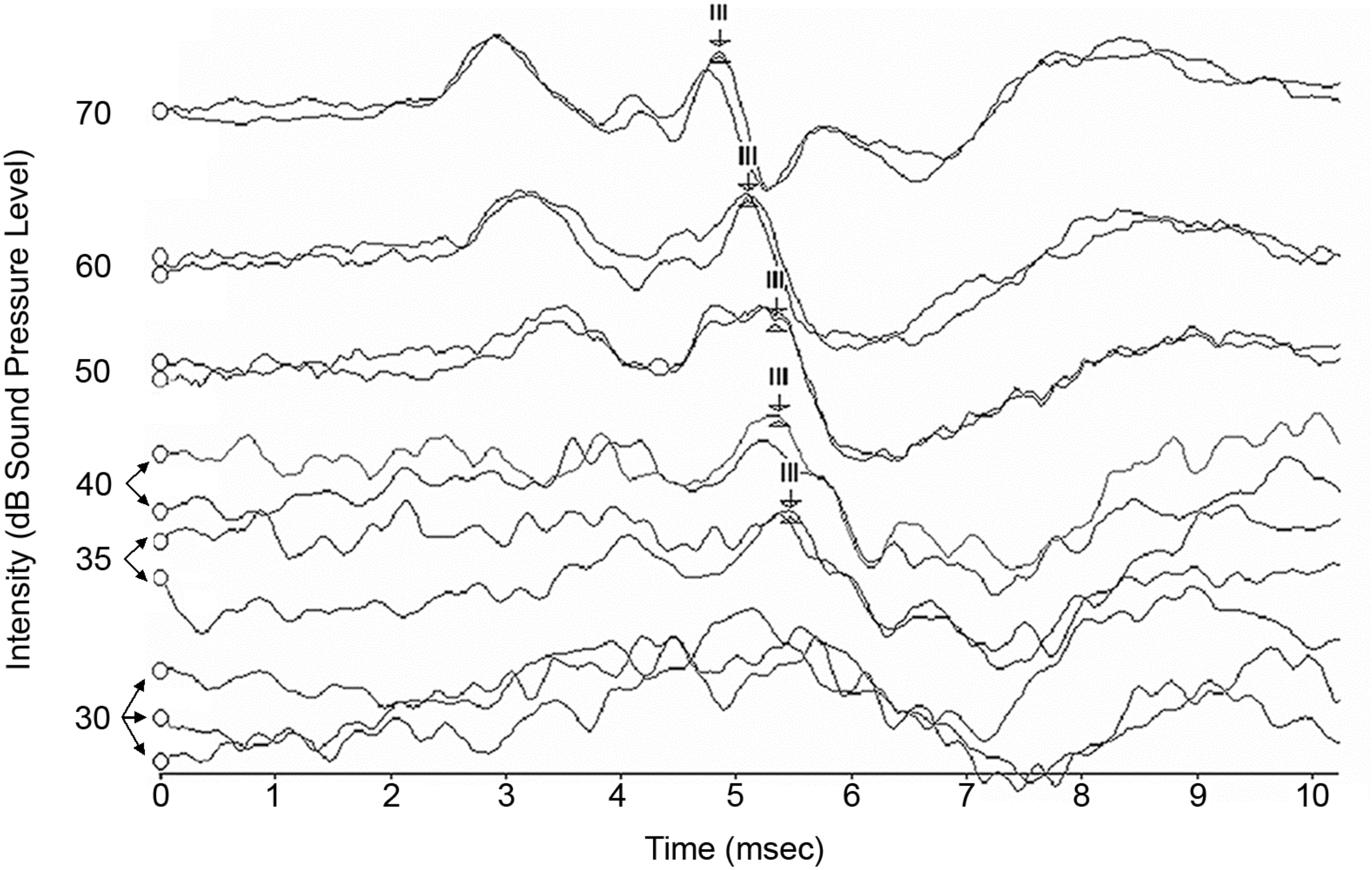
III
III
III
III
III
70
60
50
40
35
30
Intensity (dB Sound Pressure Level)
0
1
2
3
4
5
6
7
8
9
10
Time (msec)

Figure 4.2. Audiogram of mean (error bars = ± SE) frequency specific thresholds of hearing for 13 white-tailed deer as determined by auditory brainstem response at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, Athens, 2004-2005. Also included are mean frequency specific thresholds of hearing for reindeer as determined by behavioral testing (Flydal et al. 2001), for desert mule deer (A) and mountain sheep as determined by auditory brainstem response testing (DeYoung et al. 1993), and for pronghorn and desert mule deer (B) as determined by auditory brainstem response testing (Krausman et al. 2004).

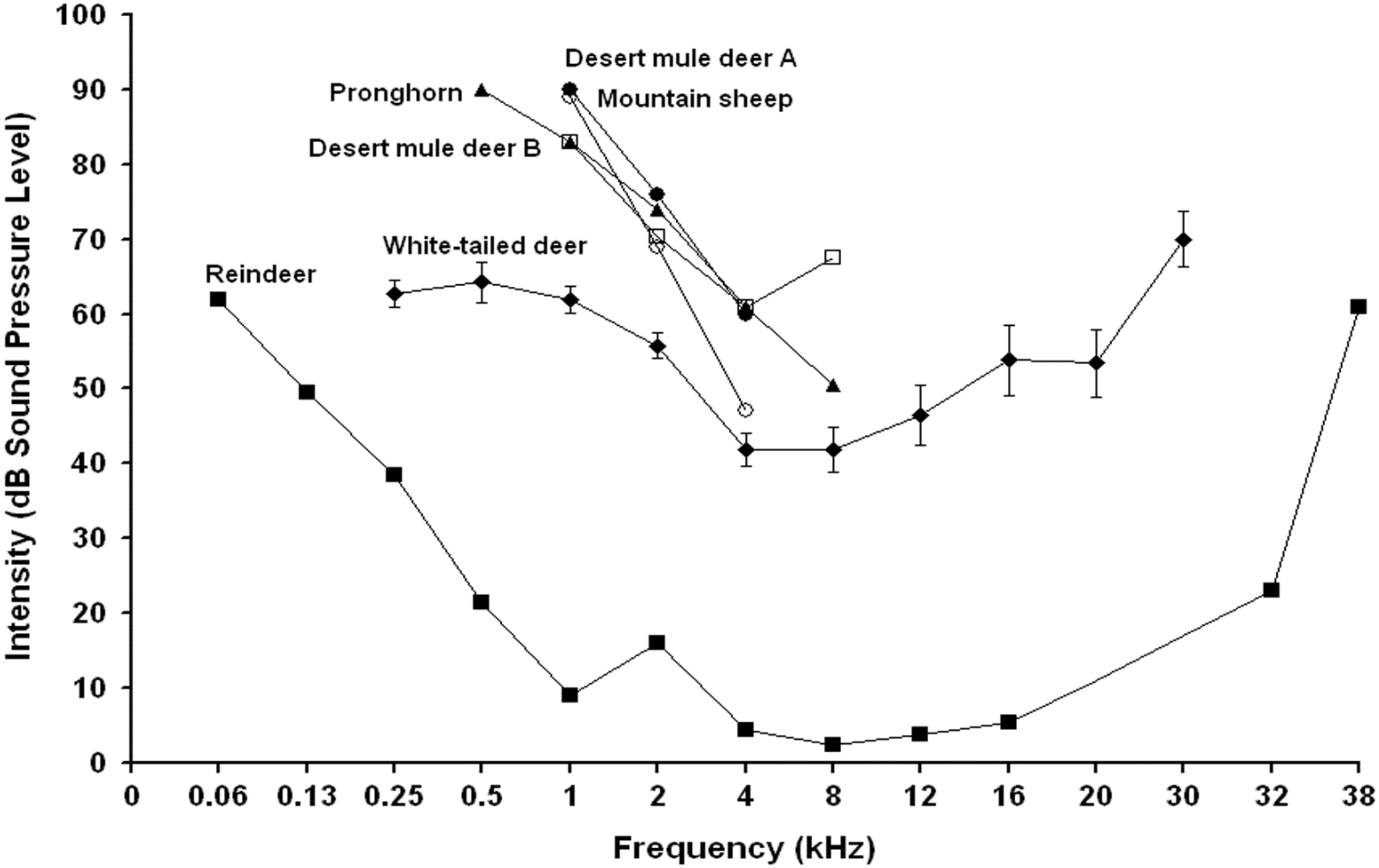
Intensity (dB Sound Pressure Level)
100
90
80
70
60
50
40
30
20
10
0
Frequency (kHz)
0
0.06
0.13
0.25
0.5
1
2
4
8
12
16
20
30
32
38
Desert mule deer A
Pronghorn
Mountain sheep
Desert mule deer B
White-tailed deer
Reindeer

Table 4.1. Mean (SE) frequency specific thresholds of hearing for 13 white-tailed deer as determined by auditory brainstem response at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, Athens, 2004-2005.

Frequency (kHz)	**Mean (dB SPL)**	**Standard error (dB SPL)**
0.25	62.7	1.8
0.5	64.2	2.6
1	61.9	1.8
2	55.8	1.7
4	41.9	2.2
8	41.9	3.0
12	46.5	4.1
16	53.8	4.7
20	53.5	4.5
30	70.0	3.7

Table 4.2. Frequency specific ambient noise levels recorded during auditory brainstem response testing at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, Athens, 2004-2005.

Frequency (kHz)	**Noise level (dB SPL)**
0.25	36.0
0.5	32.3
1	23.0
2	22.2
4	17.5
8	12.9
12	8.2
16	6.3
20	–
30	–

CHAPTER 5

CONCLUSIONS

CONCLUSIONS

Literature Review

1. Most states utilize strategies in attempts to reduce deer-vehicle collisions. However few research efforts have sufficiently examined the efficacy of such techniques and information on deer behavior relative to these mitigation efforts was limited.
2. Information on the physiology of the auditory and visual systems of white-tailed deer is limited in the scientific literature.

Evaluation of Wildlife-warning Reflectors

1. We concluded that the wildlife warning reflectors we tested did not alter deer behavior such that deer–vehicle collisions might be prevented.
2. Our data indicated that deer exhibit an increase in negative behavioral responses toward vehicles in the presence of reflectors.

Examination of the White-tailed Deer Visual System

1. The visual system of white-tailed deer is similar to other ungulates and is well suited for sensitivity in low light conditions and detection of predators in a variety of habitats.
2. The visual streak of deer is similar to other cervids, and provides deer with enhanced surveillance of a broad area.

3. The horizontal slit pupil of deer serves to protect their light-sensitive retina in bright light conditions and concentrate light on the visual streak for improved acuity.
4. The tapetum lucidum improves sensitivity in low-light conditions. The spatial association of the visual streak and tapetum and the color reflectance of the tapetum likely improves the contrast of visual scenes and perception of color in daylight.

Determination of the Hearing Range of White-tailed Deer

1. We determined that white-tailed deer hear within the range of frequencies we tested, from 0.25-30 kHz.
2. Best hearing sensitivity of deer is 4-8 kHz.
3. We demonstrated that white-tailed deer detected frequencies to at least 30 kHz, whereas the upper limit of human hearing lies at about 20 kHz.
4. The difference between deer and human hearing in ultrasonic frequencies (>20 kHz) suggests that research on the use of ultrasonic auditory deterrents is justified as a possible means of reducing deer-human conflicts.

RECOMMENDATIONS

1. Future development of strategies for reducing the incidence of deer-vehicle collisions should be based on the physiological and behavioral characteristics of white-tailed deer.
2. Transportation agencies should only deploy strategies that have undergone extensive testing in actual roadway conditions, and have been shown to consistently alter deer behavior as desired over time.

3. Until such strategies become available, management efforts to minimize deer-vehicle collisions should focus on:

   A. Implementation of proper deer herd management programs
   B. Control of roadside vegetation to minimize its attraction to deer and to maximize visibility for motorists
   C. Increasing motorist awareness of the danger associated with deer-vehicle collisions
   D. Thorough monitoring of deer-vehicle collision rates
   E. Encouraging communication and cooperation among governments, wildlife researchers, highway managers, motorists, and others involved in the issue of deer-vehicle collisions

APPENDIX A

VISUAL ACUITY OF WHITE-TAILED DEER AS ESTIMATED BY DISCRIMINATION LEARNING[4]

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[4] D’Angelo, G. J., J. G. D’Angelo, D. A. Osborn, G. R. Gallagher, R. J. Warren, and K.V. Miller.

INTRODUCTION

Despite an abundance of scientific research focusing on the senses of domestic species, relatively little is known about the visual capabilities of white-tailed deer (*Odocoileus virginianus*). Designers of livestock facilities routinely use knowledge of anatomical and physiological components that influence animal behavior to achieve effective handling and containment (Rehkämper and Görlach 1997). Yet, mechanisms intended to alter deer movements in relation to human-altered landscapes continue to be engineered without consideration for standard deer sensory processes. A clear understanding of the visual capabilities of deer may prove integral to the invention of economically effective strategies to reduce deer-human conflicts.

The ability to resolve visual details is limited by optics of the eye, size and brightness of the retinal image, the density of photoreceptors, and connections among photoreceptors and higher order neurons (Timney and Keil 1992). Cone photoreceptors are responsible for color vision and the ability to distinguish fine detail (Ali and Klyne 1985). D'Angelo et al. (unpublished data) found that the distribution of medium wavelength cones in the deer retina was characteristic of a horizontal visual streak and maximum density of medium wavelength cones averaged 35,700/mm^2. In contrast, Ahnelt et al. (2006) demonstrated that the human retina contains a fovea centralis, a small circular area with medium wavelength cone density >150,000/mm^2. The fovea centralis affords humans with visual acuity superior to many species (Ali and Klyne 1985). The visual streak of deer in combination with their wide set eyes likely provides them with enhanced ability to monitor the horizon and to detect movement, however deer likely have far less acuity than humans because the density of cones is relatively limited in the deer retina.

Larger eyes have increased distance between the cornea/lens and retina, which increases the size of the image projected on the retina (Walls 1942). Since the diameter of photoreceptors varies little among species, the number of photoreceptors that are available to absorb light is greater in the large eye (Walls 1942). By maximizing image size and the number of photoreceptors in the retina, the large eye enhances visual acuity. D'Angelo et al. (unpublished data) demonstrated that the thickness of the deer lens and the spatial arrangement of their eye likely projects an image on the retina which is moderate in size and brightness as compared to the human eye (Walls 1942, Howland et al. 2004). The density of cones and the morphological characteristics of the deer eye suggest that deer may have reduced visual acuity as compared to humans.

Discrimination trials have been used to estimate visual acuity in a variety of ungulates (Blakeman and Friend 1986, Entsu et al. 1992, Timney and Keil 1992, Harman et al. 2001). Our objective was to estimate the visual acuity of white-tailed deer by discrimination trials with a hand-reared captive deer.

STUDY AREA AND ANIMAL

We conducted our research at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, Athens. The facility was 2.4 ha in area and was encompassed by 3-m high woven-wire fencing. We hand reared the female subject deer used in this study from 3 days of age until weaning to accommodate her to humans. During this study, the subject deer was housed individually or with 1-7 other human-accommodated deer. We began the procedures described in this study when the subject deer was approximately 2 years old. However, on a regular basis throughout her life, the subject deer was used in other experiments in close association with human handlers and involving the deer she was housed with.

METHODS

Apparatus and Test Gratings

We constructed a testing apparatus within a 0.1-ha paddock which the subject deer was housed in (Figure A.1). The apparatus consisted of 2 parallel corridors 2 m in length and 0.5 m in width constructed with wooden frames and opaque silt-fence fabric. The corridors were attached to a 2.4 m x 3.6 m platform made of 1.9-cm thick plywood. At the end of each corridor was a plywood wall 2 m in height with a rectangular cutout 23 cm x 29 cm centered in the corridor at 1 m in height. On the back surface of the wall below each cutout, we mounted a plastic well for placement of food during visual acuity trials. We constructed panels to be mounted within the rectangular cutouts to hold the test targets. The panels consisted of a 22 cm x 28 cm clear acrylic sheet mounted on a 22 cm x 28 cm polypropylene sheet with a 0.2 cm space between the sheets for insertion of test targets. We secured the panels within the cutouts with hinges centered on the upper edge of the cutout and test panel. We designed test targets with Adobe Illustrator 9.0 software (Adobe Systems Inc., San Jose, California, USA) and printed the test targets with a bubble jet printer on white photo paper (Figure A.2). The test targets were spatial acuity gratings with vertical black bars evenly spaced against a white background in spatial frequencies of 2, 4, 6, 8, and 30 cycles/degree. We presented the 30 cycles/degree acuity grating to the subject deer as the negative target. Based on visual acuity information on other species, we assumed that the visual acuity of white-tailed deer was less than 30 cycles/degree and would appear gray to the subject deer (Harman et al. 2001). We designated a plain sheet of white photo paper as the positive training target.

Testing Procedures

We accommodated the subject deer to the apparatus by placing her food ad libitum in the wells with the testing panels secured open. Once she became accustomed to receiving her food in the apparatus, we closed the panels and placed food only behind the positive training target. The other panel contained the 30 cycles/degree negative target. The subject deer readily obtained her food by pushing open the panels with her nose. Over 2 weeks, we alternated daily which corridor received the positive training target. Once this behavior was established, we relocated the deer's primary food to an alternate location in the paddock. Behind the panel with the positive training target, we placed a small food reward which the deer preferred over her normal ration (e.g., fresh fruit, pelleted food sweetened with molasses, prunes). We were able to conduct multiple trials per session by restricting access of the deer to the apparatus between trials so the observer could change panels and replenish the food reward.

We conducted trials several days per week for a duration determined by the willingness of the subject deer to participate each day. We used random numbers generated previously to determine the placement of the positive target for each trial. A trial consisted of the subject deer entering the apparatus, viewing the testing panels from the end of the corridors, and walking down a corridor and pushing open the testing panel to receive the food reward (Figure A.5). To ensure that the subject deer was making the visual discrimination at the appropriate distance at the end of the corridor, we excluded trials in which the subject deer walked partially down one corridor, and exited that corridor without obtaining the food reward. After each trial, the observer encouraged the deer to exit the apparatus, closed doors at the ends of the corridors, and changed the testing targets as necessary, and replaced the food reward. Once the subject deer achieved ≥70% discrimination of the positive training target, we began to include the spatial acuity gratings as positive targets. For each trial, we assigned randomly the positive training target or 2, 4, 6, or 8 cycles/degree acuity gratings as the positive target versus the 30 cycles/degree negative target. We set 70% of trials correct as the threshold below which we assumed the subject deer was no longer discriminating between the negative and positive targets. We performed all animal use procedures in a humane manner, and received prior approval from the University of Georgia Institutional Animal Care and Use Committee (#A2004-10102-0).

RESULTS AND DISCUSSION

From May-August 2006 we conducted 150 visual acuity trials. We estimated the visual acuity of the deer as approximately 6 cycles/degree-the spatial frequency beyond which discrimination fell below 70% correct (Figure A.6). Our estimate suggests that the ability of white-tailed deer to discern fine visual details is limited relative to humans with normal vision which possess visual acuity of 30 cycles/degree (Ali and Klyne 1985). Visual acuity of white-tailed deer appears to be similar to the domestic cat (*Felis domesticus*) which was estimated to have visual acuity between 6-9 cycles/degree (Jacobson et al. 1976, Bloom and Berkely 1977, Hall and Mitchell 1991). Using methods similar to those in our study, Harman et al. (2001) estimated visual acuity of the Bactrian camel (*Camelus bactrius*) as 10 cycles/degree. The horse (*Equus caballus*), an ungulate common to open habitats, was estimated to have visual acuity of 23.3 cycles/degree, much greater than our estimate for white-tailed deer (Timney and Keil 1992). Timney and Keil (1992) attributed the high visual acuity of the horse in part to their size of their eyes which are one of the largest of all mammals.

The limited visual acuity of white-tailed deer as compared to humans and other species suggests that deer may rely more on their other senses to fulfill their life requisites. Olfaction is likely the dominant sense utilized by deer to navigate their home ranges while using established travel routes. Deer appear to use olfaction and touch to select food items while keeping their eyes fixed at further distances for detection of potential sources of danger (G. J. D'Angelo unpublished data). Correspondingly, white-tailed lack trichromatic color vision (Jacobs et al. 1994), a trait characteristic of primates which visually select foods based on coloration (Surridge et al. 2003). Further research on the accommodation abilities of white-tailed deer and the abundance of ganglion cells in the deer retina may further elucidate factors limiting their visual acuity.

The properties of the deer eye which limit their visual acuity (e.g., moderate eye size and lens thickness, limited density of cones) provide deer with greater sensitivity to light. Such a trade-off enables deer to exploit an ecological niche inaccessible to many other species (Miller and Murphy 1995).

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Figure A.1. Apparatus used to estimate visual acuity of the white-tailed deer (*Odocoileus virginianus*) at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, during May-August 2006. The panels for mounting the test targets are visible at the ends of the 2 corridors. The photograph was taken approximately at the point in the apparatus that the subject deer made her choice as to which corridor to enter during each trial.

Figure A.2. Spatial frequency grating created with Adobe Illustrator 9.0 software (Adobe Systems Inc., San Jose, California, USA) and used in visual acuity trials of white-tailed deer (*Odocoileus virginianus*) at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, during May-August 2006.

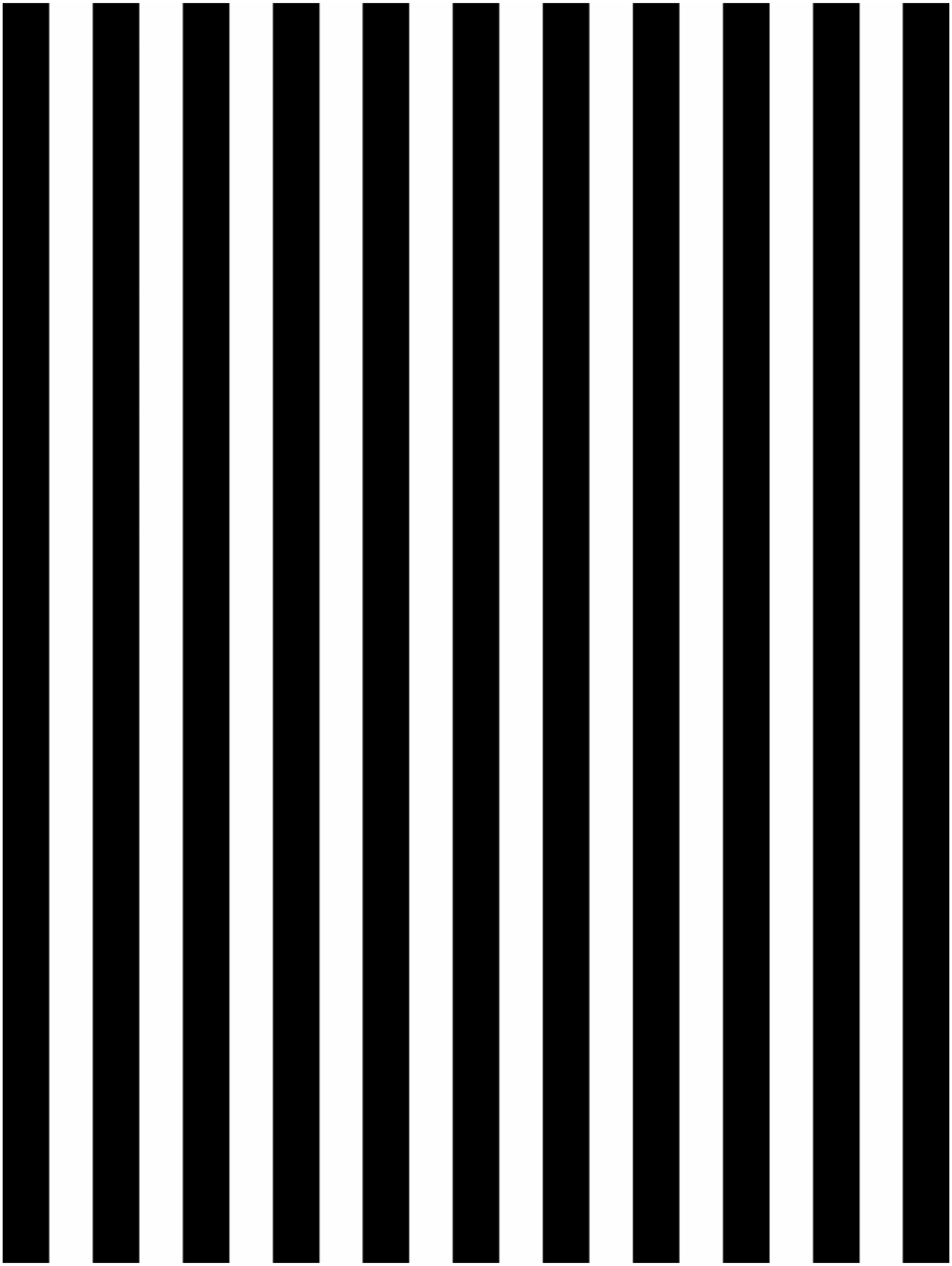
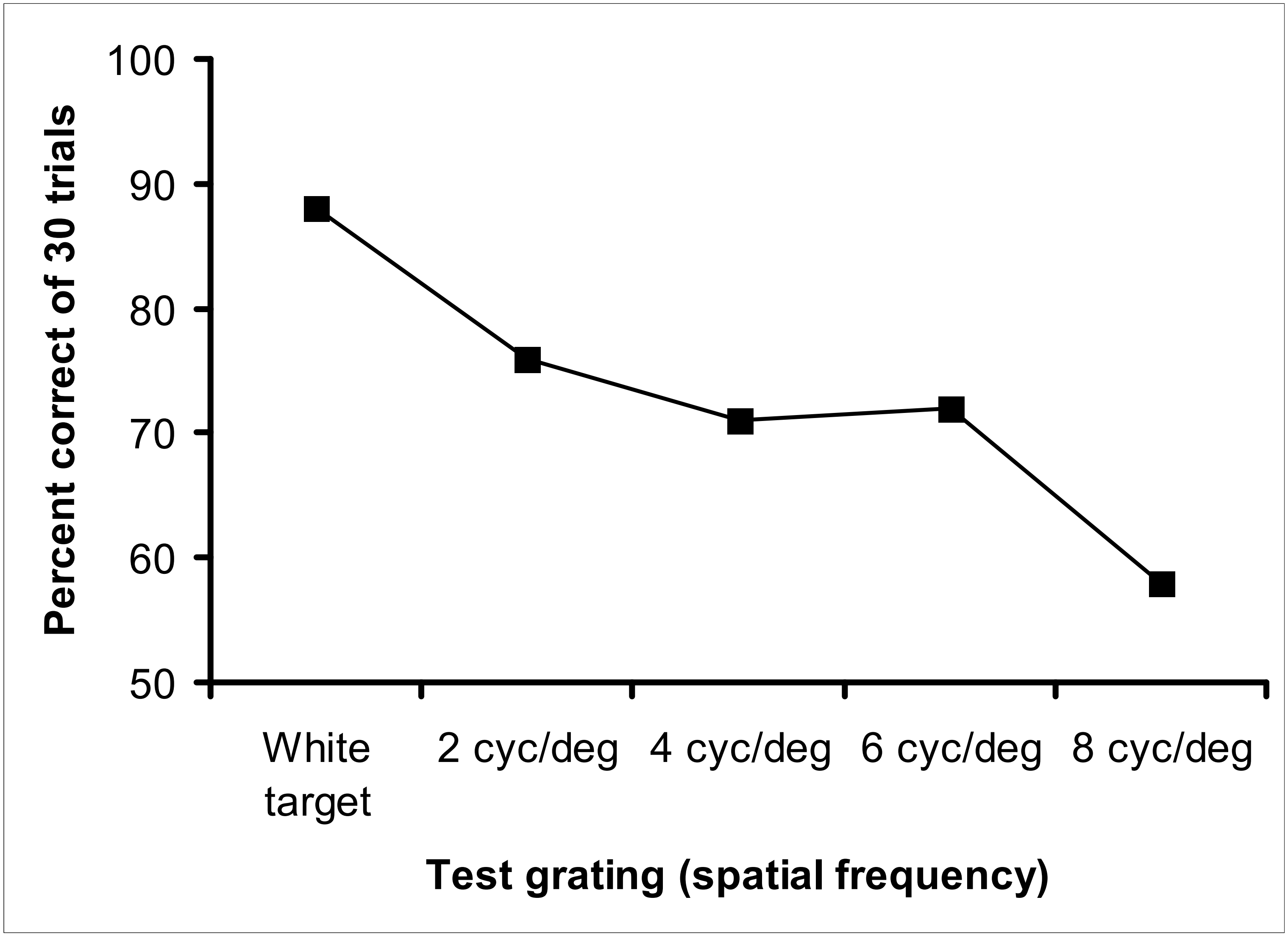


Figure A.3. Subject white-tailed deer (*Odocoileus virginianus*) entering apparatus used to estimate her visual acuity at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, during May-August 2006.

Figure A.4. Discrimination of test targets by a white-tailed deer (*Odocoileus virginianus*) during experiments to estimate the deer's visual acuity at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, during May-August 2006.


100
90
80
70
60
50
Percent correct of 30 trials
White target
2 cyc/deg
4 cyc/deg
6 cyc/deg
8 cyc/deg
Test grating (spatial frequency)