FINAL PROJECT REPORT

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

prepared by

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EXECUTIVE SUMMARY

This project was funded by Georgia Department of Transportation (GDOT) through the Governor’s Office of Highway Safety and the National Highway Traffic Safety Administration. The study was a collaborative research project initiated in 2004 and directed by Drs. Robert J. Warren and Karl V. Miller of University of Georgia (UGA) and Dr. George R. Gallagher of Berry College. The study was designed to: 1) provide a comprehensive literature review of all pertinent aspects related to deer-vehicle collisions, 2) evaluate the effectiveness of Strieter-Lite wildlife warning reflectors for altering the behavior of white-tailed deer along roadways, 3) generate basic information on the visual capabilities of white-tailed deer, 4) determine the hearing range of white-tailed deer, 5) improve on existing technologies or develop new strategies for reducing the incidence of deer-vehicle collisions. This final report is a compilation of the literature review, the Ph.D.dissertation of Gino D’Angelo (D’Angelo 2007), and the Master of Science Thesis of Sharon Valitzski (Valitzski 2007). The dissertation and thesis are presented in individual chapters including an introductory and conclusion chapter, and scientific manuscript chapters. Each scientific manuscript chapter includes an abstract, introduction, methods, results, discussion of results, and conclusions. Our findings will be described briefly in the following paragraphs.

In the planning of our research project and at the request of GDOT, we reviewed the primary literature to identify strategies with the most potential to reduce deer-vehicle collisions. Our findings indicated that most states in the U.S. have attempted to minimize deer-vehicle collisions through a variety of techniques. However, the efficacy of most of these techniques
have not empirically tested and many deer deterrent devices were not designed with an understanding of the sensory capabilities of deer. Many previous studies also were isolated in scope or were inadequately replicated to afford statistical validity. Hence, the questions regarding efficacy of many deer deterrent devices remained largely unanswered and there existed a need for further research on mitigation strategies based on the sensory abilities (e.g., hearing, vision) of deer.

In field trials with free-ranging white-tailed deer at Berry College in northwest Georgia, we evaluated the behavioral responses of deer 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. 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. 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. Our results illustrate that 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.

To gain knowledge of visual specializations influencing the roadway behavior of white-tailed deer, we examined the anatomy of the deer eye. Whereas the pupil of humans is round, white-tailed deer possess a horizontal slit pupil that is highly versatile to function in a range of lighting conditions. The slit pupil of deer extends nearly the entire horizontal width of the eye
and is capable of vertical adjustment from a narrow slot in bright light conditions to a broad oval when light is limited. The slit pupil enables deer to function in full daylight without overwhelming their highly light-sensitive retina. The tapetum lucidum is a membrane attached to the deer retina to enhance vision in low light. Reflections from the tapetum lucidum produce the characteristic eye shine of deer when they are alighted by bright sources of light. The tapetum reflects light that has already passed through the eye back to the photoreceptors (light sensitive cells) a second time to increase the absorption of light and improve interpretation of visual images. Deer possess a visual streak, a broad horizontal band of increased cone photoreceptor density. Contrasting the visual streak in deer, the human retina contains a fovea centralis, a small circular area with high cone density. The visual streak of deer likely has far less acuity than the fovea in humans because the density of cones is relatively limited in the deer retina. 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. The specializations of the deer eye which enable vision in low-light conditions in the natural environment may inhibit deer in their avoidance of collisions with vehicles. Natural changes in light (i.e., dawn, dusk) occur slowly allowing the eye to adjust appropriately. The visual system of deer likely is overwhelmed by abrupt increases in light such as that from vehicle headlights.

Using auditory brainstem response testing at the UGA captive deer research facility, we 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 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. This information
provided a basis for the development of experimental sounds in the following study designed to examine the behavioral responses of deer to sound deterrents in roadway environments.

We conducted a study to assess the efficacy of sound as a deterrent for reducing deer-vehicle collisions by observing the behavioral responses of captive and free-ranging white-tailed deer to pure tone sounds within their hearing range. Our preliminary experiments at the UGA captive deer research facility indicated that none of the sound treatments we tested elicited an aversive behavioral response (e.g., flight away from the sound) in captive deer. In experiments with free-ranging deer at Berry College, our results indicate that deer within 10 meters of roadways did not consistently alter their behavior in response to pure-tone sound treatments emitted from a moving automobile fitted with a sound-producing system. As commercially available vehicle-mounted auditory deterrents (i.e., deer whistles) are purported to emit similar consistent, continuous sounds as pure tones, this data suggests that deer-whistles are likely not effective in preventing deer-vehicle collisions.

The results of our field trials involving observations of deer-vehicle interactions (D’Angelo Chapter 2, Valitzski Chapter 2) demonstrate that the behavior of free-ranging white-tailed deer may be unpredictable in the presence of oncoming vehicles. Strategies designed to deter deer within close proximity of the roadway may pose a risk to human safety. The effectiveness of such strategies relies solely on eliciting consistent, predictable behavioral responses by deer in the desired manner to avert negative deer-vehicle interactions. In future attempts to prevent deer-vehicle collisions, we recommend that GDOT: 1) continues efforts to develop strategies for prevention of deer-vehicle collisions that are designed based on the physiological and behavioral characteristics of white-tailed deer, 2) deploys strategies that have undergone extensive testing in actual roadway conditions, and 3) seek to develop methods to
reduce access of deer to roadway corridor where feasible. In our research proposal for Phase II of this project, we have described several strategies for the reduction of deer-vehicle collisions which we feel merit further research attention.

DOCTORAL DISSERTATION AND MASTERS THESIS RESULTING FROM THIS PROJECT AND ATTACHED TO THIS REPORT:


PUBLICATIONS RESULTING FROM THIS PROJECT:


PRESENTATIONS RESULTING FROM THIS PROJECT:


EVALUATION OF STRATEGIES DESIGNED TO REDUCE DEER-VEHICLE COLLISIONS:
AN ANNOTATED BIBLIOGRAPHY
Literature Review

EVALUATION OF STRATEGIES DESIGNED TO REDUCE DEER-VEHICLE COLLISIONS

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INTRODUCTION

Upon review of literature related to deer-vehicle collision reduction strategies, several prominent themes are evident: (1) Of the mitigation technologies previously studied, fencing of adequate height combined with the proper wildlife crossing structures is the most effective method for reducing deer-vehicle collisions while providing a semi-permeable road/landscape interface. (2) Areas in need of improvement on an international level include: monitoring of deer-vehicle collision rates; scientifically rigorous evaluation of reduction strategies; and communication and cooperation among governments, wildlife researchers, highway managers, motorists, and others involved in the issue of deer-vehicle collisions.

To develop solutions aimed at reducing the occurrence of deer-vehicle collisions, we must enhance our understanding of the factors that result in hazardous encounters between deer and motorists. This requires a unique cooperative effort among disciplines to design, successfully implement, and refine mitigation techniques. Ultimately, we should possess a collection of strategies that were developed with consideration for the specific behavioral and physiological traits of deer and motorists alike.

Literature Reviews On Deer-vehicle Collision Mitigation – Annotated Bibliography


Bruinderink and Hazebroek evaluated literature related to ungulate-vehicle collisions in Europe, the U.S., and Japan. They argued that the relationship suggested in most studies, between the incidence of ungulate-vehicle collisions and traffic volume, is confounded by population dynamics, changes in traffic volume, and sampling intensity. Bruinderink and Hazebroek concluded that successful design of mitigation strategies is contingent on consideration for the
life history features of the target species. They found no strong evidence of the effectiveness of passive warning signs, warning reflectors, or scent or acoustic deterrents. For high volume roads, they recommended the use of fencing combined with wildlife passage structures to deter ungulates from roadways. For secondary roads, they recommended seasonal application of intermittently lighted warning signs triggered by ungulates entering the roadway corridor. They also encouraged the implementation of driver education programs.


Damas & Smith Limited conducted a comprehensive literature review on deer-vehicle countermeasures. They identified mitigation strategies that proved most effective in minimizing deer-vehicle collisions in Canada, the United States, and Europe and recommended experimental control techniques for selected national parks in Canada. In their assessment, they recognized fencing to “have the widest applicability and highest overall effectiveness” of techniques tested. However, they also regarded fencing as maintenance intensive and restrictive to wildlife movements without the installation of proper animal crossing devices. They recommended the testing of the following strategies for reducing deer-vehicle collisions in Canada’s national parks: chemical repellents, a microwave animal crossing detection system with flashing warning signs, alternatives to road salt de-icing agents, and a public information campaign.

Danielson and Hubbard suggested that the primary problems with previous research on deer-vehicle collisions were “(1) the studies have not included control areas to compare to treatment areas, or (2) the studies have lacked adequate replication of treatment and/or control areas”. Of those studies deemed statistically valid, Danielson and Hubbard concluded through a literature review that properly maintained fencing coupled with wildlife crossing structures was the most effective mitigation strategy for reducing deer-vehicle collisions on main roads. They indicated that such structures should be monitored for sufficient wildlife use with infrared detection systems. Danielson and Hubbard further suggested that public awareness campaigns and driver awareness programs should be evaluated in future research efforts.


The Wisconsin Departments of Transportation and Natural Resources and the Sand County Foundation invited leaders in insurance; highway safety, management, and engineering; landscape ecology; local government; law enforcement; and related fields from their region of the U.S. and Canada to participate in a working session to address the issue of >60,000 deer-vehicle collisions annually on Wisconsin roadways. Working Group participants developed and committed to a pathway of action, which promised to develop a comprehensive public education program related to deer-vehicle collisions; support of statewide deer herd reduction; create a “toolbox” of possible actions that could be tailored and implemented to reduce deer-vehicle
collisions at a specific site; and to create a regional clearinghouse to disseminate validated information on deer-vehicle collisions. They also identified areas requiring research, these included: (1) determine if local deer herd reduction can lower deer-vehicle collision rates; (2) determine if fencing and other barriers help prevent deer-vehicle collisions; (3) determine if modifying road corridor habitat can reduce deer-vehicle collisions; (4) create a “Center for Research Excellence” to address scientific standards, research quality, and funding.


Hedlund et al. conducted an intensive review of literature pertinent to deer-vehicle collisions and concluded that fencing combined with overpasses and underpasses was the only scientifically proven and publicly accepted method. However, they also stated that fencing will not eliminate deer entering roadways and such strategies are expensive to construct and maintain. Their review identified other possible mitigation strategies that require further testing; these included: herd reduction, roadside clearing, temporary and active warning signs, at-grade crossings for deer combined with signage, infrared driver vision. Hedlund et al. categorized reflectors, roadside lighting, intercept feeding, and repellents as methods with limited demonstrated effectiveness. They suggested that quality research investigating the response and habituation of deer to light beams and reflectors would be useful. Hedlund et al. determined that deer whistles and deer flagging signs were not effective, and general education, passive signs, and speed limit reduction had no promise.

The wildlife crossing toolkit located at http://www.wildlifecrossings.info is a searchable internet database resource for biologists and highway planners, which provides information on strategies to mitigate wildlife highway mortality and increase highway permeability for wildlife. Information in the Toolkit includes wildlife species-specific information relative to passage structure design and materials, criteria for mitigation technique use, and effectiveness.


Premo and Premo rated deer-vehicle collision mitigation strategies with potential for use in Michigan using information gathered during a literature review and by interviewing individuals with expertise related to deer-vehicle collisions. Methods with very good potential to reduce deer-vehicle collisions in Michigan included deer population management, modifying right-of-way vegetation and width, right-of-way clearing, warning signs, limiting driver speed, driver education, and public awareness programs. Those strategies with good potential to be effective included artificial deer feeding restrictions, modified agricultural and forestry activities, habitat modification, and alternative highway design.


Putnam reviewed literature pertaining to deer-vehicle collision mitigation techniques used in the U.S. and Europe; these included deer warning signs, roadside reflectors, chemical repellents,
sound-scarers, roadside fencing in combination with crossing structures and one-way gates, and management of roadside vegetation. Putnam concluded that for major roadways with consistently high traffic volumes, fencing was the only effective measure to significantly reduce deer crossings. He noted, however, that underpasses and overpasses should be installed with fencing constructed in a manner, which funnels animal movements to the structures to increase use and habitat connectivity. Also, one-way gates proved necessary to allow an escape passage for animals trapped in the roadway corridor. Underpass dimensions should be at least 4 m X 4 m with floor material of a natural substrate and cover-type habitat near the entrances. Putnam acknowledged that fencing and crossing structures often are prohibitively expensive for most highway projects. Although Putnam indicated that previous studies of roadside reflectors provided inconsistent conclusions, he suggested that reflectors may offer a less-expensive alternative to fencing on roads with light traffic.

Note: Animals become trapped in roadways by breaching fences at weak spots or by entering at the end of the fence. One-way gates generally are constructed of metal tines or prongs, which form a smooth funnel that flexes by spring tension in the intended direction of use and a narrow, fixed-position, pointed opening in the opposite direction. For one-way gates to be effective, the devices must be adjusted properly through spring tension and initial opening width to allow passage of the target animals only in the intended direction of travel (inside the roadway corridor to the right-of-way on the outside). This is a difficult task considering the size differences among sex and age classes of deer. Studies reporting that some animal use of gates was in both directions are indicating that the one-way gates were not totally effective.

Reed et al. evaluated the effectiveness of underpasses and overpasses, deer guards, deer fence length, highway lighting, and animated deer crossing signs in reducing mule deer-vehicle collisions on Colorado highways. They concluded that 2.44-m high deer fencing used in combination with sufficiently large underpasses or strategically placed one-way gates was the most effective method for averting deer-vehicle collisions. Deer guard prototypes were constructed either of steel rails with alternating black and white paint, large tire tubes, smaller bicycle inner tubes, or a black and white painted ray pattern. None of the deer guard designs eliminated deer crossings. Segments of 2.44-m high deer fence with one-way gates were effective in reducing deer-vehicle collisions along those sections, however, this study made no comparisons among different fence segment lengths or heights or the tendency for deer to make end runs around fences relative to segment length. Lighted, animated deer crossing signs and highway lighting did not affect driver behavior.

Note: Deer guards are a modified version of cattleguards. Both devices are placed in crossings over an excavated area of a certain depth and are designed to exclude hoofed animals while facilitating normal vehicle or pedestrian traffic. Guards have alternating lateral slats and openings spaced regularly for a total distance, which is greater than the distance that may be jumped by the animal targeted for exclusion. The slats may be sloped to make traction for hooves difficult. The excavated pit beneath the guard typically is deep enough so the target animal cannot touch the bottom through the open spaces.

Romin and Bissonette distributed mail surveys to the 50 U.S. state natural resource agencies to request estimates of deer (not reported by species) killed annually on highways, the source of the estimates, and information about methods used to reduce deer-vehicle collisions. They reported that of the 43 state agencies that responded, statistics on deer kills had limited quantitative basis and were highly variable and inconsistent among agencies. They conservatively estimated that the deer road-kill for 1991 was 500,000 deer, and deer road-kills had increased in the 26 of 29 states that had suitable trend data for 1982-1991. Nearly all respondent states had used some sort of mitigation technique; two states used highway lighting, three hazed deer, six altered habitat, seven set lower speed limits, seven built or modified underpasses or overpasses, 11 used mirrors, 11 built deer exclusion fencing along roads, 20 used warning whistles, 22 used public awareness programs, 22 installed swareflex reflectors, and 40 used deer-crossing signs. Thirteen respondents indicated their state had not conducted a scientific evaluation of these techniques. No state reported a scientific evaluation of the effects of reduced speed limits, hazing, or public awareness programs.

FENCES AND WILDLIFE CROSSING STRUCTURES

Roadside fencing is arguably the most studied of devices implemented to reduce the incidence of deer-vehicle collisions. Most research has indicated that fences are not an absolute barrier to deer, and only serve to reduce the number of animals entering the roadway. Conventional wire fencing must be at least 2.4 m high to limit the ability of deer to jump over it.
Alternative low-in-height fence designs, such as solid barrier fencing and non-traditional configurations of electric fence, may provide a less-expensive fencing option to exclude deer from roadways and other areas. Construction of fencing is prohibitively expensive for many applications, and regular maintenance is both costly and necessary for effectiveness. 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. Although fencing is not a complete barrier to deer, its presence may severely limit the natural movements and gene flow of deer populations and of other wildlife species. Fencing coupled with a variety of underpasses, overpasses, road-level crosswalks, one-way gates, and other strategies has been tested to allow animals to cross roadways at controlled areas along fenced highways. Crossing structures have proven most successful when used where traditional migratory routes of mule deer, elk, 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.

**Fences and Wildlife Crossing Structures - Annotated Bibliography**


Barnum used track counts along road shoulders and at highway underpasses to evaluate the characteristics of areas used as animal crossings on U.S. 24 and Interstate 70 in Colorado.
She correlated concentrated crossing areas to features of the surrounding landscape and roadside habitat using Geographic Information Systems-based simulations. Barnum identified a strategy for effectively identifying crossing locations along highways, which included: use habitat suitability as the primary indicator of crossing activity; consider how landscape structure interacts with habitat suitability to increase or decrease the potential level of area use by a particular species; consider how the design of the existing highway interacts with habitat suitability and landscape structure to influence animal crossing behavior; synthesize above information by mapping the landscape and roadway features known to be associated with crossing by species targeted for mitigation efforts. Barnum cautioned that each planning project should be approached individually with wildlife considerations incorporated into initial project design after consultation with individuals with expertise relative to the particular area and animal species.


Belant et al. tested the effectiveness of cattle guards as deer exclusion devices at openings in a 2.44-m fence surrounding an airport runway. They used infrared monitors to record deer crossings at the sites during pre- and post-installation periods, which were each two weeks in duration. The mean daily number of deer crossings after installation of cattle guards was reduced by ≥88%.

By conducting periodic spotlight counts, Bellis and Graves monitored white-tailed deer use of a 9.7-km portion of interstate highway right-of-way in central Pennsylvania that was fenced with 2.3-m high woven-wire mesh. They concluded that even fully maintained fencing was not a barrier to deer, and suggested that a continuously high traffic volume was responsible for the low incidence of deer-vehicle collisions on the highway by creating a “moving fence that inhibits deer from moving into traffic lanes”.


Brudin monitored drainage box culverts, arch culverts, and bridges where existing Pennsylvania highways crossed riparian areas to determine wildlife use of the structures and to define ideal characteristics of underpasses to promote wildlife use of the corridors. During phase I of the project, Brudin used infrared cameras to monitor existing underpasses in the fall during two five-day periods each separated by a month. White-tailed deer used only one of nine underpasses, and this was the largest culvert with an arch shape that was 5.8-m high by 5.8-m wide and 76.2 m long. However, other species including small and medium mammals and humans used this and all of the other structures. To better determine what size drainage culverts would most likely be used as underpasses by white-tailed deer, Brudin identified and studied 20 culverts with openness indices (openness = (width * height) / length) of 0.5 and greater. White-tailed deer
were photographed in nine of 20 (65%) culverts. Black bears were observed in two culverts, and humans were observed in three culverts. The average dimensions of those culvert structures used by deer was 2.5 m in height, 4.7 m wide, and 50 m in length. Brudin detected no deer use of culverts > 87.1 m in length, and recommended increasing height and width dimensions when length of the culvert is increased to offset a narrow openness index. Brudin further suggested tying right-of-way fencing at least 2.4 m in height into underpass openings to direct wildlife movements into the structures.


Clevenger and Waltho used track counts to monitor animal use of 11 wildlife underpasses, including nine open-space cement underpasses and two metal culverts, over a 35-month period in Banff National Park, Canada. They estimated expected crossing frequencies of wolves, cougars, black bears, grizzly bears, mule and white-tailed deer, elk, and moose from three models: radio telemetry locations; pellet counts; and habitat-suitability indices. They derived species-performance ratios for each species at individual underpasses by dividing observed crossing frequencies by expected crossing frequencies and then tested the null hypothesis that performance ratios did not differ between species. If the null hypothesis was rejected, they determined which underpass attributes (e.g. structural variables, noise level, landscape variables, and a human-use index) were most closely associated with species-performance ratios. Species use of underpasses was explained weakly by structural attributes. The only strong correlation observed was a negative relationship between wildlife use of an underpass and human activity.
Falk, N. W. 1975. Fencing as a deterrent to deer movement along highways.

Dissertation, Pennsylvania State University, University Park, Pennsylvania, USA.

and


Falk et al. concluded that 2.3-m high woven-wire mesh highway right-of-way fencing did not provide an effective barrier to deer along an interstate highway in central Pennsylvania. Using track counts in snow and soft soil, they observed high rates of deer crossing activity at fence openings near the ground.


Feldhamer et al. monitored white-tailed deer along a 40.2-km section of interstate highway right-of-way in Pennsylvania with two heights of woven-wire fencing (2.7-m and 2.2-m). They regularly monitored 22 radio-collared deer that were captured within the right-of-way, conducted 36 spotlight surveys to document deer use of right-of-ways, and obtained kill locations for 100 road-killed deer within the test section of highway. They concluded that the 2.7-m high fence reduced the number of deer on the right-of-way, but did not decrease the number of road-kills in that section.
The California State Department of Transportation developed this project to determine the effectiveness of a combination of deer-crossing underpasses, “deer-proof” fence, and one-way deer gates in preventing deer-vehicle collisions involving migrating mule deer. The structures were designed to accommodate deer migration, heavy equipment travel, and cattle passage under the highway. Three 13.2-km long sections of 2.13-m high fencing were constructed 1.6 km apart along four-lane U.S. Highway 395 in southern California. The fencing was composed of 1.83-m high woven fabric topped with three strands of high-tensile smooth wire, and was designed to direct migrating deer toward the underpasses. The fenced underpass corridors were 6.1 m wide and 104 m long. One-way gates were installed in pairs at nine locations on each fence line to allow deer trapped within the highway corridor access to outside the fence. Ford monitored deer use of the mitigation areas with track counts along fences and at crossing devices during spring migrations from 1976 through 1979. Track counts indicated that the crossing structures were very effective in safely directing deer crossings. However, it took three years for deer to adjust their movements to the structures rather than making extensive lateral movements to fence ends. In treatment areas pre-installation of the mitigation devices, deer-vehicle collisions averaged 10.8/year. During the three years post-installation, deer-vehicle collisions averaged 2.6/year, and Ford attributed seven of the nine collisions to a rancher’s access gate being left open.

Twenty-four wildlife underpasses were installed at an average spacing of 1.43 km along a 64-km fenced portion of Interstate 75 in Florida in attempts to reduce roadway mortality of the endangered Florida panther. The fencing was 3.4 m high galvanized chain–link topped with a 1-m overhang of three strands of barbed wire. Underpasses were 21.2-25.6 m wide by 48.5 m long including the open median separating the two bridges elevating traffic 3-4 m above the ground. Foster and Humphrey examined wildlife utilization of four of the underpasses with infrared-triggered wildlife cameras installed within the underpasses. They identified crossings by panthers, bobcats, white-tailed deer, American alligators, raccoons, black bears, and numerous bird species and concluded that underpasses reduced fragmentation of animals’ home ranges and prevented animal-vehicle collisions. Foster and Humphrey stressed that placement and spacing must consider the specific movement patterns of wildlife within a particular area and fence maintenance is integral to the success of a fence-underpass combination strategy.


Gallagher et al. tested the hypothesis that a virtually solid barrier of burlap cloth would provide an effective exclusion fence for free-ranging white-tailed deer in northwest Georgia. They monitored corn consumption at treatment and control feeders and used infrared game monitors to record deer events within three plots consisting of two, 10 m X 10 m squares established in pastures. Following a pre-conditioning period, data were collected during baseline periods during 10 days prior to two experimental phases. During the first experimental phase, burlap at a
height of 1.7 m was secured with wire ties to a single strand of high-tensile wire strung from four corner posts. Deer use of treatment plots was effectively eliminated (100%) over a 30-day period. During the second experimental phase, two of the three plots were reestablished 45 days later. Fence heights began at 65 cm and were raised 15 cm every five days until reaching 1.7 m in height. At a fence height of 1.7 m, corn consumption decreased by 30%. They suggested that a visually solid barrier may serve as an effective deer exclusion fence.


Gordon and Anderson monitored mule deer use of six livestock and machinery underpasses on Interstate Highway 80 and one experimental wildlife underpass on U.S. Highway 30 in Wyoming. The underpasses were all located along sections of roadway with 2.4-m high fencing. They changed the inside dimensions of the experimental wildlife underpass during periods ranging from five to 20 days. Mule deer used only one underpass along Interstate Highway 80, and that structure had the highest openness ratio (openness = (width * height) / length) of all the machinery and livestock underpasses tested. Based on mule deer use of the experimental wildlife underpass during alterations of its dimensions, Gordon and Anderson recommended that future underpasses in that area be at least 6.1 m high and 2.4 m wide.
In 2001, on U.S. Highway 30 in Wyoming, a mule deer underpass was constructed with dimensions of 6.10-m wide by 3.05-m high and 18.29-m long. This crossing replaced a passage, which consisted of a gap in a 11.27-km long, 2.44-m high fence. They used an infrared camera monitoring system to assess mule deer use of the underpass structure relative to variations in underpass height and width. Nearly 1,500 mule deer used the underpass in the fall of 2001 and spring 2002, and 1,338 mule deer used the underpass during fall 2002. Repel rates (approaches with no passage) and aversion to decreased openness of the underpass was less during fall 2002 than during spring 2002 and fall 2001, perhaps indicating that deer became more accustomed to using the structure over time.


Knight et al. evaluated elk use of different types of modifications to four-strand barbed-wire fences in rangelands. They inferred that directing elk crossings to desired locations where the modified fence would be easier for elk to cross would result in less fence damage and reduced overall fence maintenance costs. They stretched sewing thread across the 15 m wide experimental openings and maintained track beds on both sides to monitor free-ranging elk use of crossings. Broken thread and elk tracks on both sides of a fence indicated that elk crossed the
opening. The modified fence crossings used most by elk had the top wire attached to the second wire, which resulted in a lower (80 cm) crossing height than the adjacent unmodified fence (100cm). These modifications were economical and only required supplies to attach the wires together.


Land and Lotz examined wildlife use of highway underpasses designed to mitigate roadway mortality of endangered Florida panthers on State Road 29 and Interstate 75 in southwest Florida. The two State Road 29 underpasses consisted of a pre-formed concrete box culvert 2.4 m high, 7.3 m wide, and 14.6 m long. The culvert rested at ground level and the roadway gradually rose over the structure. The crossing also included a concrete span that formed a bridge across the canals adjacent to and on each side of the roadway. The surface of the concrete span was covered with a layer of soil that supported natural vegetation. The two Interstate 75 underpasses were 21.2-25.6 m wide by 48.5 m long including the open median separating the two bridges elevating traffic 3-4 m above the ground. All underpasses were installed in conjunction with 3.4 m high chain-link fencing topped with a 1-m outrigger with three strands of barbwire. They monitored wildlife use of the underpasses with infrared trail cameras and by track counts. Underpasses on both highways were used by all medium-sized to large animals that occur in southwest Florida. White-tailed deer used the Interstate 75 underpasses more than the State Road 29 underpasses probably because of the native vegetation within the crossing and the relative openness of the Interstate 75 structures.

and


Lehnert and Bissonette evaluated the effectiveness of a highway crosswalk system for reducing mortality of mule deer on a newly constructed two-lane and divided four-lane highway in northeastern Utah. Rights-of-way were fenced with 2.3-m high fencing, which restricted deer access to roadsides and directed animals to designated crosswalk zones. The crosswalk was a dirt path bordered by a field of round river cobblestones and painted cattle-guard type lines on the roadway. Four one-way gates were placed near each crosswalk to allow deer that became trapped along the highway to escape the right-of-way. A series of three warning signs was installed at a spacing of 152 m apart at each crosswalk to warn motorists of a deer-crossing zone. To evaluate the system, they: (1) monitored deer-vehicle collisions in treatment and control areas pre- and post-installation of crosswalks and compared observed and statistically expected values of deer-vehicle collisions as a basis for comparison, (2) used spotlight censuses to document deer use of the right-of-way and indirectly determine if crosswalks impeded seasonal deer migrations, (3) assessed deer behavior and movement patterns in crosswalk zones, (4) conducted motor-vehicle speed assessments to evaluate motorist response to crosswalk warning signs, (5)
evaluated the efficacy of the one-way gates at enabling trapped deer to escape the right-of-way. Based on expected kill levels, deer-vehicle collisions declined 42.3% and 36.8% along the 4-lane and 2-lane highway, respectively. However, they were unable to statistically demonstrate that observed reductions resulted from crosswalk installation. Their observations of deer suggested that the system may have reduced deer use of the right-of-way by 42% and had minimal effect on deer migration. They concluded that lack of motorist response to warning signs, the tendency of foraging deer to wander outside of crosswalk boundaries and the ineffectiveness of the one-way gates contributed to most deer mortality within the treatment areas.

**Ludwig, J., and T. Bremicker. 1983. Evaluation of 2.4-m fences and one-way gates for reducing deer-vehicle collisions in Minnesota. Transportation Research Record 913:19-22.**

Ludwig and Bremicker evaluated two segments of 2.4-m fence with one-way gates along new segments of interstate highway in Minnesota. The fences were 4.0-km long with nine pairs of gates and 5.5-km long with 10 pairs of gates. They monitored the segments for 18 months using automated counters and track counts at the one-way gates, and also by recording deer-vehicle collisions. Sixty-nine percent of 51 passages through the gates were from inside the fenced highway corridors to the outside (the intended direction of travel). Deer-vehicle collisions were reduced from 15 to 13 in the 4.0-km segment and from 15 to five in the 5.5-km segment. They concluded that the gates were effective in reducing deer entry into the roadway, and in allowing deer trapped within the roadway access to the right-of-way outside of the fenced corridor. The fence used in combination with one-way gates reduced the incidence of deer-vehicle collisions.

A series of transcontinental fences were installed in Australia beginning in the late 1800’s in attempts to reduce the impacts of vermin in crop and pastoral production areas. Fences typically were constructed of wire mesh with various diameter holes and heights to restrict movements of rabbits, marsupials (mostly red and gray kangaroos), and dingoes. Although the utility of fences was much debated at the time this article was written, the author concluded that fencing served as only a partial control measure with other forms of population control as equally necessary. Further, a rigorous fence maintenance regime was considered “the keystone of effectiveness”.


Five experimental fence designs were tested using captive deer. Individual fence types were either a variation of non-electrified high-tensile wire; electrified, high-tensile wire; or woven-wire with an overhang extension of three strands of high-tensile wire. Deer interactions with fences were observed for 30 days. This period included food restriction for up to 14 days with food always available beyond the fence perimeter. In captivity, deer penetrated all designs except a vertical electric fence, which had five strands of high-tensile electrified wire with the first strand at 25.4 cm from the ground and each thereafter at a spacing of 30.5 cm for a total height of 147 cm. This fence, the Penn State Vertical Electric Deer Fence, then was field-tested for two years on crop fields with a history of deer damage in Pennsylvania. The fence was deemed effective in excluding deer at field sites containing alfalfa, small grains, corn, vegetables, orchards, and young coniferous trees.

Perdue et al. tested the hypothesis that a slant-oriented fence would deter white-tailed deer from entering an enclosure baited daily with corn. They established three plots spaced 3 m apart and each with two paired 10-m² squares. During the first trial, they secured 5-cm wood slats to high-tensile wires at a 25.4-cm interval and a 40º angle to achieve a fence height of 1.2 m. On the adjacent square, they secured slats vertically to high tensile wires also at a 25.4-cm interval and a fence height of 1.2 m. For trials two and three, they reduced intervals between slats by 5 cm during each of the five-day periods. During all trials, deer consumed all corn provided (2.27 kg/day). Data from infrared game monitors indicated that during trials one and two deer entered enclosures with fences of slant design less, and during trial three there was no difference in deer entrance of enclosures regardless of fence type. During trials one and two, they observed deer jumping and penetrating both fence types. During trial three, deer penetrated and jumped vertical fences, but only jumped the slant fence configuration. Perdue et al. concluded that the slant fence type limited deer movement through the fence, but deer visual acuity was sufficient to allow deer to jump slanted fences at a height of 1.2 m.


The Florida Department of Transportation instituted a system of highway fencing, underpasses, and access-road deer exclusion grating in attempts to reduce endangered Florida Key deer mortality on roadways in the Florida Keys. Peterson et al. evaluated three types...
of 6.1-m X 6.1-m bridge grating for deer-exclusion efficiency at access roads by monitoring attempted Key deer crossings of the structures. Through observations with infrared trail cameras of deer attempting crossings to reach automatic feeders, they determined that grating with 10.1 cm X 12.7 cm openings with diagonal crossmembers were 99.5% effective for Key deer exclusion and also the safest for pedestrians and cyclists.


Puglisi et al. examined the characteristics of 874 white-tailed deer mortality sites along a 503.7-km stretch of Interstate 80 in Pennsylvania. The location of highway fencing was the most highly correlated variable determining where highway mortality occurred. The highest deer mortality occurred where the fence was located at the edge of a wooded area or within 22.9-m from the nearest wooded area, and the lowest deer mortality occurred where the fence was > 22.9-m from the nearest wooded area.


Quinn and Smith conducted three studies of animal passage across highways. From 1989-1991, they used radiotelemetry (species of marked animals not stated) and infrared remote cameras to monitor underpasses on Interstate 75 in Florida primarily designed to reduce roadway mortality of the endangered Florida panther. They observed over 800 passages by species other than Florida panthers. Surveys of road-killed vertebrates indicated a reduction of >3,300 road-killed vertebrates to <2,000 from pre-construction to post-construction of a roadside barrier wall and culvert underpass system at the Florida Payne’s Prairie State Reserve. After installation of the
underpass system, they observed 51 wildlife species using new and old culverts, whereas they observed only 28 species passing through existing culverts prior to installation of the new structures.


Reed et al. tested variations of a one-way gate, which was designed to allow mule deer that breached a 2.44-m fence and became trapped within a highway corridor to escape through the fence and away from the highway. They conducted preliminary tests with captive mule deer, which were required to pass through gates to reach food and water. Eight gates of the type deemed most effective were installed in 2.44-m high fences adjacent to Interstate 70, near Vail, Colorado. The 2.4 km parallel fences were used in conjunction with a deer underpass in attempts to funnel the passage of mule deer during spring and fall migrations. During a 3-year period, 96% of 558 passages through the gates were in a one-way direction away from the highway (the intended direction of use).


Reed evaluated mule deer use of a highway underpass (height = 3.05 m, width = 3.05 m, length = 30.48 m) and the extent of their behavioral reluctance associated with entering the structure during periods with and without artificial illumination inside the underpass. The underpass was constructed to allow migrating mule deer to safely cross under a four-lane interstate highway near Vail, Colorado. Reed et al. used video surveillance, track counts, and traffic counters to monitor deer passage during four migration periods. They estimated that the underpass was successful in allowing 61% of migrating mule deer in the area to safely cross the highway.
However, they determined that deer were reluctant to enter the underpass as indicated by a total of 4,450 deer approaches to the underpass and only 1,739 actual entrances over the entire study. Deer behavior and use of the underpass was not affected by artificial illumination.


Reed et al. evaluated the effectiveness of underpasses and overpasses, deer guards, deer fence length, highway lighting, and animated deer crossing signs in reducing mule deer-vehicle collisions on Colorado roadways. By conducting track counts at underpass openings, they determined that mule deer were more likely to use underpasses with an openness ratio (openness = (width * height) / length) > 0.6. They observed mule deer utilizing a substandard overpass bridge and then altered the structure to determine: (1) a threshold of width narrowness that would be tolerated by crossing deer, (2) whether deer would cross in the presence of overhead netting to simulate a pedestrian crossing structure, and wire mesh to prevent deer from jumping onto the road surface below the overpass. Deer readily crossed the structure even at the most narrow width of 2.48 m, and with the overhead netting and wire mesh. They tested five deer guard prototypes on captive deer released in a runway and allowed to voluntarily cross the deer guards. Each prototype was a derivation of a basic design constructed of flat mill steel (spacing not specified) to form a guard section with dimensions of 3.05 m X 3.66 m. Subsequent prototypes included: Prototype II) painting the steel rails to form an alternating black and white pattern; Prototype III) five large, black innertubes cut and sectioned longitudinally to form elongated rectangles stretched across and 15 cm above the Prototype II guard; Prototype IV) 93 rubber straps stretched parallel and all 15 cm above Prototype II guard; Prototype V) a black and white
ray pattern painted on a tarp placed over Prototype I guard. They deemed none of the deer guard prototypes as effective in preventing deer crossings, however, this conclusion was based on limited data of single encounters by a range of four to fourteen individual captive deer per prototype. Fences of 2.44-m in height installed in combination with one-way gates proved effective in reducing deer-vehicle collisions provided fences were properly constructed and maintained. They recommended extending fences > 0.8-km beyond mule deer concentration areas to prevent end runs, and suggested that one-way gates be placed near vegetative cover or drainages.


Reed observed the behavior of 298 mule deer exiting a highway underpass (height = 3.05 m, width = 3.05 m, length = 30.48 m) near Vail, Colorado during spring-summer migrations over a six-year period. About 67% of deer exhibited trotting and bounding modes (indicative of reluctance or wariness), compared to the walking mode usually observed some distance before encountering the underpass. This information combined with previous observations of deer at the entrance of the same underpass by Reed at al. (1975. Journal of Wildlife Management 39:361-367), indicated that behavioral responses of deer to the structure did not change over 10 years (1970-1979).


Reed et al. used benefit-cost analysis to describe the cost efficiency of 2.4-m high fencing used with underpasses and one-way gates to mitigate deer-vehicle collisions in six 1.6-km long highway projects along Interstate 70 and Colorado Highway 82 near Vail, Colorado. The
average number of deer-vehicle accidents/year in the test areas pre- and post-installation of the fences was estimated from the number of deer carcasses found on or along the road. The effectiveness of the fences was estimated by assuming that the average pre-fence deer mortality would continue to occur at a constant rate were the fence not installed. The equation used in their analyses was:

\[
(\text{1}) \times (\text{2}) \times (\text{3}) \times (\text{4}) \times (\text{5}) \times (\text{6}) + [(\text{7}) \times (\text{5})] - (\text{8}) = \text{Benefit:Cost,}
\]

where (1) = cost of vehicle repair, (2) value of deer, (3) pre-fence mortality, (4) fence effectiveness (%), (5) present value given annuity, (6) cost of 2.4-m fence, (7) cost of fence maintenance, (8) cost of 1.1-m right-of-way fence needed in absence of 2.4-m fence. They did not factor in the cost of loss of human life or injury related to deer-vehicle collisions. They estimated that at a benefit:cost ratio of 1.36:1, deer-vehicle collisions rates of eight, 16, and 12 dead deer/1.6 km/year are the minimums for 2.4m fencing on one side, both sides, and both sides with an underpass, respectively.


Roof and Wooding evaluated one experimental culvert type underpass designed to reduce roadway mortality of black bears. The inside dimensions of the crossing were 14.3 m long, 7.3 m wide, and 2.4 m high. Chain-link fencing, 3 m high topped with three strands of barbwire, was installed 0.6 km and 1.1km to either side of the underpass. Paths were bulldozed in the forest adjacent to the highway to encourage bears to walk toward the crossing. They monitored wildlife activity at the underpass by observing tracks within the dirt floor of the culvert and along disked track beds along the fencing, and by using an infrared camera within the underpass.
Also, they radio-tracked 43 radio-instrumented bears to observe their movements relative to roads. Bears used the underpass on five occasions; three crossings were by radio-collared bears. Marked bears crossed State Route 46 on 26 occasions, many of which were 100-300 m from the underpass along a river. Other species documented using the underpass included rabbit, raccoon, armadillo, opossum, gray fox, white-tailed deer, coyote, bobcat, gopher tortoise, snakes, and cattle. Sixty-nine percent of animals encountering the fence did not use the underpass, 27% used the underpass, and 4% crossed the highway by crawling under the fence or by going around the ends.


The Electrobraid fence is comprised of a 0.6-cm polyester rope with electrified copper wire woven throughout; the Electrobraid is carried on fiberglass posts set at 15-m intervals. Seamans et al. tested the fence by conducting one- and two-choice tests with free-ranging white-tailed deer. At each of 10 individual stations set > 1 km apart, a 5 m X 5 m site was established with Electrobraid fence forming a perimeter enclosing a feed trough with whole kernel corn. A trail monitoring device was used to count deer activity. Mean deer intrusions were <1/day at one- and two-choice sites where fence was electrified, while at non-electrified control sites, mean deer intrusions were 84-86/day. They concluded that Electrobraid fence was an effective deer barrier for the five weeks of the experiment.

Servheen et al. monitored seven underpasses and three culverts along Interstate 90 in Montana during 10 months with infrared cameras and by snow-tracking. Primary users of crossing structures included white-tailed deer, mule deer, elk, skunks, raccoons, house cats, foxes, coyotes, black bear, humans, and domestic dogs. Wildlife use was most common in underpasses (openness ratings range = 27.75 to 811.63) (openess = (width * height) / length), and minimal at culverts (openness ratings range = 0.12 to 0.75). They found no relationship between wildlife use and structural dimensions of the crossing devices. Ungulates most commonly used underpasses and were not observed using culverts. Servheen et al. assumed that ungulates were reluctant to use culverts because culverts lacked suitable substrate and had a low structural openness ratio.


Florida Department of Transportation developed a plan to construct fencing along U.S. Highway 1 that crosses Big Pine Key, Florida to prevent vehicle collisions with endangered Key deer. In this plan, no provisions were made to stop deer from entering the highway via the many small access roads bisecting US Highway 1. The purpose of this study was to design, construct, and test a deer guard that would allow normal passage of vehicles while preventing Key deer from
crossing. Deer guard prototypes were subjected to four tests: (1) no incentive to cross; (2) extra food and water incentive to cross; (3) fawn separated from doe; (4) doe separated from mature buck. Silvy and Sebesta recommended that Key deer guards measure at least 7.3 m with the center portion raised 0.6 m above the ground and cross-member spacing of 1.9 cm or more. Further, they suggested that the ends should be sloped to facilitate vehicular traffic and that side panels should extend the length of both sides of the guard.


Singleton and Lehmkuhl used Geographic Information Systems, automatic camera surveys, documentation of wildlife use of bridges and culverts, and track surveys to assess wildlife habitat connectivity and barriers to animal movement along 56.3 km of Interstate 90 in Washington. From January 1998 to March 2000, they observed 15 species of mammals utilizing culverts to cross the highway.


The purpose of this paper was to review biological and social issues of fences as they pertain to management of wildlife, especially free-ranging white-tailed deer in Michigan. The publication was produced in response to inquiries to Michigan Department of Natural Resources, members of the Michigan legislature, and the Michigan Natural Resources Commission by individuals and organizations concerned with the apparent increase in construction of fences in Michigan. Squib and Moritz propose two general situations where fences specifically designed to restrict deer and other wildlife movements are in the best interest of the public. The first situation utilizes high
fences to protect public health, safety, and security. The second is to protect agricultural, horticultural, or silvicultural crops. They also recognized that the state must allow landowners considerable freedom to do as they please on their private property unless such actions are proven to threaten population viability of wildlife.

Teutsch, C. 2004. Personal communication on 23 April 2004 about using Polytape Electric Fence to exclude white-tailed deer from small agricultural plots.

Chris Teutsch, a forage crop agronomist, at Virginia Polytechnic Institute and State University, used a configuration of Polytape electric fence to exclude white-tailed deer from small plots used to research ryegrass and other agricultural forage growth. The double-fence configuration had an inner layer with a strand of Polytape at 40.6 cm high and another strand at 121.9 cm high. The outer layer had a single strand of Polytape at 60.1 cm (approximately at deer nose height). Teutsch reported that the fence totally eliminated deer entry into research plots.


Ward et al. used helicopter and roadway surveys and radio-telemetry monitoring to observe the behavior of elk, pronghorn antelope, and mule deer relative to Interstate 80 in Colorado. They concluded that 1.2 m high right-of-way fencing was sufficient for deterring antelope from roadways since antelope were reluctant to cross fences and use highway underpasses. Ward et al. recommended the construction of 2.4-m fencing in combination with highway underpasses to prevent mule deer and elk road crossings. They used heart rate telemetry to monitor the physiological reaction of one female and one male elk to various stimuli including gun shots,
vehicle traffic, humans with and without a dog, a trail bike, and an airplane. However, they made no conclusions about the elk reactions due to limited sampling intensity.


Big-game fencing (2.4 m high) was installed in combination with seven wildlife underpasses along a 12.5-km section of Interstate 80 in Wyoming where annually about 1,000 mule deer crossed during spring and fall migration. Three of the underpasses were the type designed for large machinery (length = 33.5-60.7 m, width = 9.1 m, height = 4.0 m) and 4 were of a concrete box-type construction (length = 46.6-120 m, width = 3.0 m, height = 3.0-5.18 m). Ward used video surveillance cameras and track counts to document more than 4,000 mule deer passages through the underpasses during four migration periods. About 70% of the deer used the machinery underpasses to move to their winter range, and about 90% of deer used the machinery underpasses during spring migration. The remainder of deer used the box-type underpasses. The incidence of deer-vehicle collisions ranged from 37-60/year in the experiment area during the four years pre-installation of the fence/underpasses. This estimate was reduced to one deer-vehicle collision during the two years post-installation.

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-vehicle collisions within test sections either pre- and post-installation of reflectors; when reflectors were covered versus uncovered; or within reflectorized sections as compared to adjacent control sections. Such methods fail to
consider changes in deer densities, seasonal movements, or traffic patterns. Little is known about how deer react to reflector activation or if individual animals become habituated to the devices over time. Studies that use counts of deer carcasses along roadways to assess reflector effectiveness rarely use data quality controls such as video surveillance of test sections or driver surveys to account for deer-vehicle collisions that resulted in injured deer wandering from the roadside. Beyond differences in experimental design, comparison of results among different reflector studies is further confounded by the variety of reflector models tested and the distinct spectral properties of those devices.

**Wildlife Warning Reflectors - Annotated Bibliography**


*Ontario Ministry of Transportation Research and Development Branch Report No. MAT-91-12.*

Armstrong evaluated the effectiveness of Swareflex reflectors in reducing collisions with white-tailed deer on King’s Highway 21 in Ontario, Canada. Along one 3-km test section, reflectors were installed at a spacing of 14.5 m apart 3.1 m from the pavement edge on both sides of the highway. In a second test section of 1.1 km, reflectors were spaced 25 m apart in lines 8 m from the edge of the pavement. Armstrong alternated covering and uncovering reflectors for one-week periods during the 54-week study. Fifty-one deer vehicle collisions occurred within the study area, but of those only 30 were during darkness. During darkness, 14 collisions occurred while reflectors were uncovered, and 16 accidents occurred when reflectors were covered and non-operational. Accident rates did not differ statistically between covered and uncovered periods or for the different reflector spacing or placement configurations.
Boyd, R. J. 1966. “Deer mirrors” - do they work?. Colorado Department of Natural Resources, Division of Game, Fish, and Parks Game Information Leaflet No. 44.

and


Boyd tested the effectiveness of Van de Ree Deer Mirrors in reducing mule deer-vehicle collisions along U.S. Highway 6 and 24 in Colorado. Mirrors were installed at a spacing of 30.5 m between mirrors on each side of the highway along two 2-km test sections of roadway. Placement was alternating from side to side of the highway so that a mirror was present every 15.3 m along the highway. In one test section, mirrors flashed across the line of traffic. In the other test section, mirrors flashed away from the roadway. Comparison of the ratio of roadkill in the mirror section versus the control area over the eight-year study period indicated that the incidence of deer-vehicle collisions increased with mirrors in effect. They detected no difference in vehicle speeds within the test section pre- and post-installation of mirrors.


Gilbert tested roadside deer mirrors constructed of a polished stainless-steel surface with a dimple at each corner and one in the center. Mirrors were placed in 12 randomly selected 0.8 km test sections along 23.8 km of Interstate 95 in Maine. Over four years only six deer-vehicle collisions involving white-tailed deer were recorded in the study area with four in the mirrored test sections and two in the non-mirrored sections. Although no statistical inferences could be
made from this data, Gilbert used information from related literature to conclude that mirrors and other reflectors were ineffective deterrents to deer-vehicle collisions.


Ingebrigtsen and Ludwig tested Swareflex reflectors along a 1.6-km section of Interstate 94, a four-lane highway in Minnesota. They installed reflectors at 20-m intervals 4.1 m from the edge of each road surface with a total of four rows of reflectors within the roadway corridor. They recorded collisions involving white-tailed deer for one year prior to installation and for four years post-installation. During the one year prior to reflector installation, they recorded 38 deer found dead within the study area. During the four years post-installation, 13 deer were found dead for a yearly average of 3.25 deer-vehicle collisions/year. Ingebrigtsen and Ludwig did not differentiate between deer killed during daylight or darkness during the study.

Norman, P. C. Date unknown. Reducing deer-vehicle collisions by the use of reflectors—a summary of current research and literature. Howard County, Maryland Department of Recreation and Parks Internal Report.

Norman evaluated literature related to wildlife warning reflectors and deer visual capabilities, information from personal communication with persons related to the issues, and data from reflector use in Howard County, Maryland to assess the effectiveness of wildlife warning reflectors. Although he was unable to find definitive proof, Norman suggested that it was unlikely that reflectors could be effective in altering deer behavior and reducing deer-vehicle collisions. Based on his individual assessment, Norman recommended that Howard County,
Maryland cease installation of Strieter-Lite reflectors, but maintenance of the previously installed reflectors and monitoring of their effectiveness be continued.


Pafko and Kovach described anecdotal trends in deer-vehicle collision data for sections of rural and suburban Minnesota highways pre- and post-installation of wildlife warning reflectors. The Minnesota Department of Transportation installed red Swareflex reflectors or an unnamed brand of white reflectors along 16 roadway sections of unknown length. Due to limited data, Pafko and Kovach did not conduct statistical analyses of the accident data. In rural areas, reductions in deer-vehicle accidents post-installation of reflectors ranged from 50% to 97%. In the suburban areas, they observed increases in deer-vehicle accident rates. They provided possible explanations for the ineffectiveness of reflectors in the suburban areas including increases in deer population size, high traffic volume, and the inadequate maintenance of reflectors.


Reeve and Anderson evaluated the effectiveness of Swareflex reflectors for reducing vehicle collisions with mule deer in Nugget Canyon, Wyoming. They installed 350 reflectors on both sides of a 3.2-km stretch U.S. Highway 30 at a spacing of 20 m apart on straight sections of roadway and a spacing of 10 m in curves. They established a 3.2-km control section with similar roadway configuration and incidence of deer-vehicle collisions as the test section. They compared two-week alternating periods when reflectors were covered and uncovered in the test
section. Over the study period, 64 deer were killed in the test section when reflectors were covered, whereas 126 deer were killed when reflectors were uncovered. Similar numbers of mule deer were killed in the section with reflectors as the control section. Sixty-two mule deer were killed in the control section when reflectors were covered in the test section and 85 were killed when reflectors were uncovered. They concluded that Swareflex reflectors were not effective in reducing mule deer-vehicle collisions.


Schafer and Penland established four test sections ranging from 0.72 km to 1.08 km along highway SR395 in Spokane, Washington. Test sections were placed in areas with history of high deer-vehicle collision rates. Reflectors were mounted on 1.1-m posts set 1 m from the roadway and placed at a 20-m spacing along straight stretches of road and at a 10-m spacing in curves. Reflectors in each test section were alternately covered and uncovered at one-week or two-week intervals. Fifty-eight deer (56 white-tailed deer and two mule deer) were killed at night in the test sections. Fifty-two (90%) were killed when the reflectors were covered and six (10%) when uncovered. They concluded that Swareflex Reflectors were responsible for significantly reducing the number of deer-vehicle collisions.

Sielecki described the Wildlife Accident Reporting System (WARS), a database used by the British Columbia Ministry of Transportation to store and analyze information on animal-vehicle collisions. In 2000, about 80% of animal-vehicle accidents in British Columbia involved white-tailed and mule deer, and the province used WARS to select areas to implement deer-vehicle accident mitigation strategies including fencing and wildlife warning reflectors. Wildlife warning reflectors have been used in British Columbia since the late 1980’s at over 95 locations by 2001. Sielecki reported on trends in deer-vehicle accident rates that “were not observed as part of a controlled scientific experiment” in reflectorized (reflector type not stated, but were either Swareflex or Strieter-Lite wildlife warning reflectors) portions of highway versus equal length adjacent sections with no reflectors. When comparing 9.37-km and 7.45-km experimental sections to their respective control road sections, Sielecki concluded, “it appears the installation of reflectors did not alter the overall local accident trends” from 1985-2000. Sielecki recorded the reflected light intensity of Swareflex and Strieter-Lite reflectors, and found that all models, regardless of lens color, reflected < 0.1 lux at a distance of 2 m. Of those tested, the Strieter-Lite “new” style reflector with a clear lens had the highest intensity of reflected light. Sielecki also observed a “white first 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”.

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Ujavári et al. examined the habituation of fallow deer to repeatedly occurring light reflections from a WEGU reflector at a supplemental feeding area in the 5,600-ha Gribskov forest, Denmark. The reflector was composed of a black plastic cover and two symmetrically sloping mirror sides each with 10 vertical rows of 4-mm mirror facets. The reflector was built into a non-reflective triangular box with the reflector placed in the middle of the long side of the box. The corner opposite the reflector was open and four bulbs were situated in another corner. Light reflections for this study were 60° for the horizontal angle and 30° for the vertical angle. An observer hidden in a shed activated the reflector remotely. This person also classified and recorded deer behaviors. On two control nights, Ujavári et al. did not activate the reflector and the fallow deer only seldom showed flight behavior or alarm. During the first experimental night, deer fled from the stimulus in 99% of the cases, but over the remaining 16 experimental nights, fallow deer exhibited increasing indifference to reflections, which was explained by habituation to the stimulus.


Waring et al. observed white-tailed deer road-crossing behavior in Crab Orchard National Wildlife Refuge, Illinois. Before reflectors were installed, 70% of observed deer crossed or attempted to cross a roadway bordered on one side by a cornfield and on the other by hardwood forest. After Swareflex reflectors were installed along the same stretch of roadway, 76.5% of all
deer crossing attempts were completed. They observed only 14 deer making dusk to dawn crossing attempts in the presence of vehicles with reflectors in place. Of those 14, 11 continued to move toward the pavement, while the other three turned and ran back toward the woods. Dusk to dawn deer roadkills occurring in the reflector test section were the same with reflectors installed as during the two years pre-installation.


Woodham installed Swareflex reflectors along two 3.2-km test sections on State Highway 121 near Denver, Colorado. Reflectors were covered and uncovered alternately during two-week periods over three months in the fall of 1988 to test the effectiveness of the reflectors for reducing vehicle collisions with mule deer. No comparisons could be made because no deer-vehicle collisions occurred within the test area during the three-month experiment. Woodham also conducted photometric evaluations of the reflectors under field conditions at varying levels of ambient light and vehicle headlight intensities and distances. Since little was known about deer vision, for comparison purposes Woodham described how the human eye would react to visual stimulation from the reflectors. The measured luminance of the reflectors was below the threshold required for the human eye to accurately detect an object, however, the human eye would not have difficulty detecting the presence of the reflectors. Woodham further suggested that the reflectors had reduced visual impact due to their small size and the amount of time (5-6 seconds) that a reflector lit up from vehicle headlights moving at speeds of 80.1-96.5 km/hour.

and

Zacks, J. L. 1986. Do white-tailed deer avoid red? An evaluation of the premise underlying the design of Swareflex wildlife reflectors. Transportation Research Record 1075:35-43.

Zacks used discrimination learning to assess the spectral sensitivity of a single female white-tailed deer. The deer was trained to lick a water tube when it recognized a visual stimulus projected on a screen. Zacks results suggested that deer possess a peak in spectral sensitivity at 540-550 nm and perhaps a higher peak at 500 nm. Zacks also evaluated the behavior of 10 white-tailed deer relative to Swareflex warning reflectors. The deer were penned in a 1.4-ha enclosure and provided with an unlimited supply of commercial game feed. Water was dispensed only during daily experimental trials by a remotely controlled toilet flush valve into aluminum pans with small holes in the bottom. The rapid draining (about 1.5 minutes) of the water encouraged the deer to cross the line of reflectors. Reflectors were installed on individual posts 107 cm above the ground at a spacing of 20 m. Zacks used two automobile headlights powered at 12 volts AC through a transformer to illuminate the reflectors. During 18 sessions, Zacks recorded 720 observations of deer crossing the line of reflector posts: 264 crossings when no reflectors were installed, 256 crossings when red reflectors were activated, and 200 crossings when white reflectors were activated. No statistical difference was found among deer crossings during the three experimental conditions, thus suggesting that the reflectors were ineffective in altering deer crossing behavior.
MOTORIST WARNING DEVICES

Active and passive driver warning devices have proven largely ineffective at reducing vehicle speeds and deer-vehicle collisions. Drivers ignore the common “deer crossing” sign, a likely result of its overuse. Although reduced speeds are not the only desired effect of warning drivers about site-specific dangers associated with wildlife crossings, it is the most common method of assessing warning device effectiveness. 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, has been unclear despite the high cost of such devices. Research indicating that non-redundant command type messages impact driver behavior more than notification style messages 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.

Motorist Warning Devices - Annotated Bibliography


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Gordon et al. evaluated the effectiveness of a flashing light animal sensing host (FLASH) and a geophone deer detection system in identifying deer crossing a highway at a fence opening. The FLASH consisted of infrared sensors that detected animal body heat, which activated flashing lights at deer crossing signs 300 m to either side of the crossing to warn motorists of animals in the roadway. They also conducted a series of experimental manipulations to determine motorist response to the FLASH. The geophone deer detection system detected ground vibrations caused by animals crossing the opening. Deer did not cause 50% of FLASH activations, whereas the geophone system did not activate falsely. Nighttime motorists reduced their speed (6 km/hour) the most (6%) when the FLASH operated normally. They detected reduced speeds the least (7%) for the activated warning signals. Vehicle speed was reduced (20%) when deer or deer decoys were present adjacent to the road and the warning signs were activated.


Huijser and McGowen reviewed literature related to animal detection and animal warning systems to identify locations in North America and Europe where such strategies have been implemented and they gave an assessment of each system’s operation and effectiveness. As of September 2003, they identified 27 locations where systems were or had been in place, and
another 20 locations where systems were to be installed. They defined animal detection systems as those devices, which sensed large animals near the roadway and then warned drivers usually with active signage. Animal warning systems were those devices, which detected vehicles and then warned animals with visual or auditory signals. Of those systems evaluated, Huijser and McGowen found that only a few operated well and likely reduced animal-vehicle collisions. Those systems, which proved reliably operational, included passive infrared systems in Switzerland; microwave radar devices in Finland; a geophone system, which detected ground vibrations of moving ungulates in Wyoming, U. S.; and a system in which the sensing of nearby radio-collared lead cows in elk herds triggered warning activation in Washington, U.S. For systems to operate properly and reduce the incidence of false detections, many design and maintenance issues must be addressed including weather conditions, vehicle engine heat, and small animals and birds using the structures for nesting thus interfering with the system’s function.


Lee et al. evaluated message style, the physical grouping or location, and visual messages of in-vehicle warning systems to identify how message characteristics affect driving safety and compliance. They observed the actions of human test subjects presented with various warning system stimuli while operating a driving simulator. Their results suggest that command messages, as compared to notification style messages, promote greater compliance but may reduce safety. In-vehicle messages presented without redundant roadway signs displaying a similar message led to lower levels of safety.


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The Wildlife Protection System (WPS) used infrared cameras to detect wildlife approaching roadways, which triggered flashing signs to warn drivers in Kootenay National Park, British Columbia. Technical difficulties prevented the system from being fully operational during the first test season in 2002, therefore, they were unable to evaluate the effectiveness of the WPS in reducing deer-vehicle collisions or the speed response of drivers to warnings produced by the WPS in 2002. During that year, however, Newhouse did use the WPS to document wildlife behavior near highways using 24-h infrared video footage. Deer activity was greatest at night, intermediate in the evening, and lowest during daytime hours. During midday, deer reacted to vehicles more often with behaviors of concern as displayed by higher rates of approaches to the highway and crossing in front of cars. During summer and fall 2003, the WPS was deployed again and its performance and ability to reduce driver speeds was evaluated. They found that driving speeds were about 6 to 9 km/hour lower within the test section than the rest of the park when the lights were not flashing. They attributed this to the presence of the equipment, signs, and radar guns associated with the WPS. When lights were flashing, speeds were reduced 10 to
21 km/hour. The WPS worked best on cool nights with an 89% proper operation rate, and it detected animals at distances >1 km. On warm days, the WPS operated most poorly, functioning properly only 25% of the time. Major maintenance problems with the WPS were attributed to power supply being unreliable and inconsistent data logging by the system. They indicated that most power supply problems could be eliminated in locations where power could be accessed from power lines, rather than be generated on-site.


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This study evaluated the effect of two types of deer-crossing signs on vehicle speeds on a four-lane Colorado highway. Sign type one had a reflective yellow, diamond-shaped background with the message “DEER XING” formed by lighted, neon tubing covered with a 0.64-cm thickness sheet of plexiglass. Sign type two had a reflective yellow background with four deer silhouettes formed with neon tubing. The deer figures were lighted in sequence from right to left to mimic a running deer. Below the animated portion of the sign, the message “DEER XING”
was displayed in black letters on a rectangular, reflective yellow background. They used an automatic vehicle speed recorder to monitor traffic speeds during 16-day control periods during which each sign was turned away from passing motorists and during a 28-day test period with sign type one turned toward traffic and a four-day test period with sign type two turned toward motorists. During test periods, they activated each sign from 6:30 PM to 10:00 PM. Average vehicle speed during the control period was 87.7 km/hour. Whereas, during the test phases, average vehicle speed was reduced to 85.34 km/hour during sign type one activation, and 83.02 km/hour when sign type two was activated.


Pojar et al. compared rates of deer crossings per deer-vehicle collision during periods when lighted, deer-crossing signs were alternately activated and deactivated on State Highway 82 in Colorado and detected no difference in ratios during the two periods. They also monitored traffic speeds pre- and post-placement of three deer carcasses on the highway with the signs alternately activated and deactivated. With carcasses in place, mean vehicle speed dropped 10.09 km/hour when the signs were activated as compared to a reduction of 12.63 km/hour when signs were deactivated. Although motorists apparently responded to the signs by reducing speeds, this awareness was not sufficient to affect the deer crossings per kill ratio.

**ALTERNATIVE MITIGATION STRATEGIES**

No “alternative strategy” has proven effective in reducing vehicle collisions with white-tailed deer. Intercept feeding for migratory mule deer proved marginally effective, however, successful adaptation of this technique to white-tailed deer in the eastern U.S. is unlikely.
Alfred Williams, a citizen motorist in Georgia, suggested a novel technique where he drives over center lane reflective markers to deter deer from entering his lane of traffic. Although Mr. Williams’ technique has not been scientifically investigated, it is an excellent example of how hope may exist for developing innovative techniques to reduce deer-vehicle collisions.

**Alternative Mitigation Strategies – Annotated Bibliography**


Graves and Bellis tested the effectiveness of placing rear-view silhouette models of deer with raised tails near highway fence openings in reducing deer crossings. Models consisted of painted or unpainted plyboard cutouts with either a painted tail or an actual deer tail taken from a road-killed deer. They monitored deer use of control and treatment (with silhouettes in use) areas by spotlighting at night from vehicles and by inspecting fence openings for deer tracks or deer hair. They deemed all models as ineffective for deterring deer that gained access to the highway right-of-way through fence openings.


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This study evaluated whether highway lighting effectively reduced deer-vehicle collisions on State Highway 82 in Colorado. Highway lighting was turned on and off for one-week periods. Deer-vehicle collisions, vehicle speeds, and deer crossing rates within the section of roadway were monitored daily. They detected no differences in the ratio of deer crossings per deer-vehicle collision, deer-crossing sites, or average vehicle speeds among periods when lights were on or off. However, during one evening when a deer simulation was placed in the emergency lane and lights were on, motorists significantly reduced their speed.

Williams, A. 2004. Email communication with E. Woodall, Georgia Department of Transportation, about driving over highway markers to deter deer from approaching the roadway.

Alfred Williams, a citizen motorist, reported that by driving over highway markers (reflectors partially implanted in the roadway surface) on the left of his driving lanes, he effectively deterred deer from entering the roadway. He further explained that when he drives over the markers deer always take flight away from the road rather than across it. On State Highway 119 between Stilson and Guyson, Georgia, Williams hit eight deer in eight years of driving before using the markers as deer deterrent devices. But, during four years while using the tactic, he did not hit any deer. Williams suggested placing two or three reflectors in a cluster offset to the right of the normal wheel contact area so motorists could choose to drive over the markers if desired when deer are present in the right-of-way.

Wood and Wolfe tested the efficacy of intercept feeding in reducing deer-vehicle collisions by diverting mule deer activity away from Utah highways. They established treatment (feed) and control (no feed) sections equal in distance and separated by unmanipulated buffer zones along three 20.8-km to 24-km sections of interstate highway. In each treatment and control zone, they selected four feeding stations ranging from 0.4-km to 1.2-km from the highway. Feed consisted of alfalfa hay, apple mash, and pelleted deer rations. In one area they replenished feed two out of three days. In a second area, they replenished feed one out of three days, and in the last area they replenished feed daily. Although the number of roadkilled deer was greater in the control sections for the first of the two experiment years, the difference was not statistically significant. During the second experiment year when the treatment and control sections were reversed, they observed significantly fewer deer-vehicle collisions in two of three test sections. Wood and Wolfe also conducted spotlight counts of deer adjacent to the test sections of roadway. They observed more deer in control zones during both years. The authors concluded that intercept feeding may reduce deer-vehicle collisions by <50% and cautioned that more subtle costs of deer feeding programs should be considered since deer may become dependent on supplemental food and be attracted to roadside areas.

**TIME AND LOCATION OF DEER-VEHICLE COLLISIONS**

Most research indicates that peaks in deer-vehicle collision rates occur late in the evening, at night, and in the early morning on a diurnal basis, and seasonally in the spring and fall. Modern analyses of deer-vehicle collision sites typically involve Global Information...
Systems (GIS) technology combined with regression modeling to identify areas likely to experience an elevated deer-vehicle collision rate. GIS modeling also is used to select areas for implementation of mitigation strategies based on landscape and economic feasibility along with many other criteria.

Time and Location of Deer-vehicle collisions – Annotated Bibliography


Allen and McCullough analyzed information from police reports on 2,566 deer-vehicle collisions occurring in 1966 and 1967 to identify the time, location, and characteristics of traffic and deer that were related to collisions. Most accidents occurred at dawn, dusk, or after dark with peaks at sunrise and 2 hours after sunset. Accidents were highest on weekends when evening traffic was greatest. A seasonal peak in collision rates occurred in November and a lesser seasonal peak occurred in May. The deer was killed in 92% of the collisions, and < 4% resulted in human injury.


Bashore et al. analyzed 19 habitat variables thought to influence numbers of deer-vehicle collisions along Pennsylvania two-lane highways. They used the information to develop a statistical model to predict probabilities of sections of highways of being high deer kill sites. They collected information on habitat characteristics at high kill sites and low kill control sites using maps and field observation. In the model, two variables (in-line visibility along the roadway and non-wooded areas) increased the probability of a section of highway being a high kill site. Seven variables (residences, commercial buildings, other buildings, shortest visibility,
speed limit, distance to woodland, and fencing) decreased this probability. Removal of the variables speed limit and other buildings did not significantly change the model. The model showed strong discrimination between high kill and low kill sections of highway. Bashore et al. suggested that fencing was the cheapest and most effective strategy for preventing deer-vehicle collisions along short sections of highway.


Along a 12.9-km stretch of Interstate 80 in central Pennsylvania, Bellis and Graves monitored the distribution of 286 deer-vehicle collisions and the sex and age of individual deer killed over a 14 month period beginning two months after the first opening of the highway to traffic. They observed no difference in the sex of fawns and yearling deer killed, however many more adult females were killed than adult males. The number of deer killed per month was strongly correlated with the number observed grazing in the planted right-of-way. Mortality was highest in fall and spring. They suggested the construction of continuous fences close to the highway to allow deer access to the right-of-way and prevent end runs.


and

The purpose of this study was to provide baseline information on deer/highway relationships and to serve as a resource for future projects aimed at reducing deer-vehicle collisions. They conducted nighttime observations of white-tailed deer by spotlighting along Interstate Highway 80 in central Pennsylvania. They observed over 6,500 deer along a 12.9-km section of highway in a forested region and along a 12.4-km section of highway in an agricultural region. They classified each deer sighted by location, age, sex, and behavior. Sex and age classification of deer was undetermined for nearly 90% of sightings. They observed most deer at night, and peaks in deer movements occurred at dawn and dusk. In the agricultural area, they observed most deer in crop fields, whereas a greater proportion of deer sightings in the forested areas were in the right-of-way. Seasonal peaks in deer sightings occurred during March-May and a larger peak during October-December. They observed no relationship between the number of deer sighted and weather variables or traffic volume.


Case analyzed seven years of data on roadkilled wildlife obtained from the Nebraska Department of Roads emergency service logs for a 732-km stretch of Interstate Highway 80 to identify trends in roadkill rates relative to month, year, average traffic speed, and average daily traffic volume. Data on nine species of wildlife were included in analyses including: ring-necked pheasant, cottontail rabbit, raccoon, skunk, opossum, white-tailed deer, coyote, badger, and muskrat. Roadkill rates peaked in May and October, likely due to breeding and dispersal activities of the wildlife species involved. Annual road-kill rates were correlated with average vehicle speed.

Craighead et al. developed Geographic Information Systems (GIS) models to determine potential sites for wildlife crossing structures on Interstate 90 in southcentral Montana. They compiled information on carnivore (black bear, mountain lion, gray wolf, raccoons, and red fox) and ungulate (elk, moose, mule deer, and white-tailed deer) movements relative to the roadway using road-kill data, track surveys, and remote-sensing cameras. That information was integrated with GIS data on species-specific habitat suitability and complexity; and road and building densities to construct least-cost path corridor models for placement of wildlife crossing structures.


Enderle and Tappe compared site-level factors of 3,170 deer-vehicle collision sites to an equal number of randomly selected locations on state and federal highways in Arkansas. They used logistic regression to develop and test a statewide model and six Arkansas ecoregion models to identify areas at high-risk for deer-vehicle collisions on those highways. Based on test data, the statewide model correctly classified 63% of known collision locations. Ecoregion models correctly classified 56-70% of known collision sites. Five factors were selected for inclusion in all models, including: (1) presence and amount of water, (2) diverse association of land cover types, (3) amount and patch density of urban area within 1,200 m, (4) coniferous forest patch...
density and deciduous forest patch size and irregularity, and (5) pasture edge density within 1,200 m.


Farrell and Tappe used a multivariate statistical approach to examine the influence of county-level factors on the number of reported deer-vehicle collisions in Arkansas counties during 1998-2001. They examined factors including human and deer population densities, urban growth, numerous roadway characteristics, daily traffic counts, timber harvests, and land composition and spatial characteristics. Roadway features (specific features not described), level of urbanization, and human population densities appeared to have greater influence of deer-vehicle accident occurrence than deer densities or landscape characteristics.


Finder et al. used remotely sensed data to determine habitat characteristics associated with areas of high incidences of deer-vehicle collisions. Around high accident road segments (≥15 accidents from 1989-1993) and randomly selected control sites, they measured topographic features and highway construction variables within a 0.8-km radius considered conducive to deer-vehicle collisions. A logistic regression model predicted that greater distance to forest cover decreased the probability of a road segment being a high deer-vehicle collision site. The presence of adjacent gullies, riparian travel corridors crossing the road, and public recreational land within the 0.8-km radius of the site increased this probability. A model using only
landscape metrics derived from satellite imagery predicted that greater landscape diversity and shorter distances between nearby forest patches increased the probability of a site being a high deer-vehicle collision site. Finder et al. suggested that remote sensing and geographic information systems may be used to implement proactive management strategies to reduce the likelihood of deer-vehicle accidents.


Grist et al. used a GIS model to identify optimum areas for wildlife crossing structures to reduce vehicle collisions involving endangered Florida Key deer. They used a global positioning system to collect location information on road-kill sites, visible wildlife trails, fences, buildings, right-of-way habitat, and areas with road grade separation ideal for installation of crossing structures. The model integrated this information with data on property ownership, landuse, and property value to select potential wildlife corridors based on cost and logistic feasibility.


Hansen et al. fitted seven adult mule deer (four male, three female) with Global Positioning System collars. They retrieved locations from three collars with 3,900-4,900 locations stored in each. They identified 817 road-crossing locations, of which 59.6% were across local residential roads and 21.9% were across collector roads.

Hubbard et al. examined the influence of landuse patterns and highway characteristics on 32,296 deer-vehicle collision sites on federally and state maintained highways within Iowa during 1990-1997. They used Geographic Information Systems to collect spatial information on 2.59-km$^2$ plots centered on 1,284 randomly selected milepost locations. Stepwise logistic regression produced a six-variable model that included four landscape variables, the number of bridges, and the number of lanes of traffic. Over 25% of deer-vehicle collision sites occurred at 3.4% of all mileposts in Iowa. Ninety-seven percent of milepost plots with greater than or equal to four bridges experienced high rates of deer-vehicle collisions ($\geq$ 14 deer-vehicle collisions). The logistic model correctly classified 63.3% of 245 sites in a validation data set. Their results suggest that mitigation efforts may be concentrated on areas with a high number of bridges.


Nielson et al. used remotely sensed data, multivariate statistics, and a geographic information system to quantify landscape factors associated with deer-vehicle accidents in two suburbs of Minneapolis, Minnesota. They classified deer-vehicle accident sites as those 0.5-km road sections with greater than or equal to two collisions involving deer and control areas where zero or one deer-vehicle collision occurred within the 0.5-km section. They initially considered 66 variables, but the most important two variables were number of public land patches and number of buildings. Using a logistic regression model containing these variables, they correctly
classified 31 of 40 areas not used for model building and only used for testing purposes. Nielson et al. suggested that managers of public lands should alter deer habitat to minimize deer-vehicle collisions by reducing forest cover and shrubby areas near public roads.


Premo and Rogers described how the suburban/urban community of Amherst, New York used an GIS approach to compile and analyze information on deer population estimates, deer-vehicle collision locations, and land use patterns. The information was used to direct lethal deer control efforts at areas of deer-vehicle collision “hotspots”, and to formulate an adaptive deer-vehicle accident management plan. The multi-faceted management plan included modification of driver behavior, redirection of deer movements, and periodic deer population control.


Reilly and Green reported the trend in deer-vehicle accidents near a wintering area for white-tailed deer in upper Michigan over a 13-year period pre- and post-construction of Interstate 75 through the area in 1963. Post-construction of the interstate in 1964, highway deer kills increased by about 500% over the average kill rate of the previous four years. The highway mortality rate decreased slightly through 1967 and then fluctuated an average of twice the pre-construction yearly mortality estimate. Reilly and Green also reported that deer discontinued winter yarding on the side of the highway opposite their migration route, perhaps because the
highway presented a barrier or animals that yarded in that area pre-construction of the highway were killed attempting crossings.

**HUMAN DIMENSIONS ASSOCIATED WITH DEER-VEHICLE COLLISIONS**

The general public greatly values deer as a public resource. Surveys show, however, that public opinion about deer management and deer-vehicle collision mitigation is affected significantly by human perception of personal risk and cost of implementation. Human dimensions researchers suggest 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.

**Human Dimensions Associated with Deer-vehicle Collisions – Annotated Bibliography**


Conover used information from scientific literature to calculate a net value for deer in the U.S. at >$12 billion. This figure resulted from subtracting >$2 billion in negative monetary values ($1 billion in car damages + >$100 million in crop damages + $750 million in damage to the timber industry + >$250 million in damage to metropolitan households) from the >$14 billion in recreational value (expenses by recreationists + consumer surplus). Conover excluded from this analysis the “value” of human life and suffering resulting from deer-vehicle accidents and Lyme disease and the intangible values of deer. Conover hypothesized that as deer populations increase, the negative monetary values of deer will increase at a faster rate than the deer population. Further, as deer populations approach biological carrying capacity, Conover predicted that the number of deer-vehicle collisions would increase exponentially because deer
would be forced to increase their home ranges and movements in search of forage. Conover concluded that the goal of deer management should be to keep deer populations at the point where the net positive benefit of deer is highest.


Drake et al. conducted a telephone survey of 500 randomly chosen adults from New Jersey to assess suburban residents’ attitudes and opinions of, and experiences with deer and deer management; and to quantify impacts from deer in suburban areas. Despite 95% of respondents expressing a positive attitude toward deer, 50% perceived that there were too many deer in New Jersey. Seventy-eight percent of respondents had a negative experience with deer (e.g. collision, landscape damage) with damage cost estimates ranging from $50 to over $4,000. Although 57% of respondents felt that deer control measures were necessary, 60% were unaware of current deer management options. Drake et al. concluded that public education of deer management should be heightened.


Hansen determined the average cost of deer-vehicle accidents in Michigan during 1978 based on the responses of 234 completed mail questionnaires sent to a systematic sample of Michigan drivers that had been involved in deer-vehicle accidents reported to Michigan State Police. In 1978, the average cost of a deer-vehicle accident in Michigan was $648 for property damage, injury, and loss of life with an average damage to vehicle cost of $569 including repair, substitute automobile costs, and towing.

Johnson interviewed 20 experts in the fields of transportation, planning, engineering, environmental services, project development, civil engineering, wildlife biology and management, and citizen transportation groups to compile criteria for evaluating mitigation measures for reducing wildlife-vehicle collisions in Teton County, Wyoming.  Of 10 broad categories of criteria, the six most frequently mentioned in order of most mentioned to least mentioned included: economic possibility (e.g. cost, cost-benefit), technical feasibility (e.g. engineering constraints, land ownership constraints), political viability (e.g. compliance with laws, publicly acceptable), measurable results (e.g. technique must allow evaluation, new techniques should be tested), effectiveness (ultimate goal is to reduce accidents), and ungulate biology (e.g. strategy must not compromise integrity of habitat, must allow ungulates freedom of movement).


Stout hypothesized that public preference for deer population levels are influenced in part by perceptions of risk from deer-vehicle accidents.  They sent a self-administered mail-back questionnaire to a systematically selected sample of 650 people drawn from a Tomkins County, New York telephone directory.  They developed survey questions to study an individual’s
perception of risk from two viewpoints: (1) a personal assessment of his or her chance of being in a deer-vehicle collision; and (2) a societal assessment of the severity, probability, and acceptability of deer-vehicle collisions in general. Of 397 useable responses, 91% of respondents claimed to enjoy deer to some extent, and 15% hunted deer. Most (88%) were aware of deer-vehicle accidents in the county usually through personal observation of an accident event, 28% had been involved in a deer-vehicle accident, and the most frequent deer-related concerns (83%) involved deer-vehicle collisions. Despite their awareness of deer-vehicle collisions, about half (49%) of respondents preferred to maintain deer population levels at current levels, 37% wanted a decrease, and 14% wanted an increase. Stout et al. suggested that wildlife professionals should combine public risk-assessment data with biological data to make decisions about alternative management strategies.


Schwabe and Schuhmann surveyed the literature related to the cost of deer-vehicle collisions. They reported a value range of $23 million to nearly $1 billion, depending on the calculation method used, for the deer-fatality component of deer-vehicle collisions in the U.S. In literature related to deer-vehicle collisions, estimates of single deer values range from $671 to $1,468, whereas values estimated using nonmarket valuation techniques range from $35 to $209. They concluded that the proper measure to use when estimating loss to hunters from deer mortalities related to collisions is the consumer surplus or net Willingness to Pay estimate.

West et al. surveyed 732 Virginia landowners in 1996 to determine the occurrence and severity of deer-vehicle collisions and to evaluate what impact they have on the attitudes of Virginia motorists. Overall, 9.2% of respondents reported hitting a deer in 1995, and of those, 79.1% were involved in only one deer-vehicle collision. Only 3.1% of respondents involved in a deer-vehicle collision reported that they or one of their passengers was injured, and 68.8% did not report the incident(s) to law enforcement. The average cost of vehicle repairs resulting from a single collision was $1,386 with a range of $100 to $4,700. Nearly 53% of all respondents rated the risk level of experiencing a deer-vehicle collision in their county as moderate.

DEER HEARING

Information on white-tailed deer hearing abilities and their response to sound frightening devices is limited. Previous research on deer hearing was preliminary in nature, and investigations of the efficacy of sound deterrents were of poor experimental design. Studies have indicated that deer likely have hearing abilities similar to humans, thus suggesting that current sound deterrent devices are probably not within the hearing thresholds of deer and have no promise of being effective.

and


Belant et al. tested three ultrasonic devices; the motion-activated Yard Guard, the motion-activated Usonic Sentry, and Electronic Guard; in attempts to develop a technique for reducing deer depredation of agricultural crops, winter livestock food supplies, and ornamental plantings. The Yard Guard was evaluated at the medium frequency setting (20 to 28 kHz, 114 dB at 1 m), which was emitted for about 7 seconds at a time. The Usonic Sentry was evaluated at 23 to 35 kHz with sound pressure of 160 dB at 1 m, and sound was emitted for 8 to 28 seconds when activated. Electronic Guards were equipped with a white strobe light (70,000 candlepower, flash rate = 60/minute) and a 1.4 kHz modulating (15 to 20 modulations/minute) siren with 116 dB output at 1 m. Electronic Guards also had a photocell, which allowed operation only during night. During two 4-week experiments, they monitored deer use (number of intrusions into plot and corn consumption) at eight feeding stations in a 2,200 ha fenced facility with a high deer density (≥38 deer/km²). During experiments, one of the devices was positioned at each of four sites. The mean daily number of deer intrusions at feeding stations during treatment was greater than or equal to the mean daily number of deer intrusions during pre- or post-treatment. Corn
consumption declined only at stations with Usonic Sentries for one week. They concluded that the devices were ineffective at deterring deer from preferred feeding stations.


Bender conducted laboratory and field evaluations of the ROO-Guard, an ultrasonic device manufactured by the Shu-Roo company and designed to protect agricultural areas from kangaroo depredation. Bender’s laboratory trials indicated that the ROO-Guard had only a small component of ultrasonic frequencies. The device did not alter the behavior of captive eastern gray kangaroos or red kangaroos in any way. Bender found that the ROO-Guard did not reduce the density of free-ranging eastern gray kangaroos at sites where the device was operating as compared to control sites, and she observed no change in kangaroo density with distance from the device.


Bomford and O’Brien reviewed literature related to the mechanisms by which sonic devices may affect animals, and evaluations of sonic devices. They concluded that although numerous devices had been developed and assessed, many reported tests were inconclusive. They recommended that future tests would be improved by: adequate experimental control and replication, avoidance of pseudoreplication (occurs when treatments are not replicated or replicates are not statistically independent), appropriate measures of device effect, and quantitative description of the sound produced.

Flydal and Enger determined audiograms for two yearling male reindeer using conditioned suppression/avoidance procedure. Trials were started as the animal drank from a metal bowl of water while pure tone signals were played at random intervals and followed by an electric shock in the bowl. By breaking contact with the bowl at sound signals, the animal avoided the shock and indicated that it heard the sound. They found that the reindeer detected sounds at intensities of 60 dB or less from 70 Hz to 38 kHz. The frequency range of best sensitivity was relatively flat from 1 kHz to 16 kHz, with best sensitivity of 3 dB at 8 kHz.


Gilsdorf et al. developed a bio-acoustic frightening device to reduce deer damage to agricultural crops. The device included an infrared detection system used to detect the presence of deer entering the edge of a cornfield, which then activated an audio alarm system designed to broadcast deer distress calls. They recorded the distress calls while handling deer live-captured in netted cage traps within the study area at the DeSoto National Wildlife Refuge, Nebraska. They placed two frightening devices on the perimeter of each experimental field adjacent to wooded areas where the highest crop damage was expected to occur. They conducted trials starting at the onset of the silk-tasseling stage of corn growth and until corn maturity. They used indices of track counts, corn yields, crop damage assessments, and use-areas of radiomarked deer to evaluate the efficacy of the devices in experimental fields versus in control fields. They
concluded that the bio-acoustic device, which cost about $600 per unit, was not effective in protecting corn fields.


Gilsdorf evaluated the effectiveness of propane exploders and Electronic Guards for reducing deer damage in corn fields during the silk-tasseling stage of corn growth at the DeSoto National Wildlife Refuge (DNWR) and Loess Hills State Forest (LHSF), Nebraska. Gilsdorf et al. connected propane exploders to a bottle of propane and set the units to discharge at 15 minute intervals throughout the night at a sound level of 130 dB (as measured at 75 m). Electronic Guards consisted of a photo cell (to activate the device at sunset and to shut it off at sunrise), timer, flashing white strobe light (70,000 candlepower, flash rate = 60/minute) and a 1.4-kHz modulating siren (15-20 modulations/minute, 116-dB output at 1 m). They set the Electronic Guard to randomly activate sound for 7-10 seconds at 6-7 minute intervals throughout the night. They selected four groups of three test fields each on DNWF and LHSF. Each field was about 9 ha and was greater than or equal to 1 km from the other fields used in the experiment. They randomly assigned treatment (experimental = either two propane exploders or two Electronic Guards/field, control = no devices in the field). They used indices of track counts, corn yields, crop damage assessments, and use-areas of radiomarked deer to evaluate the efficacy of the devices in experimental fields versus in control fields. They concluded that neither propane exploders nor Electronic Guards were effective in reducing deer damage to corn fields.

Krausman et al. evaluated whether routine military activities (airplane noise, noise from ordinance delivery, and ground-based activity) on the Barry M. Goldwater Range, Arizona affected the behavior of the endangered Sonoran pronghorn. They compared behavior and activity of Sonoran pronghorn to other pronghorn in an adjacent population, which were not regularly exposed to military activity. They contrasted the hearing of pronghorns not in the Sonoran population and that were not exposed to regular military activity (they could not test Sonoran pronghorn because of their endangered status) to two different groups of desert mule deer that were and were not exposed to sound pressure levels from military activity by testing hearing thresholds using auditory brainstem responses (ABR). ABRs are electrical potentials generated by the brainstem when the ear is stimulated by sound. Krausman et al. recorded mean thresholds at intensity levels up to 90 dB and obtained responses from 0.5 kHz to 8 kHz for the pronghorn and mule deer, and found no difference in the ABR thresholds between the control and exposed animals. They concluded that military activity had no apparent effect on pronghorn auditory characteristics and only a marginal influence on their behavior.


Hearing range in white-tailed deer. Abstract for The Wildlife Society Texas Chapter Meeting.

Risenhoover et al. determined audiogram hearing thresholds for five sedated white-tailed deer by recording brainstem evoked potentials in response to stimuli consisting of 45-millisecond pure-tone pips delivered using headphones held against the ears. They recorded evoked potentials at
intensity levels up to 85 dB in a frequency range of 0.5 to 16 kHz. At intensity levels of 95 dB a response was obtained up to 16 kHz. The range of greatest hearing sensitivity was between 1-8 kHz with a marked peak at 4 kHz.


Romin and Dalton tested two models of deer warning whistles, Game Tracker’s Game Saver and the Sav-a-life Deer Alert. They separately tested each device on free-ranging mule deer along a dirt road at a wildlife management area in Carbon County, Utah, on which 0.28 deer-vehicle collisions/km occurred annually. Testing was done in two passes with the research vehicle traveling at 65 km/hour. In the first pass, they recorded distance of deer from the road and deer reaction to the passing vehicle without activating the whistles. Immediately following, they traveled greater than or equal to 0.8 km past the deer group, activated the whistles, turned the vehicle around and passed the group again to record their distance and reaction. In observations of 150 deer groups that were within 100 m of the road, they recorded 152 responses and detected no difference between responses with or without either type of whistle.


Scheifele et al. recorded the frequencies and intensities generated by six deer whistles (no make or model specified, the authors only distinguished the devices by referring to “closed end” and “open end” designs, but did not describe these classifications). They made laboratory recordings with a digital audio tape recorder while forcing air directly into the mouth of each whistle until a strong sound was emitted. In road tests, they mounted “the two loudest whistle pairs” on the
bumpers of two separate vehicles. They recorded ambient noise levels and sounds from the
vehicles mounted with whistles during 10 duplicate runs at speeds of 48 km/hour, 56 km/hour,
64 km/hour, and 88 km/hour. Scheifele determined the primary frequency of operation for the
“closed-end” whistles to be 3.3 kHz, and 12 kHz for the “open-end” whistles. Scheifele used
information provided by Risenhoover et al. (Texas A&M University) to compare white-tailed
deer hearing thresholds to the effective sound emission of the deer whistles tested. However,
they failed to make any definitive evaluation of the effectiveness of the whistles.

Weisenberger, M. E., P. R. Krausman, M. C. Wallace, D. W. De Young, and O. E.

Maughan. 1996. Effects of simulated jet aircraft noise on heart rate and behavior

Weisenberger et al. implanted heart rate transmitters in captive desert mule deer and mountain
sheep to evaluate the effects of simulated low-altitude jet aircraft noise on their behavior and
heart rate. They conducted simulated overflights one to seven times per day at noise levels
between 92-112 dB during three seasons. The heart rates of the desert mule deer and mountain
sheep increased related to dB levels, but returned to pre-simulation levels within 60-180 seconds.
They also observed changes in animal behavior that lasted <252 seconds after simulated
overflight. All animal responses decreased with increased exposure suggesting that they
habituated to simulated sound levels of low-altitude aircraft.

DEER VISION

Electrophysical examination and behavioral research has established that white-tailed
deer are capable of limited color vision. During the day, deer likely can discriminate in the color
range of blue to yellow-green, and at night in the blue to blue-green color range. Little else is
known about how white-tailed deer perceive the world. Information on their visual acuity and depth perception are lacking.

Deer Vision – Annotated Bibliography


Jacobs et al. used electroretinogram flicker photometry to study the spectral mechanisms in the retinas of white-tailed deer and fallow deer. 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 cone sensitivity was about 537 nm (yellow-green), and the fallow deer peak 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.


VerCauteren and Pipas reviewed and summarized literature related to white-tailed deer color vision and arrived at the following conclusions. White-tailed deer possess two types of cone mechanisms with sensitivity in the short (450-460-nm range) and medium wavelengths (maximum sensitivity of about 497 nm). During the day, it is likely that deer see colors in the range that humans would define as blue to yellow-green, and they may be able to discern longer
wavelengths (red and orange) from medium wavelengths (green). At night deer perceive color in the human-defined blue to blue-green portion of the spectrum.


Witzel et al. established that white-tailed deer retinas are composed of rods and cones. They used histology, light microscopy, and electron microscopy on eyes taken from dead deer; and electrophysical examinations of the eyes of sedated deer to identify the presence of both rods and cones. Previous belief was that deer retinas were composed entirely of rods.

**CONCLUSION AND RECOMMENDATIONS**

Although many aspects of deer biology have been well studied, we lack a basic understanding of the anatomy and physiology related to the hearing and visual capabilities of deer, information which may prove integral to the invention of economically effective strategies to minimize deer-vehicle collisions. Further, our knowledge of deer behavior relative to roads is inadequate. Limiting our evaluations of deer-vehicle collision mitigation devices to comparisons of deer road-kill statistics, for example, tells little about the complex interaction of deer and motorist behavioral traits that leads to collisions. When conducting future tests, we should make detailed observations of deer behavior relative to the implementation of mitigation techniques and, when possible, also document motorist awareness and response to the strategies. Such data may be used to improve strategies during the design and planning stages rather than as a basis for critique after mitigation strategies are widely instituted or enter the manufacturing process.

At present, fences of the appropriate height may be the most effective method to exclude deer from roads. However, transportation and wildlife managers have an ethical responsibility
to consider the potential ecological impacts of fencing on animal populations. Traditional fence designs may severely limit gene flow among populations separated by fenced roads. Fencing also may restrict wildlife access to resources critical to their survival. Crossing structures within fenced roadway corridors may provide partial habitat connectivity for some wildlife species, and have proven most successful when used where traditional migratory routes of mule deer, elk, and other migratory species intersect highways. However, white-tailed deer generally do not make mass seasonal migrations, and are more likely to cross roads within their home ranges on a daily basis. Over a single kilometer, a roadway may be intersected many times by the home ranges of different white-tailed deer in an area. A stark example of the crossing rate of white-tailed deer was reported in a study of deer mortality on a new Pennsylvania highway where Bellis and Graves (1971) documented an average of more than 22 road-killed deer/km over a 14-month period. Previous reports rated wildlife crossing structures as cost prohibitive for most applications. Considering the road-crossing behavior of white-tailed deer and the cost of wildlife crossing structure installation, reliance on fencing to prevent deer-vehicle accidents likely is not a feasible option.

Currently there is no simple, low-cost solution for reducing the incidence of deer-vehicle collisions. Like fencing, other devices, including wildlife warning reflectors and motorist warning systems, are used where deer regularly cross roads. Only instituting collision reduction techniques at select areas or “hotspots” will not guard against non-habitual deer road crossings, which typically occur during the peak seasons for deer-vehicle collisions (breeding and fawning). To guard against these collisions and to provide the most effective system for minimizing deer-vehicle collisions, we have three general conclusions and recommendations:
(1) Vehicle-mounted deer warning systems may have the best potential for minimizing deer-vehicle collisions; however, to date none of these systems has been designed in accordance with the senses of deer. Therefore, future research and development of vehicle-mounted deer warning systems must be based on detailed knowledge of deer vision, hearing, and behavior.

(2) Every year, motorist awareness of the danger of deer-vehicle collisions can decline over time. Therefore, agencies should develop and routinely implement education programs and/or highway warnings to enhance motorist awareness prior to and during the seasons of greatest danger for deer-vehicle collisions (breeding and fawning).

(3) Deer overabundance can increase the potential for deer-vehicle collisions. Therefore, agencies and municipalities should implement proper deer herd management programs designed to control deer abundance.
DEVELOPMENT AND EVALUATION OF DEVICES DESIGNED TO MINIMIZE
DEER-VEHICLE COLLISIONS

by

GINO JUDE D’ANGELO

(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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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/mm² 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/mm². 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 of 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.

LITERATURE CITED


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Walls, G.L. 1942. The vertebrate eye and its adaptive radiation. Cranbrook Institute of Science, Bloomfield Hills, Michigan, USA.


CHAPTER 2

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


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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 $\geq 38.1$ 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 $\geq 90°$ 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 ($\chi^2 = 25.99, P \leq 0.001$). 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 ($\chi^2 = 42.65, P \leq 0.001$).

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 ($t = -5.77, df = 341, P \leq 0.001$). 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; $\chi^2 = 14.37, P = 0.006$). 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; $\chi^2 = 52.69, P \leq 0.001$).

*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%, $n = 24$, $\chi^2$
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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**LITERATURE CITED**


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Associate editor: Jacob Bowman
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.
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.
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.
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<tr>
<td>+1</td>
<td>Active parallel to road</td>
<td>Active away from road</td>
</tr>
<tr>
<td>+2</td>
<td>Active toward road</td>
<td>Active away from road</td>
</tr>
<tr>
<td>+2</td>
<td>Within road</td>
<td>Passive</td>
</tr>
<tr>
<td>+2</td>
<td>Within road</td>
<td>Active away from road</td>
</tr>
<tr>
<td>+2</td>
<td>Within road</td>
<td>Active parallel to road</td>
</tr>
<tr>
<td>+2</td>
<td>Within road</td>
<td>Active toward road</td>
</tr>
</tbody>
</table>
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.
<table>
<thead>
<tr>
<th>Test area</th>
<th>Experimental phase</th>
<th>n</th>
<th>−2</th>
<th>−1</th>
<th>0</th>
<th>+1</th>
<th>+2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main campus</td>
<td>Pretreatment</td>
<td>161</td>
<td>3.73</td>
<td>2.48</td>
<td>70.81</td>
<td>18.01</td>
<td>4.97</td>
</tr>
<tr>
<td>Red reflectors</td>
<td></td>
<td>182</td>
<td>6.04*</td>
<td>7.14*</td>
<td>69.78</td>
<td>16.48*</td>
<td>0.55*</td>
</tr>
<tr>
<td>White reflectors</td>
<td></td>
<td>295</td>
<td>7.12*</td>
<td>10.50*</td>
<td>51.10*</td>
<td>21.02*</td>
<td>10.20*</td>
</tr>
<tr>
<td>Mountain campus</td>
<td>Pretreatment</td>
<td>307</td>
<td>2.61</td>
<td>3.58</td>
<td>72.96</td>
<td>16.94</td>
<td>3.91</td>
</tr>
<tr>
<td>Blue-green reflectors</td>
<td></td>
<td>226</td>
<td>3.09**</td>
<td>6.63**</td>
<td>80.00**</td>
<td>8.85**</td>
<td>1.33**</td>
</tr>
<tr>
<td>Amber reflectors</td>
<td></td>
<td>199</td>
<td>9.04*</td>
<td>7.54*</td>
<td>54.77*</td>
<td>20.10*</td>
<td>8.54*</td>
</tr>
</tbody>
</table>

* $P \leq 0.001$ 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.
<table>
<thead>
<tr>
<th>Test area</th>
<th>Experimental phase</th>
<th>$n$</th>
<th>Period 1</th>
<th>Perpendicular distance moved</th>
<th>Total distance moved</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main campus</td>
<td>Pretreatment</td>
<td>161</td>
<td>10.4 (7.8)</td>
<td>8.9 (7.1)</td>
<td>4.8 (4.2)</td>
</tr>
<tr>
<td>Red reflectors</td>
<td></td>
<td>182</td>
<td>15.5 (8.6)*</td>
<td>5.9 (4.4)</td>
<td>6.0 (3.8)</td>
</tr>
<tr>
<td>White reflectors</td>
<td></td>
<td>295</td>
<td>12.1 (8.0)**</td>
<td>4.2 (3.7)**</td>
<td>4.8 (3.4)</td>
</tr>
<tr>
<td>Mountain campus</td>
<td>Pretreatment</td>
<td>307</td>
<td>13.6 (7.9)</td>
<td>4.7 (3.7)</td>
<td>6.4 (5.0)</td>
</tr>
<tr>
<td>Blue-green reflectors</td>
<td></td>
<td>226</td>
<td>12.9 (7.8)</td>
<td>4.4 (3.0)</td>
<td>3.6 (2.4)*</td>
</tr>
<tr>
<td>Amber reflectors</td>
<td></td>
<td>199</td>
<td>11.9 (8.2)**</td>
<td>3.3 (2.9)**</td>
<td>3.6 (1.9)*</td>
</tr>
</tbody>
</table>

* $P \leq 0.001$ 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 1 and 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 DEER²

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/mm² 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-mm² 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-mm² sampling windows using a fluorescent light microscope (Nikon, Melville, USA) and a CCD camera.
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/mm² for each retina labeled in immunohistochemical experiments was calculated and the photoreceptor density/mm² 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
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/mm². 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.

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. We acknowledge the technical support of J.G. D’Angelo, J.L. D’Angelo, J.M. D’Angelo, J.S. Falzone, A.E. Faulkner, S. Geva, and M.K. Kim. We thank G.H. Jacobs for his advice and use of laboratory facilities. J.C. Carroll, B.C. Faircloth, and R.N. Winn provided laboratory equipment. J. Nathans provided JH455 and JH492 antisera. S.B. Castleberry, A.R. De Chicchis, and M.T. Mengak provided helpful comments on this manuscript.

REFERENCES


white-tailed deer (*Odocoileus virginianus*) and fallow deer (*Dama dama*). Journal of Comparative Physiology A 174:551-557.


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.
<table>
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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.
**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.
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.
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.
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 16414/mm² (range = 4717, \(n = 3\)) ranging from an average minimum of 7322/mm² (range = 500, \(n = 3\)) to an average maximum of 35 700/mm² (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.
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/mm² (range = 317, *n* = 2) ranging from an average minimum of 442/mm² (range = 50, *n* = 2) to an average maximum of 4883/mm² (range = 1433, *n* = 2).

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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 subdermal 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.

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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.
LITERATURE CITED


Occupational Safety and Health Administration. 2006. OSHA Technical Manual TED 01-00-015. United States Department of Labor, Washington, DC, USA.


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.
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).
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.
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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.
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<td>30</td>
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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

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/mm². 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/mm². 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).

**LITERATURE CITED**


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.
White target

Test grating (spatial frequency)

Percent correct of 30 trials
EVALUATION OF SOUND AS A DETERRENT FOR REDUCING
DEER-VEHICLE COLLISIONS

by

SHARON ANN VALITZSKI

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

ABSTRACT

I evaluated the efficacy of sound as a deterrent for reducing deer-vehicle collisions by observing the behavioral response of captive and free-ranging white-tailed deer (*Odocoileus virginianus*) to a range of sound frequencies within their hearing range. Captive deer exhibited no behavioral response when exposed to any of 5 different pure-tone sound treatments. I then evaluated the effects of a moving automobile fitted with a sound-producing device and speakers on roadway behavior of free-ranging deer. My results indicated that deer within 10 m of roadways did not alter their behavior in response to any of the 5 pure-tone sound treatments tested in a manner that would prevent deer-vehicle collisions. Many commercially available wildlife-warning whistles (deer whistles) are purported to emit similar consistent, continuous pure-tone sounds; however, my data suggest that deer-whistles are likely not effective in altering deer behavior along roadways to help prevent deer-vehicle collisions.

INDEX WORDS: Auditory deterrent, Deer-vehicle collisions, Deer-whistle, Hearing, *Odocoileus virginianus*, Sound, White-tailed deer, Wildlife-warning whistle
EVALUATION OF SOUND AS A DETERRENT FOR REDUCING

DEER-VEHICLE COLLISIONS

by

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Maureen Grasso
Dean of the Graduate School
The University of Georgia
August 2007
DEDICATED TO MOLLY, ELSIE, RALLY, AND ELVIRA.

Though you were lost before this was finished, you made it fun while you were here. You will never be forgotten.

“The best fertilizer is the foot steps of the landowner.”

“Find a job you love and you will never have to work a day in your life.”

~Confucius
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I am thankful to have had the opportunity to work under Drs. Karl V. Miller and Robert J. Warren. Their endless wisdom and confidence in my abilities made me return to school and kept me working hard. I thank Dr. George R. Gallagher for supporting me during my field season at Berry College. I also thank Drs. Steven B. Castleberry and W. Dale Greene for editorial advice.

Special thanks to Gino J. D’Angelo, who provided technical support, editorial advice, encouragement, and friendship. In other words, he answered my endless questions! Thanks to David A. Osborn, who helped with the captive trials and ate lots of lunches with me. Joseph G. D’Angelo provided technical support in the construction of the sound-emitting equipment and spent late nights setting up the field trials. I’d like to thank all of the students at Berry College who gave their time for the success of this project.

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INTRODUCTION

Deer (*Odocoileus* spp.)-vehicle collisions are an increasingly important concern for the public and agencies charged with managing wildlife populations or highway safety. Increasing deer populations, coupled with expanding transportation systems, have led to a rise in the number of deer-vehicle collisions (Romin and Bissonette 1996). Annually, there are approximately 1.5 million deer-vehicle collisions at a cost of nearly $1 billion in damages (Sullivan and Messmer 2003). On average, 51,000 collisions are reported each year within the state of Georgia (J. Beardon, Georgia Department of Natural Resources Wildlife Resources Division, personal communication).

Despite public demand for more effective measures to keep deer off of roadways, few states have conducted scientific research on mitigation techniques before deployment (Romin and Bissonette 1996). Deer whistles are perhaps the most widely marketed and utilized mitigation technique available. Manufacturers of deer whistles state that the devices produce ultrasonic frequencies that should deter deer from roads by warning them of an approaching vehicle (Hornet Deer Whistle 2002, Deer Alert 2007, Save-A-Deer Whistle 2007). The manufacturers also claim that deer whistles emit consistent, continuous sounds when activated. Pure tones are defined as continuous sounds of equal intensity at a single frequency (Martin 1994), which can be produced using standard commercially available equipment. Scheifele et al.
(2003) tested the actual frequencies emitted from deer whistles, and found they produced pure tone sounds. Based on this study and other similarities between sounds elicited by deer whistles and pure tones, the objective of this research was to evaluate the efficacy of pure-tone sounds throughout the full range of deer hearing for altering the behavior of free-ranging deer along roadways.

LITERATURE REVIEW

There has been little scientific research conducted on the perception and behavioral response of white-tailed deer (O. virginianus) to sound. As a preliminary step towards developing an understanding of hearing abilities of deer, auditory brainstem response tests were conducted on captive deer at the University of Georgia’s Whitehall Captive Deer Research Facility (D’Angelo et al. 2007). By recording the neurological responses of 13 sedated white-tailed deer to a range of sound frequencies at varying intensities, D’Angelo et al. (2007) determined that the range of white-tailed deer hearing included frequencies of sound from 0.25 kHz-30 kHz, with best hearing sensitivity from 4 kHz to 8 kHz. The upper limit of human hearing is approximately 20 kHz (Durrant and Lovrinic 1995), and any sound greater than this is considered ultrasonic. As deer could hear >20 kHz, these results suggest that ultrasonic sounds have potential for use as auditory deterrents for prevention of deer-vehicle collisions.

Measurements of the actual frequencies emitted from a selection of commercially sold deer-whistles showed that those whistles tested did not produce the ultrasonic sounds claimed by the manufacturer (Scheifele et al. 2003). Closed-end deer-whistles produced sound at 3.3 kHz, while open-end whistles produced sound at 12 kHz. Schildwachter et al. (1989) reported that deer-whistles did not emit recordable sounds at manufacturer-recommended vehicle speeds (<89 km/h), but when hand-blown, produced sound at 18-20 kHz accompanied by an audible whistle.
(2 kHz). They also reported no behavioral responses of deer exposed to traveling vehicles equipped with whistles.

Bender (2003) found that the ROO-Guard, a sound device designed to deter kangaroos (*Macropus rufus*) by masking their ability to hear their natural predators, did not alter behavior of captive kangaroos and there was no reduction in free-ranging kangaroo density compared to control sites where the device was not used. She also found that the ROO-Guard sound comprised only a small component of ultrasonic frequencies and concluded that the ROO-Guard would be ineffective at reducing kangaroo damage to crops or deterring them from roadsides.

Information is limited regarding ungulate responses to auditory deterrents in actual roadway conditions. Romin and Dalton (1992) noted no differences in behavioral responses of 150 groups of mule deer (*O. hemionus*) exposed to either of two brands of deer whistles (brand not specified). They indicated that auditory deterrents may be ineffective at reducing deer-vehicle collisions and outlined the need for more research on the effects of sounds on behavior of ungulates along roadways.

The behavioral response of target animals to an auditory deterrent may depend on the type of sound emitted. Pure tones are single frequency, continuous sounds at equal intensity (Martin 1994). Complex sounds resemble sounds occurring in nature (i.e., deer vocalizations) and are composed of two or more pure tones of different frequencies that are generated simultaneously and repeated over time. Complex sounds are rapid-change stimuli, with fast neurological onset caused by simultaneous firing of the auditory nerve fibers (Hall 1992, Jacobson 1994).

In contrast to complex sounds, pure tones are considered prolonged-onset stimuli which produce a slower neurological response that lasts for the duration of the sound stimuli.
Therefore, if the purpose of sound is to produce a rapidly changing behavioral response, complex sounds may be more applicable than pure tones for management of wildlife damage. However, direct testing of complex sounds on deer feeding behavior has shown that these auditory deterrents either have no effect on deer behavior, do not produce the desired responses by deer, or the effectiveness of the devices diminishes after a short time interval of exposure. For example, sound devices such as propane exploders have proven ineffective at reducing deer damage to corn fields (Gilsdorf et al. 2004a). Bioacoustic frightening devices, which used distress and alarm calls from live-captured deer, were also shown to be ineffective, as track-count indices and use-areas of radio-collared deer did not differ among control plots and plots where the frightening device was active (Gilsdorf et al. 2004b). VerCauteren et al. (2005) found that elk (Cervus elaphus) and mule deer did not change their feeding behavior when the Critter Gitter™ acoustic frightening device was in place. The Critter Gitter device was designed to protect gardens and landscaping from wildlife damage by producing beeps that vary in pattern when the device is activated by the detection of an animal with passive-infrared sensors. Likewise, Belant et al. (1998) tested motion-activated acoustic frightening devices, which also emit sound only when activated by the deer, and found that although these sound devices had an initial effect, deer quickly habituated to the sound and continued using corn fields at levels comparable to before the sound devices were put into use. When testing the effectiveness of the Yard-Guard, a regular-interval acoustic frightening device, Curtis et al. (1995) found no significant difference in apple consumption among test areas. Similarly, Ujvari et al. (2004) found that fallow deer (Dama dama) visiting a feeding station exhibited increasing indifference over time to pre-recorded sounds produced by acoustic road markings and concluded that the deer habituated to the acoustic stimulus.
The results of previous research suggest that auditory deterrents may be an unreliable method for altering deer behavior such that deer-vehicle collisions may be prevented. These studies looked primarily at commercially available devices. We investigated behavioral responses of deer to sounds within their known hearing range in a controlled field application. As sound stimuli must be neurologically significant to the animal to produce a behavioral response (Jacobson 1994), Belant et al. (1998) suggested that the lack of negative reinforcement associated with auditory deterrents prevents frightening devices from being effective deterrents for white-tailed deer. Thus, testing pure tones sounds to investigate the efficacy of sound deterrents is necessary to gauge if there is potential for these devices to reduce deer-human conflicts.

**OBJECTIVES**

1. Determine the behavioral responses of captive white-tailed deer to a range of sound frequencies within their hearing range.
2. Evaluate the effect of sounds on altering behavior of free-ranging deer along roadways.

**Thesis Format**

This thesis is written in manuscript format. Chapter 1 presents a literature review and background for this study. Chapter 2 is a manuscript that will be submitted to Journal of Wildlife Management describing my experiments evaluating the behavioral responses of white-tailed deer to a vehicle-mounted sound-production system. Chapter 3 summarizes and concludes the findings of my thesis research.

**LITERATURE CITED**

Pest Conference 18:107-110.


CHAPTER 2

BEHAVIORAL RESPONSES OF WHITE-TAILED DEER TO A VEHICLE-MOUNTED SOUND PRODUCTION SYSTEM

ABSTRACT

We evaluated the efficacy of sound as a deterrent for reducing deer (*Odocoileus* spp.)-vehicle collisions by observing the behavioral responses of captive and free-ranging white-tailed deer (*O. virginianus*) to pure-tone sounds within their documented range of hearing. For captive adult deer, frequency and response were considered independent, as their behavior did not change when exposed to any of the 5 pure-tone sound treatments. We then monitored roadway behavior of free-ranging deer in response to a moving automobile fitted with a sound-producing device and speakers that produced the same 5 sound treatments. Our results indicated that deer within 10 m of roadways did not alter their behavior in response to pure-tone sound treatments emitted from a moving automobile. Many commercially available, vehicle-mounted auditory deterrents (i.e., deer whistles) are purported to emit similar consistent, continuous pure-tone sounds; however, our data suggest that deer whistles are likely not effective in altering deer behavior and are unlikely to prevent deer-vehicle collisions.

**Key words:** Auditory deterrent, Deer-vehicle collision, Deer-whistle, Hearing, *Odocoileus virginianus*, Sound, White-tailed deer, Wildlife-warning whistle

INTRODUCTION

Deer (*Odocoileus* spp.)-vehicle collisions are an important highway safety issue throughout much of North America. Increasing deer populations, coupled with expanding transportation systems and vehicular volumes, have led to a rise in the number of deer-vehicle collisions (Romin and Bissonette 1996). Annually, there are approximately 1.5 million deer-vehicle collisions resulting in nearly $1 billion in damages (Sullivan and Messmer 2003). Most
states in the U.S. employ mitigation techniques for reducing deer-vehicle collisions. However controlled scientific evaluations of these techniques generally are lacking (Romin and Bissonnette 1996).

Vehicle-mounted auditory deterrents (i.e., deer whistles) are a widely accepted and commercially available device for prevention of deer-vehicle collisions. Deer whistles are purported to produce ultrasonic frequencies that deter deer from roads by warning them of an approaching vehicle (Hornet Deer Whistle 2002, Deer Alert 2007). These devices are advocated as humane, inexpensive, easy-to-use, and scientifically sound (Bomford and O’Brien 1990), but scientific evidence of their efficacy is lacking. Although several studies indicated that some commercially available deer whistles do not produce the ultrasonic frequencies as claimed (Schildwachter et al. 1989, Scheifele et al. 2003), many motorists rely solely on these products to prevent deer-vehicle collisions.

Previous research has evaluated the effects of auditory deterrents on white-tailed deer (Odocoileus virginianus) feeding behavior (Belant et al. 1998, Gilsdorf et al., 2004a, 2004b, VerCauteren et al. 2005). These studies concluded that auditory deterrents either have no effect on deer behavior, do not produce the desired responses by deer, or the effectiveness of the devices diminishes over a short time due to habituation. The effects of pure-tone sound on roadway behavior of free-ranging white-tailed deer has not been studied.

Recently, D’Angelo et al. (2007) conducted auditory brainstem response experiments to record the neurological responses of sedated white-tailed deer to a range of sound frequencies at varying intensities. They reported that the range of white-tailed deer hearing included frequencies from 0.25 kHz-30 kHz, with best hearing sensitivity between 4 kHz-8 kHz. Because the upper limit of human hearing is approximately 20 kHz (Durrant and Lovrinic 1995),
ultrasonic sounds may have potential for use as auditory deterrents for resolving deer-human conflicts.

Deer whistles are claimed to emit consistent, continuous sounds when activated (Hornet Deer Whistle 2002, Deer Alert 2007). Pure tones are continuous sounds of equal intensity at a single frequency (Martin 1994), which can be produced using standard commercially available equipment. Scheifele et al. (2003) tested the actual frequencies emitted from deer whistles, and found they produced pure tone sounds. Based on this study and other similarities between sounds elicited by deer whistles and pure tones, the objective of this research was to test the effects of pure-tone sounds on white-tailed deer behavior. Our objective was to evaluate behavioral responses of captive deer to a range of pure tones and to test the efficacy of pure tones for altering the behavior of free-ranging white-tailed deer along roadways for prevention of deer-vehicle collisions.

**STUDY AREA**

We conducted experiments on the responses of captive deer to sounds at the Daniel B. Warnell School of Forestry and Natural Resources, Whitehall Deer Research Facility at the University of Georgia, Athens (herein, captive deer facility). The captive deer facility encompassed 2.4 ha, with 19 covered barn stalls, a rotunda with moveable internal walls to direct deer movements, 5 outside paddocks, and 3 outside holding/sorting pens. The captive deer facility houses 60-100 white-tailed deer annually.

We conducted the field portion of our study on the 1,215-ha Berry College Wildlife Refuge (BCWR), contained within the Berry College Campus in northwestern Georgia. BCWR is within the Ridge and Valley physiographic province (Hodler and Schretter 1986) with elevations ranging from 172-518 m. BCWR is characterized by campus-related buildings and
facilities interspersed with pastures, woodlots, and larger forested tracts. Forested areas are
dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), and pines (*Pinus* spp.).

BCWR had an abundant deer herd with an estimated 40 deer/km² (J. Beardon, Georgia
Department of Natural Resources, personal communication). There were 12-24 deer-vehicle
collisions reported annually on the approximately 24 km of paved roads (Berry College Police
Department, unpublished data). BCWR roads were 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. Average traffic volume was 26 cars/hour (24 hour average, SE = 4) during
our study.

On BCWR, we observed free-ranging white-tailed deer on 2 test areas separated by >5
km: (1) main campus test area (280-m long segment of road) and (2) mountain campus test area
(220-m long segment of road). 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 (*Festuca arundinacea*), 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**

**Sound-emitting Equipment**

We used a tone generator (Model 555, ACK Electronics, Atlanta, Georgia, USA) to
produce pure-tone sound stimuli across a range of frequencies. We controlled sound intensity
levels using a Madisound 5150 amplifier (Madisound Speaker Components, Madison, Wisconsin, USA), and a receiver (Model 2400, KLH Audio Systems, Sun Valley, California, USA). We transmitted sound to a 4-channel speaker selector with amplifier protection (Monster Cable SS4, Monster Cable Products, Inc., Brisbane, California, USA), which allowed us to select which speakers would emit the pure tones. We used Fostex 127E full-range speakers (Fostex America, a Division of Foster Electric, U.S.A., Inc., Gardena, California, USA) and Madisound high-frequency speakers (Madisound Speaker Components, Madison, Wisconsin, USA).

We calibrated the sound-emitting equipment to deliver the proper frequencies and levels of intensity. For calibration purposes, we recorded sample sound stimuli with a M30BX measurement microphone (free-field frequency response of 9 Hz-30 kHz; Earthworks Precision Audio, Milford, New Hampshire, USA) routed to an Edirol UA-25 USB sound card (Roland Corporation, Los Angeles, California, USA) connected to a laptop computer. We used RAVEN-Interactive Sound Analysis Software (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, New York, USA) to analyze sound stimuli. The same sound-emitting and calibration equipment was used for both the captive and field trials.

D’Angelo et al. (2007) concluded that ultrasonic pure tones (>20 kHz) had to be emitted between 45 and 60 db Sound Pressure Level (SPL) at the deer’s ear to be heard reliably by the deer. To ensure that the sound treatments in our study were audible to deer, we set the minimum intensity at 70 db SPL at calibrated distances for all pure tones. 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).
Captive Trials

Based on D’Angelo et al. (2007) we selected pure-tone sound treatments within the hearing range of white-tailed deer. For all trials with captive deer, we observed behavioral responses of focal deer to 1 of 5 pure tone sound treatments: 0.28 kHz, 1 kHz, 8 kHz, 15 kHz, and 28 kHz. We assigned the treatments for each trial randomly. During each trial, we classified the behavior of the focal deer during 3 observation periods: 1) pre-treatment-15 sec, 2) treatment-5 sec of pure tone sound, and 3) post-treatment -15 sec, with a recovery period of 2 min between trials.

We classified the deer’s behavioral responses as: 1) passive, 2) alert-head held high, movement of ears, 3) active-movement away from or towards speakers, or 4) flight-a swift movement away from the speakers. We recorded the position of the deer in relation to the speakers as away or towards for each observation period. One researcher made all observations to minimize observer bias.

During March-April 2006 at our captive deer facility, we housed 8 semi-tame, adult (>2.5 years) deer in an outside paddock (0.2 ha). We mounted speakers on evenly spaced posts along 2 sides of the perimeter of the paddock at 1.5-m above the ground. We placed 4 speakers serving each side of the paddock for a total of 8 speakers. From a blind near the midline of the paddock, the observer selected a focal animal randomly and recorded its behavior. During each trial, we set the speaker selector so that only speakers from one side of the paddock emitted sound stimuli. As calibrated, the sound was ≥70 db SPL at the midline of the paddock to ensure that sound was audible to the deer, but also allowed the deer a chance to respond and escape.

We also evaluated the behavioral responses of 5 adult deer housed individually in barn stalls (3 x 6 m) at our captive deer facility. We attached 1 speaker to the door of the barn stall
and calibrated the sounds to ensure they were audible ≥70 dB SPL throughout the stall. We mounted video cameras (Panasonic pro-line WV-BP310, Panasonic Broadcast and Digital Systems Company, Secaucus, New Jersey, USA) in each stall that linked to a time lapse recorder (Panasonic AG-RT600P, Panasonic Broadcast and Digital Systems Company, Secaucus, New Jersey, USA), a color video monitor (Panasonic CT-1386YWD, Panasonic Broadcast and Digital Systems Company, Secaucus, New Jersey, USA), and a sequential switcher (Panasonic WJ-SQ208, Panasonic Broadcast and Digital Systems Company, Secaucus, New Jersey, USA) to observe behaviors of individual deer.

For each trial, we categorized changes in deer behavior between pre-treatment, treatment, and post-treatment observation periods. These changes were scored as: 1) negative reaction – focal deer moved towards the source of the sound, 2) positive reaction – focal deer moved away from the source of the sound, and 3) neutral reaction – no change in behavior of focal deer. We used a chi-square test of independence (Sokal and Rohlf 1995), allowing us to make comparisons of the independence of behavior score categories among all 5 sound treatments. We analyzed the behavioral responses of deer within a group and individual deer in barn stalls in independent analyses. We examined significance in shifts of deer behavior among the pure tone sound treatments using $\alpha=0.05$.

**Field Trials**

We used the same sound-emitting equipment as in the captive trials, altered for vehicle mounting (Figure 2.1). For all trials, we used a 1993 Buick station wagon with 4 high-frequency speakers (Madisound Speaker Components, Madison, Wisconsin, USA) mounted forward of the grill at an approximate height of 0.75 m above the road surface. Two speakers emitted sound
directly in front of the vehicle (mounted 90° from the grill) and 2 speakers emitted sound to the sides of the vehicle (mounted 45° from the grill).

We conducted field trials during April and June 2006. We did not hold trials during May to avoid fawning and its possible influence on deer behavior. Within the 2 test areas on BCWR, we delineated an area of influence, which encompassed a 10–m buffer on both sides of the road for the entire length of the test area (Figure 2.2). Based on our calibrations of sound stimuli emitted from the test vehicle traveling through the test areas at 48 km/hour, we determined that sound stimuli was ≥70 dB SPL at 1.5 m above the ground within the 10 m buffer and ≥30 m ahead of the test vehicle. All sound treatments were >25 dB SPL above operating noise of the test vehicle at the calibrated distances.

To delineate the area of influence, we installed distance markers 10 m perpendicular to the road edge at 20-m intervals along the roadway segment of each test area. We observed deer behavior from a 3-m high elevated platform placed approximately 6 m from the road edge near the mid-line of each test area. We used a forward-looking infrared (FLIR) ThermaCAM B1 (FLIR Systems, Inc., Boston, Massachusetts, USA) with a 12 degree lens (360° rotation and 90° vertical tilt) mounted on the safety rail of the platform. The FLIR was connected to a 33 cm, black and white monitor with a Video Cassette Recorder, powered by a 12-volt deep-cycle marine battery and a 750-watt power inverter. The distance markers delineating the area of influence were made to collect heat during the day and store and radiate more heat than the surrounding environment at night to be visible in the FLIR (D’Angelo et al. 2006). We established test areas 2 weeks before our observations began.

We recorded deer behavior during 2, 3-hr observation periods per day, from 0600-0900 hours and from 1900-2200 hours. We held one observation period per test area per day,
alternating AM and PM observation times. We concentrated our observations around dawn and dusk to maximize the number of deer in the test area. The observer entered the viewing platform 30 min before observations began to reduce disturbance to deer in close proximity to the test area. To minimize observer bias, the same researcher made all observations. The observer randomly selected a focal deer within the area of influence, and alerted a co-worker with a 2-way radio to drive through the area at 48 km/hour in the vehicle equipped with the sound-emitting equipment.

For each trial, we exposed the deer within the area of influence to 1 of 6 randomly assigned treatments. The 6 treatments consisted of a control (no sound stimuli from vehicle) and the 5 pure tones used in our experiments with captive deer: 0.28, 1, 8, 15, and 28 kHz. We did not conduct trials on days with heavy precipitation, fog, or high winds as these conditions would prevent sound from traveling at the calibrated intensities.

We characterized deer behavior into 1 of 5 categories: 1) passive, 2) alert - lifted head, movement of ears, 3) active - movement away or toward roadway, 4) flight - a swift movement away from the roadway and 5) within road - deer was within the roadway. Every trial consisted of recording focal deer behavior to each treatment at 2 observation periods: Period 1 (before the vehicle entered the test area), and Period 2 (during interaction between deer and vehicle). For each trial, we categorized changes in deer behavior between periods 1 and 2. These changes were scored as: 1) a negative interaction – the behavior of the animal was more likely to cause a deer-vehicle collision, 2) a positive interaction – the deer was less likely to cause a deer-vehicle collision and 3) a neutral interaction – no change in risk of a deer-vehicle collision (Table 2.1). For example, a trial in which the behavior of the focal deer was passive during Period 1 (before the vehicle entered the test area), after which the focal deer was active towards the road during
Period 2 (the interaction between the deer and vehicle) would have been categorized as a negative interaction. We used a chi-square goodness of fit test (Sokal and Rohlf 1995), with $\alpha < 0.05$ indicating significance, to compare deer behavior when exposed to each pure-tone treatment to deer behavior when exposed to the control.

**RESULTS**

**Captive Trials**

During 15 days of observation from 22 March 2006-7 April 2006, we recorded 406 observations of captive deer responses to pure-tone sound treatments. For focal deer in a group, we held 30 trials/day for 8 days ($n = 240$ observations). For focal deer housed individually, we held $\leq 25$ trials/day for 7 days ($n = 166$ observations).

Pure-tone sound treatments and behavioral responses of the focal deer were independent for all observations of captive deer within a group (Table 2.2, 0.28 kHz, $\chi^2 = 0.36, P = 0.999$; 1 kHz, $\chi^2 = 2.54, P = 0.959$; 8 kHz, $\chi^2 = 2.14, P = 0.976$; 15 kHz, $\chi^2 = 6.02, P = 0.645$; 28 kHz, $\chi^2 = 0.12, P = 0.999$). For deer within a group, $\geq 74\%$ of the observations we scored were in the neutral behavior category for all frequencies tested. For focal deer housed individually, there also was no difference in behavioral response of deer to all 5 pure-tone sound treatments (Table 1.3, 0.28 kHz, $\chi^2 = 2.69, P = 0.952$; 1 kHz, $\chi^2 = 0.61, P = 0.999$; 8 kHz, $\chi^2 = 1.74, P = 0.988$; 15 kHz, $\chi^2 = 0.05, P = 0.999$; 28 kHz, $\chi^2 = 1.70, P = 0.989$). We scored $\geq 69\%$ of the observations as neutral behavior for deer housed individually.

At first exposure to sound, deer behavior was categorized as more alert, but reactions degraded to passive after multiple exposures to pure-tone sound treatments. We observed normal captive deer behavior of feeding, grooming, and laying down during all 3 observation
periods. Deer behavior did not change with exposure to pure-tone sound treatments. We did not observe flight responses conducive to preventing deer-vehicle collisions.

**Field Trials**

During 26 observation periods from 10 April 2006-26 April 2006 and 5 June 2006 through 13 June 2006, we recorded 319 observations of focal deer relative to the test vehicle. All pure-tone sound treatments were used for both April and June observations. For all treatments, deer behavior did not change between periods 1 and 2, as we classified >53% of the observations in the neutral category (Table 2.4). For the 0.28 kHz treatment versus the control, we observed a decrease in the proportion of neutral and positive responses by deer and an increase in the proportion of negative responses by deer ($\chi^2 = 7.58, P<0.023$). For the other 4 treatments, we observed no differences in the proportions of behavioral response categories between the treatment and the control ($1\text{ kHz}, \chi^2 = 0.13, P=0.937$; $8\text{ kHz}, \chi^2 = 3.44, P=0.179$; $15\text{ kHz}, \chi^2 = 0.89, P=0.641$; $28\text{ kHz}, \chi^2 = 4.54, P=0.103$.)

In ≥ 35 % of trials, deer exposed to vehicles with no pure-tone sound treatments responded in a positive manner (i.e., moved away from the road in a manner that a deer-vehicle collision might be prevented). Likewise, as deer were exposed to pure-tone sound treatments from a traveling vehicle, the proportion of positive responses did not vary significantly among treatments ($0.28\text{ kHz}, 33\%; 1\text{ kHz}, 37\%; 8\text{ kHz}, 24\%; 15\text{ kHz}, 33\%; 28\text{ kHz}, 24\%$)

**DISCUSSION**

Our intent was to investigate responses of captive deer to pure-tone sound treatments to determine which were most applicable in a roadway setting (i.e., flight response by deer away from the sound). Because the responses of captive deer did not differ among the sound treatments we tested, we elected to test all 5 pure tones in our field trials.
We found that the pure-tone sounds we tested did not alter the behavior of captive or free-ranging white-tailed deer in a manner that would prevent deer-vehicle collisions. Based on deer hearing abilities (D’Angelo et al. 2007) and our calibration of the sound treatments, all of the treatments we tested were audible to focal deer in the area of influence. However, only the 0.28 kHz pure tone elicited behavioral responses by deer and those deer were more likely to enter the roadway in the presence of the test vehicle. Given the general lack of response to sound treatments, deer confronted with a vehicle and additional stimuli from auditory deterrents may: 1) have too little time to react as desired, 2) lack the neurological ability to process the alarm information efficiently to respond as desired, or 3) may not recognize the sounds we tested as threatening.

Pure tones are similar to the sounds deer-whistles are purported to emit. We tested pure tones at frequencies similar to manufacturer claims (>15 kHz, Hornet Deer Whistle 2002, Deer Alert Animal Warning Device 2007) as well as frequencies within the range that several designs of deer whistles have been shown to produce (Scheifele et al. 2003; 3-12 kHz). Therefore, we suggest that deer whistles likely would not be effective for prevention of deer-vehicle collisions. Correspondingly, Romin and Dalton (1992) reported no differences in behavioral responses of mule deer (O. hemionus) exposed to either of 2 brands of deer whistles (brand not specified) compared to vehicles without whistles.

To effectively reduce the incidence of deer-vehicle interactions, auditory deterrents should be transmitted as far ahead and to the sides of the vehicle as possible to provide deer with ample time to react. For our field trials, we set minimum standards for pure tones being audible ≥70 db SPL within the 10-m area of influence and ≥30 m in front of the test vehicle traveling at 48 km/hr. Although our experiments were conducted under ideal conditions, with weather
conditions conducive to sound transmission and few roadside obstructions, exceeding our minimum 10-m area of influence would be difficult, particularly at the higher frequencies. For example, we could not produce intensities for the ultrasonic treatment (28 kHz) greater than the minimum standards, or beyond the area of influence, without damaging the sound-producing equipment. Hearing safety of humans also must be considered because they would be exposed to sounds within proximity of passing vehicles. We limited intensities to \( \leq 115 \) dB SPL at 1 m from the speakers based on standards set by the Occupational Safety and Health Administration (2006) for maximum permissible noise exposure for \( \leq 0.25 \) hours/day.

Sound stimuli must have neurological significance to the animal to produce a behavioral response (Jacobson 1994). Natural sounds (e.g., deer vocalizations) are complex, being composed of several pure tones of different frequencies generated simultaneously, repeating over time (Martin 1994). Complex sounds are rapid-change stimuli, with a relatively fast neurological onset caused by simultaneous firing of the auditory nerves (Hall 1992, Jacobson 1994). Pure tones are considered slow onset and long-duration stimuli producing slower neurological responses which last for the duration of the sound stimuli. To produce a rapid change in deer behavior, complex sounds may be more appropriate than pure tones.

Nevertheless, research on auditory deterrents has shown that some types of complex sounds are ineffective for altering deer behavior. Gilsdorf et al. (2004b) found that recorded distress and alarm calls used as a bio-acoustic frightening device did not deter deer from using agricultural fields. Similarly, elk (Cervus elaphus) and mule deer were not deterred from feeding sites by the Critter Gitter™, a deterrent device with an auditory alarm that “approached 120 dB in volume (manufacturer statement) and consisted of a repeated series of low and high pitched beeps that varied in pattern each time the device was activated” (VerCauteren et al. 2005:1283). Other
studies found no change in deer feeding behavior with motion-activated or regular-interval acoustic frightening devices (Curtis et al. 1997, Belant et al. 1998).

MANAGEMENT IMPLICATIONS

Considering the challenges of producing sound at appropriate intensities and distances from a moving vehicle, deer hearing capabilities, human safety concerns, and our observed lack of behavioral responses of deer to sound treatments, auditory deterrents do not appear to prevent deer-vehicle collisions.

ACKNOWLEDGMENTS

Our study was funded by the Georgia Department of Transportation through the Governor’s Office of Highway Safety and the National Highway Traffic Safety Administration, with special thanks to David Jared of the Georgia Department of Transportation. J. G. D’Angelo provided technical support and constructed the sound-emitting equipment. S. B. Castleberry and W. D. Greene provided earlier reviews of the manuscript. We thank the animal science students at Berry College who contributed to the field work.

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Bacon, Boston, Massachusetts, USA.


Occupational Safety and Health Administration. 2006. OSHA Technical Manual TED 01-00 015. United States Department of Labor, Washington, D.C., USA.


Figure 2.1. Test vehicle equipped with sound-emitting equipment used for observations of behavior of free-ranging white-tailed deer in response to sound treatments at Berry College Campus and Wildlife Refuge, Mount Berry, Georgia, 2006.
Figure 2.2. Depiction of an experimental roadway section established for testing vehicle-mounted sound deterrents on white-tailed deer roadway behavior on Berry College Campus and Wildlife Refuge, Mount Berry, Georgia, USA, 2006.
Table 2.1. Behavior score categories for white-tailed deer exposed to vehicle-emitted sound treatments based on changes in deer behavior along roadways, comparing periods before the deer was exposed to treatment to when the vehicle passed the deer or interacted with the deer, Berry College Campus and Wildlife Refuge, Mount Berry, Georgia, USA, 2006. Negative scores indicated a higher risk of a deer–vehicle collision (DVC), neutral scores indicated no change in DVC risk, and positive scores indicated a lower risk of a DVC.

<table>
<thead>
<tr>
<th>Observation period</th>
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<td><strong>Behavior Score</strong></td>
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Table 2.2. Percent change of white-tailed deer behavioral response scores exhibited by captive deer within a group, using Chi-Square Test of Independence, during pure-tone sound trials at the University of Georgia Captive Deer Research Facility, Athens, Georgia, USA, 2006.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N</th>
<th>Negative</th>
<th>Neutral</th>
<th>Positive</th>
<th>$\chi^2$</th>
<th>P-value</th>
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<td>75.00</td>
<td>20.83</td>
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<tr>
<td>8 kHz</td>
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<td>15 kHz</td>
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<td>28 kHz</td>
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<td>0.12</td>
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Table 2.3. Percent change of white-tailed deer behavioral response scores exhibited by captive deer housed individually, using Chi-Square Test of Independence, during the pure-tone sound trials at the University of Georgia Captive Deer Research Facility, Athens, Georgia, USA, 2006.

<table>
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<tr>
<th>Treatment</th>
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<th>Negative</th>
<th>Neutral</th>
<th>Positive</th>
<th>$\chi^2$</th>
<th>P-value</th>
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</thead>
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<tr>
<td>0.28 kHz</td>
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<td>2.69</td>
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<tr>
<td>1 kHz</td>
<td>24</td>
<td>8.33</td>
<td>79.17</td>
<td>12.50</td>
<td>0.61</td>
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<td>8 kHz</td>
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<td>1.70</td>
<td>0.9889</td>
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Table 2.4. Percent change of white-tailed deer behavioral response scores for free-ranging deer exposed to vehicle-mounted sound-producing devices, using a Chi-Square Goodness of Fit Test, at Berry College Campus and Wildlife Refuge, Mount Berry, Georgia, USA, 2006.

<table>
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<th>Treatment</th>
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<th>Neutral</th>
<th>Positive</th>
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<th>P-value</th>
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<td>67.27</td>
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CHAPTER 3
SUMMARY AND CONCLUSIONS

As public concern over deer-vehicle collisions increases, agencies charged with managing wildlife populations or highway safety are interested in the effectiveness of mitigation techniques, such as deer whistles. Little scientific research has been conducted on the perception and behavioral response of white-tailed deer to sound. Results of previous research on other types of auditory deterrents suggest that sound deterrents may not be a reliable method for altering deer behavior such that deer-vehicle collisions may be prevented. There are similarities between sounds produced by deer whistles and pure tones. Therefore, I evaluated the efficacy of pure-tone sounds throughout the full range of deer hearing for altering the behavior of free-ranging deer along roadways.

I first investigated responses of captive deer, looking for a flight response by deer away from the sound, to pure-tone sound treatments to determine which were most applicable in a roadway setting. Because the responses of captive deer did not differ among the sound treatments I tested, I elected to test all 5 pure tones in our field trials. I found that the pure-tone sounds I tested did not alter the behavior of free-ranging white-tailed deer in a manner that would prevent deer-vehicle collisions. Free-ranging white-tailed deer within 10 m of roadways did not change their behavior relative to 4 of the 5 pure tone sound treatments. The 0.28 kHz pure tone sound treatment elicited negative responses from deer in our field trials (i.e., deer were more likely to move towards the roadway and create a dangerous situation along the road edge).
Based on the lack of behavioral responses of deer to any of the sound treatments, deer confronted with a vehicle and additional stimuli from auditory deterrents may: 1) have too little time to react as desired, 2) lack the neurological ability to process the alarm information efficiently to respond as desired, or 3) may not recognize the sounds I tested as threatening. Considering the challenges of producing sound at appropriate intensities and distances from a moving vehicle, deer hearing capabilities, human safety concerns, and my observed lack of behavioral responses of deer to sound treatments, auditory deterrents appear to lack applicability for prevention of deer-vehicle collisions.