Response of beach-nesting American Oystercatchers to off-road vehicles: An experimental approach reveals physiological nuances and decreased nest attendance

RESEARCH ARTICLE

Response of beach-nesting American Oystercatchers to off-road vehicles: An experimental approach reveals physiological nuances and decreased nest attendance

Shilo K. Felton,[1]* Kenneth H. Pollock,[2] and Theodore R. Simons[3]

[1] North Carolina Cooperative Fish and Wildlife Research Unit, Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina, USA
[2] Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina, USA
[3] U.S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit, Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina, USA
* Corresponding author: skfelton@ncsu.edu

ABSTRACT

Shorebird populations face increasing challenges as rising sea levels and growing human populations constrain their breeding habitats. On recreational beaches, the nesting season often coincides with a season of high visitor use, increasing the potential for conflict, which may negatively influence beach-nesting shorebird species. We designed a field experiment to study the responses of nesting American Oystercatchers (*Haematopus palliatus*) to off-road passenger vehicles (ORVs) at Cape Hatteras and Cape Lookout National Seashores in North Carolina, USA. We used continuous video and heart rate recordings to assess changes in the behavior and physiology of incubating oystercatchers. We conducted driving experiments affecting 7 nesting pairs in 2014 and 19 nesting pairs in 2015, between April and July of each year. Experimental treatments were repeated throughout the incubation period for each nest. Although responses were highly variable within and among pairs, paired randomized permutation tests indicated that, overall, oystercatcher pairs spent a greater proportion of time with their heads up and exhibited slower heart rates during driving treatments. Pairs also left their nests more frequently and attended their nests for a lower proportion of time during driving treatments, although these responses diminished over time. Higher nest attendance and lower departure rates late in incubation may have reflected a stronger attachment to nests closer to hatching or habituation to the driving treatment, although individuals continued to exhibit physiological responses to passing vehicles throughout incubation. Beach-nesting birds may benefit from reduced vehicle traffic at their nesting sites, allowing parents to spend more time attending the nest and less time on defensive behaviors.

Keywords: Field experiment, in situ, paired design, flight response, freezing behavior, American Oystercatcher

Respuesta de los individuos de *Haematopus palliatus* que anidan en la playa a los vehículos todoterreno: Un enfoque experimental revela matices fisiológicos y una disminución del cuidado del nido

RESUMEN

Las poblaciones de aves playeras enfrentan desafíos crecientes a medida que el aumento del nivel del mar y el crecimiento poblacional humano restringen sus hábitats reproductivos. En las playas recreacionales, la estación de anidación usualmente coincide con la estación de alto uso de visitantes, aumentando el potencial de conflictos que pueden influenciar negativamente a las especies de aves playeras que anidan en la playa. Diseñamos un experimento de campo para estudiar las respuestas de los individuos anidando de *Haematopus palliatus* a los vehículos de pasajeros todoterreno en las Costas Marinas Nacionales Cabo Hatteras y Cabo Lookout. Usamos grabaciones continuas de video y del ritmo cardíaco para evaluar los cambios en el comportamiento y la fisiología de incubación de individuos de *H. palliatus*. Realizamos experimentos de conducción vehicular ante siete parejas anidando en 2014 y ante 19 parejas anidando en 2015, entre abril y julio de cada año. Los tratamientos experimentales fueron repetidos a lo largo del período de incubación de cada nido. Aunque las respuestas fueron altamente variables en y entre parejas, las evaluaciones de permutación aleatoria de pareja indicaron que, en general, las parejas de *H. palliatus* pasaron una mayor proporción del tiempo con la cabeza erguida y presentaron ritmos cardíacos más lentos durante los tratamientos de conducción. Las parejas también dejaron sus nidos más frecuentemente y cuidaron sus nidos por una menor proporción de tiempo durante los tratamientos de conducción, aunque estas respuestas disminuyeron enormemente a lo largo del tiempo. Un mayor cuidado de los nidos y tasas de salida más bajas al final de la incubación pueden reflejar una vinculación más fuerte a los nidos a medida que se acerca la eclosión y un acostumbramiento a los tratamientos de conducción, aunque los individuos continuaron exhibiendo respuestas fisiológicas a los vehículos

circulantes a lo largo de la incubación. Las aves que anidan en las playas pueden verse beneficiadas por una reducción del tráfico vehicular en sus sitios de anidación, permitiendo que los padres pasen más tiempo cuidando el nido y menos tiempo en comportamientos de defensa.

Palabras clave: comportamiento de congelamiento, diseño pareado, experimento de campo, *Haematopus palliatus*, in situ, respuesta de vuelo

INTRODUCTION

Human–wildlife conflict threatens biodiversity globally. Understanding how sensitive species respond to potential sources of disturbance can help managers to mitigate negative interactions for wildlife in human-dominated landscapes (Blackwell et al. 2016). Shorebird species are at particular risk of this conflict due to limited resource availability (Defeo et al. 2009), as demonstrated by high declines relative to other bird communities (Bart et al. 2007). High visitor use of beaches in the form of boating, pedestrian, and off-road vehicle activity can reduce hatching success and chick survival through direct mortality (Sabine et al. 2006, Schulte and Simons 2015) and indirect effects (Burger 1991, 1994, Ruhlen et al. 2003, Sabine et al. 2008).

It is often difficult to quantify the indirect effects of off-road vehicles (ORVs) on nesting shorebirds. Studies have documented vehicles causing direct mortality of chicks and nests (Weston et al. 2012, Schulte and Simons 2015), but the effects of vehicles on the survival rates of adults and nests are less certain. Heavy vehicle traffic can reduce suitable habitat and restrict access to foraging sites (Anders and Leatherman 1987, Goldin and Regosin 1998, Verhulst et al. 2001, Schlacher and Thompson 2008). Experimental field studies have demonstrated that driving on beaches reduces shorebird feeding efficiency by flushing foraging flocks (Tarr et al. 2010, Burger and Niles 2014). This occurs regardless of drivers' attempts to avoid disturbing flocks (Weston et al. 2014). Previous observational studies have suggested that vehicles regularly flush incubating oystercatchers from their nests, and that nest survival decreases with increased exposure to vehicles (McGowan and Simons 2006, Sabine et al. 2008, Borneman et al. 2016). Unattended eggs are more vulnerable to environmental factors that may reduce hatching success. Increased activity around the nest (such as flushing in response to vehicles) can also attract nest predators (Sabine et al. 2008). However, such observational studies often fail to eliminate sources of variation that may confound the observed response.

In order to reduce the uncertainty introduced by confounding factors and to better understand the mechanisms driving the potential influence of vehicles on beach-nesting birds, we assessed the direct effects of off-road vehicles on the incubation behavior and physiology of a beach-nesting shorebird in an experimental framework.

Our study focused on the American Oystercatcher (*Haematopus palliatus*), a species that has emerged as an important focal species for tracking changes to coastal environments along the Atlantic and Gulf coasts of the United States (American Oystercatcher Working Group et al. 2012). The sensitivity of oystercatchers to a variety of factors affecting coastal resources, including habitat loss, coastal development, pressure from human recreation, pollution, and nonnative predators, makes them important indicators of coastal ecosystem health (Carlson-Bremer et al. 2010, Ogden et al. 2014).

At Cape Hatteras National Seashore in North Carolina, USA, as in many other coastal communities, beach access has become a particular source of contention surrounding management efforts to preserve oystercatcher populations and shorebird communities in general. Vehicles have been driven on what is now Cape Hatteras National Seashore since the 1930s, with access to the unpaved islands originally via ferry. Vehicle traffic to Cape Hatteras National Seashore dramatically increased following the paving of North Carolina Highway 12 (N.C. 12) in 1954 and the completion of Bonner Bridge, which connected Hatteras Island to mainland North Carolina in 1963. Cape Hatteras National Seashore saw an 8-fold increase in visitation between 1955 and 2007 (National Park Service 2010). Located immediately to the southwest is Cape Lookout National Seashore, which has no paved roads and is accessible to visitors only by ferry.

The managers of these seashores enact different policies for closures of vehicle routes around oystercatcher nests. At the time of our study, Cape Lookout National Seashore allowed vehicles to pass oystercatcher nesting areas in order to access other parts of the beach, but Cape Hatteras National Seashore did not, potentially aggravating conflict over vehicle management policies at Cape Hatteras National Seashore. In cases such as this, land managers may need to consider the interests of conflicting stakeholders. Federal law requires the National Park Service to protect natural resources and preserve public access to recreation. Doing so, however, requires an understanding of the natural systems that may be negatively affected by recreation and their responses to these potential disturbances. Understanding the immediate effects of vehicles on nesting shorebirds can provide insights into the mechanisms driving breeding success in shorebird populations and can better inform managers of their options when making decisions to protect shorebird populations.
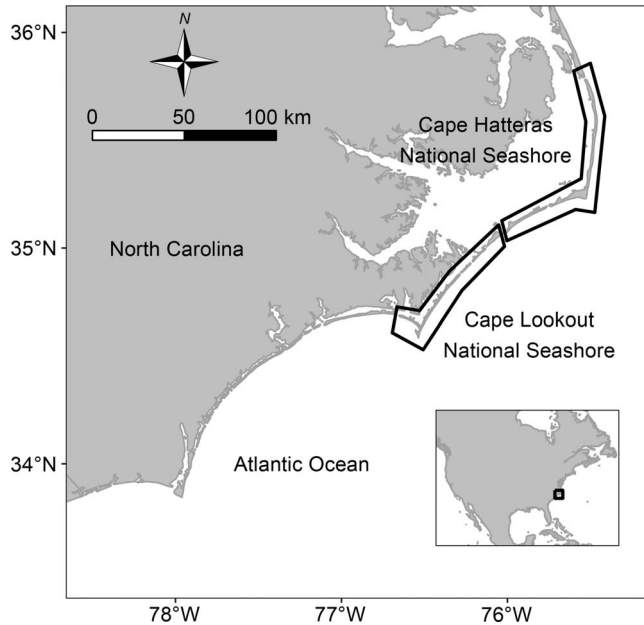
FIGURE 1. Sites at Cape Hatteras and Cape Lookout National Seashores, North Carolina, USA, where we studied the responses of beach-nesting American Oystercatchers to off-road passenger vehicles (ORVs) in 2014 and 2015.

We employed an experimental design to assess the potential effects of allowing vehicles to drive through closure areas at a fixed distance from incubating oystercatchers. Specifically, we tested the hypothesis that passing vehicles would alter the behavior (e.g., nest attendance, flightiness, and alertness) and physiology (e.g., heart rate) of oystercatchers during incubation.

METHODS

Study Area

We conducted our field research at Cape Hatteras National Seashore in 2014 and at both Cape Hatteras and Cape Lookout National Seashores in 2015. Together, these 2 National Seashores are made up of a network of barrier island beaches off the northeastern coast of North Carolina (Figure 1). We focused on nesting pairs of American Oystercatchers on Hatteras Island, Cape Hatteras National Seashore, and on South Core Banks, Cape Lookout National Seashore, because these 2 islands contain the largest numbers of nesting pairs for each of these parks. Both islands are part of the Atlantic Flyway and have been designated Globally Important Bird Areas by the American Bird Conservancy.

Cape Lookout National Seashore extends from Ocracoke Inlet to Beaufort Inlet (Figure 1). South Core Banks has a general northeast–southwest orientation and is 40 km long. It is accessible only by ferry or private boat. Current management at Cape Lookout allows both vehicle

and pedestrian traffic in areas of the beach where oystercatchers are actively nesting, but prohibits visitors from stopping, parking, or camping on the beach within 91.44 m of any nest (National Park Service 2006). Within these 91.44-m buffer zones, nests are protected by a 37.16-m^2 area that is completely closed to vehicle traffic. Neither pedestrians nor vehicles are permitted within these complete closure areas.

Cape Hatteras National Seashore is the northernmost of these barrier islands (Figure 1). Hatteras Island is a narrow barrier island that extends up to 45 km into the Atlantic Ocean from the mainland coast of North Carolina. Visitors can access Hatteras Island from the north via N.C. 12 and a network of bridges. At the time of this study, management practices closed beach access to both vehicle and pedestrian traffic in areas where oystercatchers, Piping Plovers (*Charadrius melodus*), or Least Terns (*Sternula antillarum*) were actively nesting. For oystercatchers, these closures were 300-m (minimum) in diameter, centered around the oystercatcher nest.

Field Methods

We assessed the effects of vehicle activity on the behavior and physiology of incubating American Oystercatchers using an experimental approach with a paired experimental design because we could not select experimental nests randomly. Each nest included in the study was exposed to several (2–15) experimental driving treatments throughout the 27-day incubation period. Because oystercatchers can renest following failed nesting attempts, we exposed multiple nests of some pairs to experimental driving treatments. Three hundred meter (minimum) vehicle and pedestrian access closure areas were established around all study nests.

The driving treatments were meant to mimic the type of disturbance that incubating oystercatchers might experience if drive-through corridors were opened at Cape Hatteras National Seashore. Based on vehicle traffic data at this seashore and current beach access hours, ~5–40 vehicles on average might drive through such a corridor during each hour of the nesting season (National Park Service 2017; see also Discussion). Driving treatments consisted of 1 person driving a 4-wheel-drive off-road passenger vehicle through the 300-m access closure zone parallel to the shoreline and 25 m from the nest at its closest point. We chose this distance because it maximized the number of nests that we were able to include in our study. We increased this distance to 40 m at 1 nest in 2014 to avoid an adjacent Least Tern colony. In 2015, we reduced the distance to 20 m at 1 nest because the beach was too narrow to allow a 25-m nest buffer. Drivers were instructed to maintain a speed of ~16 kph (~10 mph; the speed limit near wildlife imposed by Cape Hatteras National Seashore). After completing each pass, we turned
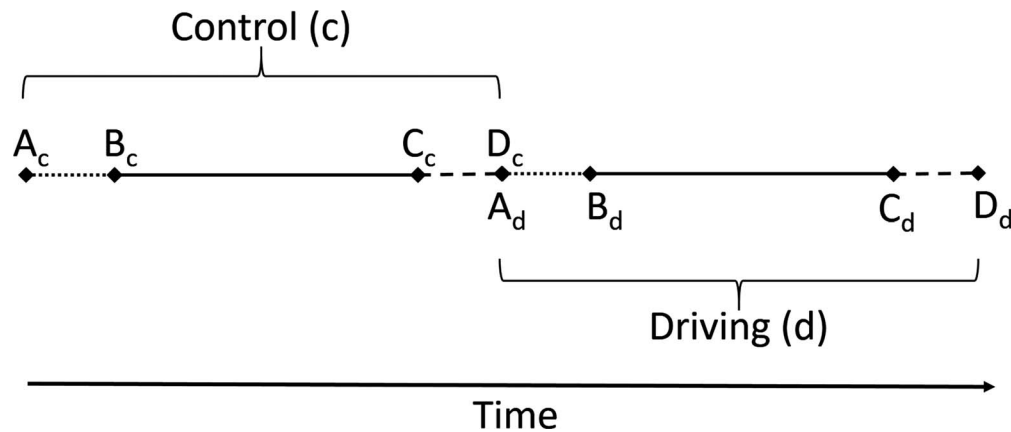
FIGURE 2. Schematic of video sampling periods of beach-nesting American Oystercatchers in relation to driving experiments using off-road passenger vehicles (ORVs) in areas closed to public vehicle access in Cape Hatteras National Seashore, North Carolina, USA. A_d is the point at which the bird first leaves the nest (if this occurs before the vehicle enters the closure), B_d is the point in time at which the vehicle first enters the closure, C_d is the point when the vehicle leaves the closure after the last scheduled pass, and D_d is the point when the bird returns to the nest (if this occurs after the last vehicle pass). Points A_c–D_c represent equivalent points in time during the control period. Segments drawn using similar dash types are equal in length of time. For example, the amount of time that passes between points C_d and D_d (i.e. the time elapsed between the end of the last vehicle pass and the return of the bird to the nest) is equivalent to the time between points C_c and D_c (i.e. the time between the end of the control period and the time that the bird leaves the nest as the vehicle approaches the experimental area). Behaviors recorded during periods B_c–C_c and B_d–C_d were included in analyses.

around at the end of the closure area and waited for the oystercatcher to return to its nest before beginning the next pass. The driving treatment began the second that the vehicle entered the 300-m buffer to begin the first pass and ended the second that the vehicle exited the buffer at the end of the final pass.

For both years, each driving treatment was defined by the amount of time that our vehicle remained inside the 300-m buffer zone to complete all driving passes (20 passes in 2014 and 10 passes in 2015). However, incubating adults often seemed to respond to our vehicles before we entered the buffer to begin the treatment and occasionally did not return to their nests until after we had left. For this reason, we also included in our driving period observations the time that an individual first left the nest upon our vehicle's first approach and the time that the bird returned to the nest following our exit from the buffer. The control periods that we observed occurred over the same length of time and immediately preceded the driving periods (Figure 2).

2014 driving protocol. We attempted 2 experimental driving treatments daily in 2014; 1 treatment during morning hours (06:00–12:00) and 1 treatment during afternoon and evening hours (12:00–20:00). During each driving treatment, we drove a 4-wheel-drive passenger vehicle from one end of the 300-m closure area to the other, passing the nest at a perpendicular distance of 25 m, as described above. Each driving treatment consisted of 20 vehicle passes by a nest. This procedure was repeated for 3 days in a row. After the first 3 days of driving treatments at

a nest, we refrained from conducting driving treatments at that nest for the subsequent 3 days. The entire process was repeated, with 3 days of driving treatments and 3 days of no driving treatments, until the nest either hatched or failed.

2015 driving protocol. In 2015, we modified the driving protocol to strengthen our study design. Most notably, we included an additional study site at Cape Lookout National Seashore, which allowed us to increase our sample size substantially. To minimize impacts to the beach and allow for a more structured sampling procedure, while maintaining the same rate of driving events per trial, we reduced the number of passes per driving treatment to 10 passes. As in 2014, we waited for the bird to return to its nest before beginning each pass, but, while we waited for the bird to return to its nest, we further standardized our protocol by orienting the vehicle so that the front faced the ocean, to mimic the position in which many visitors park their vehicles on the beach.

In the summer months, visitors are permitted to drive on beaches between 07:00 and 19:00. Therefore, to maintain consistency and to control for variations in responses associated with time of day, we limited driving treatments to 3 times of day: morning (07:00–10:00); afternoon (12:00–15:00); and evening (17:00–20:00, so that treatments ended before sunset).

We used a period of time equivalent to the duration of the experimental treatment and immediately before the driving treatment as a control period for each driving

treatment (Bókony et al. 2012). This pairing of control and driving treatments reduced variability associated with the tidal cycle and weather, which could change considerably over longer (e.g., 3-day) intervals. Driving treatments were assigned using a randomized blocking design so that, within a 6-day interval, each nest was sampled during all 3 driving treatment times of day, with each day of driving treatment separated by a day of no driving treatment. We rerandomized the order in which we implemented driving treatments (morning, afternoon, and evening) for each consecutive 6-day block. This procedure continued until the predicted hatching date for each nest (27 days from the laying date of the second egg in the clutch). This stratified random design was used to reduce bias associated with time of day.

Nest monitoring equipment. We assumed that egg laying was complete when no new eggs appeared in a nest for 3 days in a row. At this point, researchers installed monitoring equipment, which was replaced every 4–6 days to provide fresh batteries and download recorded data. In 2014, we accessed nests for equipment maintenance using the same vehicles that were used for the driving experiments. In 2015, equipment maintenance was performed by accessing the nest either on foot, by utility terrain vehicle (UTV), or using a truck not used in the driving experiments so that the experimental pairs did not associate our experimental vehicle with additional forms of disturbance. In 2015, we installed camera equipment at least 1 day prior to any driving treatments. While this was also true for most cases in 2014, there were some occasions during which we installed monitoring equipment earlier on the same day. Any occasions on which the monitoring equipment was installed during a control period were removed from analyses.

A continuous 24-hr video recorder monitored incubation behavior. The system was composed of an infrared outdoor security camera, digital video recorder, 2 12-V 35-amp-hr AGM (absorbed glass mat) sealed lead acid batteries, and voltage regulator, all housed within a 37.85-L bucket (Borneman et al. 2016). We positioned video cameras 3.05–4.57 m from incubating oystercatchers, with the adjacent beach habitat in the field of view so that we could record passing vehicles.

Heart rate monitors were comprised of a small microphone (Electret Condenser Microphone, PUI Audio, Dayton, Ohio, USA; 6-mm diameter, sensitivity of −46 dB ± 3 dB) mounted on the surface of a plastic egg and connected to an external digital audio recorder (Borneman et al. 2014). The plastic eggs and microphones were covered with a balloon to protect and conceal the microphone, and the entire apparatus was painted to resemble an American Oystercatcher egg. We placed the audio recorder and a battery in a plastic bucket between 3.05 m and 4.57 m from the nest, burying both the bottom

half of the bucket and the wire connecting the microphone and audio recorder. We replaced artificial eggs as their outer membranes deteriorated. On occasion, the artificial egg became separated from the rest of the clutch due to the activity of the incubating adult. When this occurred, we moved the artificial egg (usually just a few cm) to the location of the other eggs. Heart rate recorders were only installed in nests with ≤3 eggs, so the total number of "eggs" in the nest never exceeded the number of eggs that American Oystercatchers are known to successfully incubate (Nol et al. 1984, Borneman et al. 2014).

In 2015, we additionally installed trail cameras (Reconyx, Holmen, Wisconsin, USA) at some treatment nests so that we could identify individuals by their field-readable leg bands as they approached and left their nests.

Data Extraction

Behavioral video review. We conducted continuous focal observations of all experimental nests to gather activity budgets for each incubating pair at the nest during every recorded driving period and its paired control period. For each driving and control period video, we recorded the activity state (see below), the times at which individuals of the pair departed from or arrived at the nest, and the number of times that an experimental vehicle drove past (for use in heart rate collection). We defined activity states to be exclusive and exhaustive so that the pair was always considered to be in exactly one of these states in relation to its nest at any given time during the observation period. We used the following activity states: off the nest, sitting, standing, shading (i.e. a posture between sitting and standing in which the bird's tarsometatarsus was resting on the ground but the brood patch was elevated off the eggs), shifting (i.e. the bird was moving between any of the states: sitting, standing, shading, or off the nest), head tucking, not visible (for poor visibility at the nest or a brief lapse in video coverage, so that we could not distinguish whether a bird was on or off its nest), and other (generally when we could determine that a bird was on its nest, but we could not determine the bird's posture). Periods during which individuals were not visible were removed from analysis. Standing, shading, shifting, sitting, head tucking, and other states were those during which we considered that the pair was "On" the nest. Standing, shading, and sitting states were considered "Head up" states.

Incomplete driving treatments were removed from the analysis. Driving treatments containing more passes than were specified in the protocol were used in the analysis, but these were reduced by ending the treatments at a time that we estimated the vehicle would have exited the buffer after the last scheduled pass. Although we conducted 2 driving treatments per day in 2014, we included only the first treatment in each day in our analyses in order to

reduce any bias due to the nonindependence of samples taken within the same day.

Heart rate recordings review. We reviewed heart rate recordings using Adobe Audition (Adobe Systems, San Jose, California, USA) audio-editing software. We counted heart beats as we heard them in the recording, and compared our counts to the number of spikes in the visual waveform produced in Adobe Audition, verifying that both the auditory and the visual counts were the same. When necessary, we slowed the playback speed of rapid heart rate recordings to facilitate these analyses. If a bird was not on its nest at the time of the driving treatment or if we were unable to obtain an unambiguous measure of heart rate, we discarded the sample. We took 10-s samples of heart rates centered on the time that a vehicle passed an incubating bird (as in Nephew et al. 2003 and Borneman et al. 2014). We then extrapolated these samples to beats per minute. We took 10-s heart rate samples from comparable times during the corresponding control periods. This equated to 20 potential 10-s heart rate samples for each sampling period in 2014 and 10 in 2015. The observed number of samples could be lower depending on the number of vehicle passes for which an individual stayed on the nest. In 2015, we assigned individual oystercatcher identifications to the heart rates for which the bird's identity could be verified using the trail camera images.

Data Analysis

We used program R for all data analyses (R Core Team 2015). Analyses were performed for each year separately using a nonparametric randomized permutation procedure (Adams and Anthony 1996). We summarized the behavioral responses of each pair of oystercatchers, averaging the responses for all driving and control periods sampled for each of the pairs. We calculated the differences between the averages across pairs and the means of those differences, referred to as the observed effect size ($\hat{\mu}_d$), such that:

$$\hat{\mu}_d = \frac{\vec{y}_{driving} - \vec{y}_{control}}{n},$$

where $\vec{y}$ is the vector of responses, averaged for each pair, and n is the number of pairs. Under the null hypothesis, in which there is no effect of treatment on the response, $\hat{\mu}_d = 0$. To determine whether effect sizes were significant, we compared them (or their absolute values for 2-tailed tests) with distributions of randomly generated effect sizes. We created these distributions by first randomly assigning observed pair averages to treatments. We then calculated the new effect sizes for these permutations. The permutation procedure was repeated 9,999 times, creating 9,999

randomly generated effect sizes. We determined the P-value for one-tailed tests by dividing the rank of the observed effect size by the total number of permutations (9,999 random + 1 observed). For 2-tailed tests, we determined the P-value by dividing the rank of the observed effect size minus one by the total number of permutations and then subtracting that value from 1.

The paired 2-sample test results from each year were evaluated jointly with Fisher's method for combined statistics, using the sumlog function from the metap library (Dewey 2016). This method was used in order to allow for the slight changes to experimental design between 2014 and 2015 and for duplication in the pairs included across years at Cape Hatteras National Seashore.

We used general linear mixed models (GLMM) with the glmer function from the lme4 library (Bates et al. 2015) to assess the interactive effects of treatment with island, time of day, and nest age on each response variable in 2015 (Bolker et al. 2009). Pair ID and paired treatment (Treat ID) were included as random effects to account for our paired study design. Responses of proportional value (e.g., proportion of time spent on the nest and with the head up) were logit transformed, adding an adjustment to the numerator and denominator of the logit function to account for 0 and 1 values in the datasets. The adjustment was determined by the minimum nonzero value in each dataset (as in Warton and Hui 2011). We evaluated these models using the Anova function in the stats library (R Core Team 2015), using the Type III sums of squares Wald F test statistic for hypothesis testing. These methods are robust to errors in inference associated with nonnormality and overdispersion, which occurred in our data, even following transformation. Because the heart rate data fit the assumptions of normality, for this analysis we used a classical ANOVA F test with a Satterthwaite approximation for degrees of freedom (Bolker et al. 2009). Sample sizes in 2014 were insufficient to assess interactions.

We considered results to be significant if the corresponding P-values were less than a type I error rate (alpha) of 0.05. It is important to note that performing multiple hypothesis tests increases the probability of falsely rejecting one of the null hypotheses (Verhoeven et al. 2005). However, we chose not to lower our alpha values because of our low sample sizes.

Oystercatcher behavior. We assessed the behavioral responses of American Oystercatchers to ORVs by quantifying, for each pair, the percentage of time spent on the nest, the percentage of time spent with the head up while incubating, and the rate at which departure events from the nest occurred during each paired control and driving period. Of the 10 nests exposed to experimental driving tests in 2014 (Figure 3), only 6 were included in behavioral data analyses due to equipment failure and early nest failure. The 6 nests used in our analyses for 2014 were
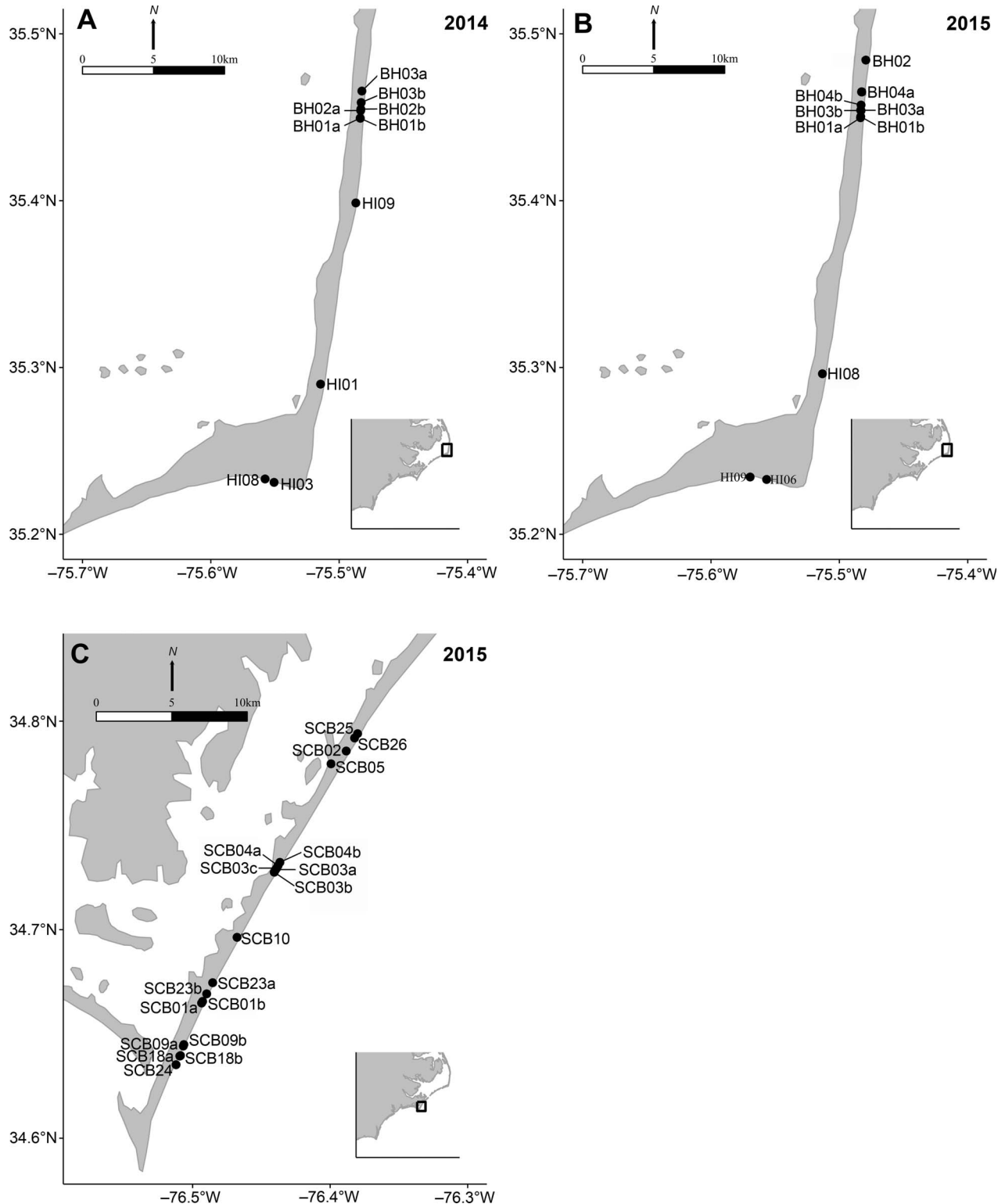
FIGURE 3. Experimental driving nest locations by pair of American Oystercatchers at (**A, B**) Cape Hatteras National Seashore and (**C**) Cape Lookout National Seashore, North Carolina, USA. Experimental driving nests were those exposed to experimental driving treatments in 2014 and 2015 using off-road passenger vehicles (ORVs). Pairs identified by the prefix "HI" were in the Hatteras Island district, while pairs identified by the prefix "BH" were in the Bodie-Hatteras district, in Cape Hatteras National Seashore. Nests with the prefix "SCB" were located on South Core Banks in Cape Lookout National Seashore. In some cases, pairs made multiple nesting attempts over the course of the season. Multiple nests of the same pair are indicated with a, b, or c following the pair number. This illustration does not included all nests laid, only those which were exposed to experimental driving treatments.

associated with 6 independent pairs of oystercatchers. One oystercatcher pair from 2015 was excluded from our behavioral analyses because equipment failure and early nest failure limited the number of subsamples.

Nest attendance. Our analysis was one-tailed, with the alternative hypothesis that the percentage of time spent on the nest would be lower for experimental driving periods than for control periods ($\hat{\mu}_d < 0$).

Head-tucking behavior. This analysis was also one-tailed, with the alternative hypothesis that the percentage of time spent with the head up would be higher during experimental driving periods than during control periods ($\hat{\mu}_d > 0$).

Nest departures. This analysis was also one-tailed, with the alternative hypothesis that the rate of departures would be higher for experimental driving periods than for control periods ($\hat{\mu}_d > 0$).

Heart rate. We assessed the physiological responses of American Oystercatchers to driving by quantifying, for each pair, the average heart rate during each control and driving period. Of the 10 nests exposed to experimental driving treatments in 2014, only 6 were included in the heart rate analysis due to equipment failure and early nest failure. The 6 nests used in our analysis for 2014 were associated with 6 independent pairs of oystercatchers. Of the 19 pairs of oystercatchers exposed to experimental driving treatments in 2015, 14 were included in our heart rate analysis. Additionally, we were able to calculate average heart rates for control and driving periods for 11 individuals identified using trail camera images. Equipment failure and early nest failure created some limitations on the number of subsamples. Poor heart rate recordings also limited the number of subsamples available for analysis. Nests of 2 pairs did not receive heart rate monitors because the nests had too many eggs (>3) or were in locations unsuitable for installing monitoring equipment.

The heart rate analysis was 2-tailed, with the alternative hypothesis that heart rate would differ between driving and control periods ($\hat{\mu}_d \neq 0$).

RESULTS

In 2014, we conducted experimental driving treatments at 10 nests of 7 breeding oystercatcher pairs (Figure 3). In 2015, we conducted experimental driving treatments at 10 nests of 7 breeding oystercatcher pairs on Hatteras Island and 19 nests of 12 breeding oystercatcher pairs on South Core Banks (Figure 3).

Oystercatcher Behavior

Nest attendance. On average, oystercatcher pairs spent 8% less time on their nests during driving periods than during control periods in 2014 and 25% less time in 2015 (Figure 4). We did not detect a statistically significant difference in the percentage of time that oystercatchers spent on their nests in 2014 ($\hat{\mu}_d = -0.08 \pm 0.06$, $n = 6$, $P = 0.12$; Figure 4). However, paired permutation test results from 2015 did suggest a significant decrease in the amount of time spent on the nest in response to driving treatments ($\hat{\mu}_d = -0.25 \pm 0.04$, $n = 18$, $P < 0.001$; Figure 4). Fisher's method for combining tests revealed a significant decrease in the proportion of time that pairs spent on their nests during driving treatments over the 2-yr study period ($\chi^2_4 = 22.62$, $P < 0.001$), and the analysis of variance confirmed this result (Table 1). The interaction between treatment and time of day was significant for determining the proportion of time that each pair spent on its nest (Table 1). On average, pairs spent more time on their nests during control treatments than during driving treatments, but this difference dropped dramatically during afternoon treatments (Figure 5). There was limited evidence that the driving treatment effect interacted with island and nest age, but these effects were not statistically significant (Table 1).

Head-tucking behavior. On average, oystercatcher pairs spent 13% more time in a "head up" posture when they were attending their nests during driving periods than during control periods in 2014 and 13% more time in 2015. These results equated to a statistically significant difference in 2015 ($\hat{\mu}_d = 0.13 \pm 0.03$, $n = 18$, $P < 0.001$), but not in 2014 ($\hat{\mu}_d = 0.13 \pm 0.07$, $n = 6$, $P = 0.09$; Figure 4). Combining tests over the 2 yr revealed a significant increase in the proportion of time that incubating pairs spent in a "head up" posture during driving treatments ($\chi^2_4 = 22.33$, $P < 0.001$).

The generalized linear mixed model showed no evidence of a treatment effect (Table 1). Similarly, none of the interaction effects were significant (Table 1, Figure 5).

Nest departures. Results from 2014 alone did not support a statistically significant difference in the rate at which incubating oystercatcher pairs left their nests during driving vs. control periods ($\hat{\mu}_d = 0.0003 \pm 0.0003$ departures s^{-1}, $n = 6$, $P = 0.11$; Figure 4). Although the difference in rate was small, results from 2015 indicated that nesting oystercatchers left their nests at a significantly higher rate during driving periods than during control periods ($\hat{\mu}_d = 0.0010 \pm 0.0003$ departures s^{-1}, $n = 18$, $P < 0.001$; Figure 4). Combining tests over the 2 yr revealed a statistically significant increase in the rate at which incubating pairs departed their nests during driving treatments compared with control periods ($\chi^2_4 = 19.67$, $P < 0.001$).

The analysis of variance indicated a statistically significant effect of treatment on nest departure rate for incubating birds (Table 1). There was limited evidence that the interactions of treatment with island and nest age influenced departure rate, but these interaction effects
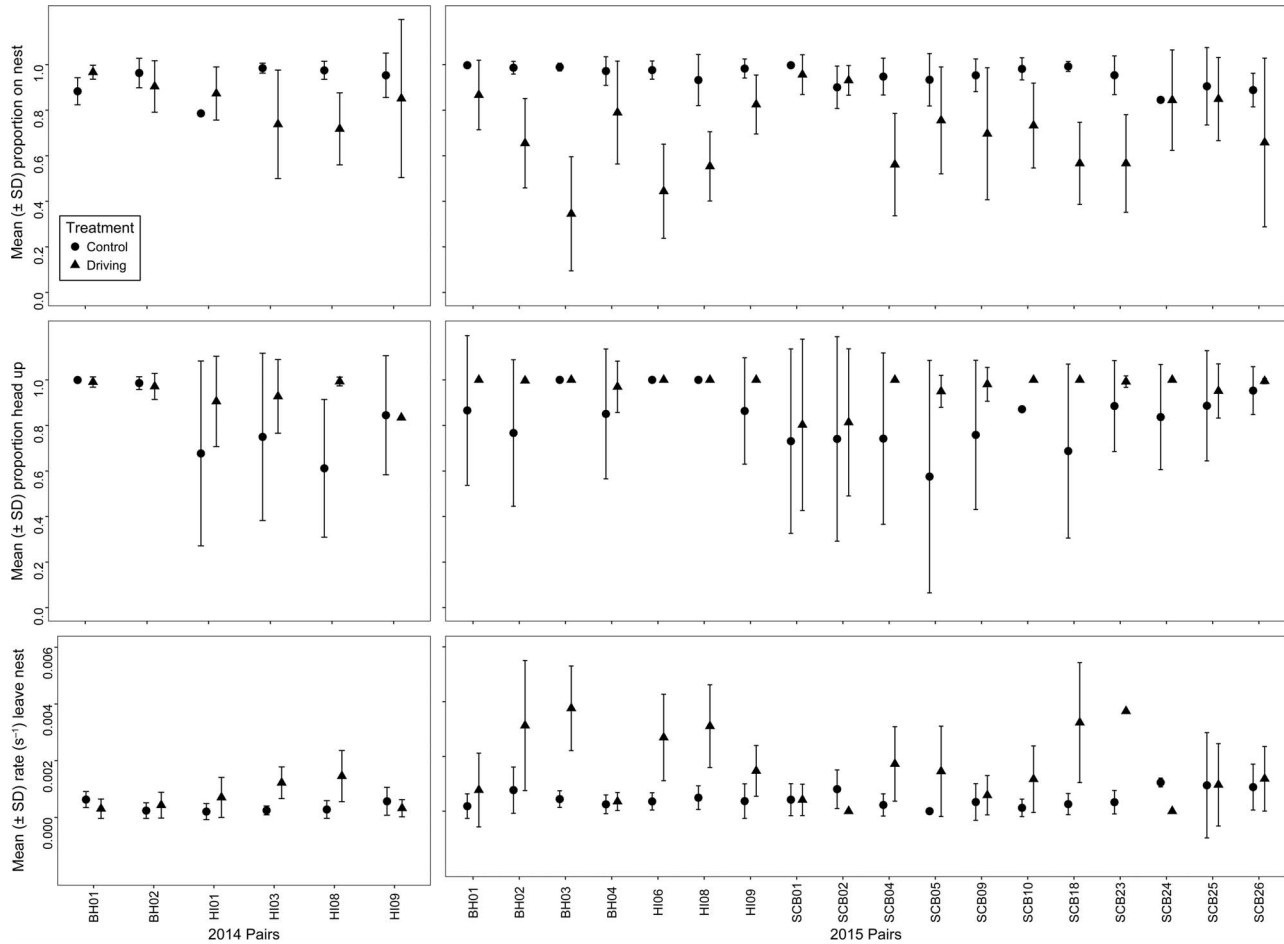
FIGURE 4. Behavioral response paired randomized permutation results for pairs of American Oystercatchers exposed to off-road passenger vehicles (ORVs) during driving experiments in Cape Hatteras and Cape Lookout National Seashores, North Carolina, USA, 2014 and 2015. BH and HI indicate pairs from Hatteras Island, Cape Hatteras; SCB indicates pairs from South Core Banks, Cape Lookout. Plots illustrate the behavioral responses of pairs across control and driving treatments; symbols show the mean response, and error bars indicate ±1 SD. "Mean proportion on nest" indicates the proportion of time that a pair remained on the nest, "Mean proportion head up" shows the proportion of time that an incubating oystercatcher had its head up in an alert posture, and "Mean rate leave nest" refers to the average number of times (per second) that an incubating oystercatcher left the nest.

were not statistically significant (Table 1). There was no evidence that the interaction effect of treatment with time of day was significant (Table 1, Figure 5).

Heart Rate

In 2014, oystercatcher heart rates decreased 25.39 beats min^{-1} during driving periods compared with control periods. Variation among pairs was high, but results from 2014 indicated a statistically significant difference in the heart rates of incubating oystercatcher pairs between control and driving periods ($\hat{\mu}_d = -25.39 \pm 10.07$, $n = 6$, $P = 0.001$; Figure 6). Results from 2015 did not indicate a significant difference in heart rate between control and driving periods, although the direction of change was the same as for 2014 ($\hat{\mu}_d = -3.93 \pm 13.22$, $n = 13$, $P = 0.76$; Figure 6). Combining tests over the 2 yr indicated a

statistically significant decrease in the heart rates of incubating birds during driving periods compared with control periods ($\chi^2_4 = 13.70$, $P = 0.008$). However, the analysis of variance showed no response of heart rate to treatment (Table 2). Similarly, none of the interaction effects were significant (Table 2, Figure 5).

The result of the paired test for 2015 nests was likely due in part to the large sample variance between individuals of a pair: Control period heart rates across all nests ranged from 108 beats min^{-1} to 498 beats min^{-1}. The permutation procedure to test the change in heart rate across treatment types for individually identifiable oystercatchers revealed a high amount of variation between individuals ($\hat{\mu}_d = 7.23 \pm 0.11$, $n = 11$, $P = 0.55$; Figure 7). Figure 7 also reveals that individuals within the same pair may have responded differently to the experimental driving treatments, sug-

TABLE 1. Generalized linear mixed model results of behavioral responses of beach-nesting American Oystercatchers exposed to off-road passenger vehicles (ORVs) experimentally driven in areas closed to public vehicle access in Cape Hatteras and Cape Lookout National Seashores, North Carolina, USA, in 2015. Effects of interest are in bold font. See Figure 4 for definitions of responses.

Response	Effect	df	df residuals	F-value	P-value
Proportion on nest [‡]	**Treatment (Trtmt)** [†]	1	97	9.297	**0.003**
	Time of day (Time)	2	182	0.279	0.76
	Nest age (Age) [†]	1	184	0.938	0.33
	Island	1	204	0.005	0.95
	Trtmt*Time [†]	**2**	**102**	**3.790**	**0.03**
	Trtmt*Age	**1**	**105**	**0.235**	**0.63**
	Time*Age	2	180	0.282	0.76
	Trtmt*Island	**1**	**102**	**0.990**	**0.32**
	Time*Island	2	183	0.036	0.97
	Age*Island	1	184	0.464	0.50
	Resid(Trtmt*Time*Age) [†]	2	102	4.749	0.01
	Resid(Trtmt*Time*Island)	2	102	2.839	0.06
	Resid(Trtmt*Age*Island)	1	105	0.007	0.93
	Resid(Time*Age*Island)	2	182	0.167	0.85
	Resid(Trtmt*Time*Age*Island) [†]	2	102	5.488	0.005
Proportion in head up posture [‡]	**Treatment (Trtmt)**	**1**	**116**	**0.046**	**0.83**
	Time of day (Time)	2	197	0.435	0.65
	Nest age (Age)	1	212	0.138	0.71
	Island	1	223	0.188	0.67
	Trtmt*Time	**2**	**108**	**0.054**	**0.95**
	Trtmt*Age	**1**	**114**	**0.204**	**0.65**
	Time*Age	2	197	0.609	0.55
	Trtmt*Island	**1**	**116**	**1.742**	**0.19**
	Time*Island	2	200	0.669	0.51
	Age*Island	1	215	0.049	0.83
	Resid(Trtmt*Time*Age)	2	108	0.093	0.91
	Resid(Trtmt*Time*Island)	2	108	0.048	0.94
	Resid(Trtmt*Age*Island)	1	115	1.760	0.19
	Resid(Time*Age*Island)	2	202	0.410	0.67
	Resid(Trtmt*Time*Age*Island)	2	109	0.063	0.94
Rate of nest departure events	**Treatment (Trtmt)** [†]	**1**	**100**	**7.615**	**0.007**
	Time of day (Time)	2	194	0.019	0.98
	Nest age (Age)	1	200	0.011	0.92
	Island [†]	1	208	0.297	0.59
	Trtmt*Time	**2**	**102**	**0.284**	**0.75**
	Trtmt*Age	**1**	**105**	**1.632**	**0.20**
	Time*Age	2	196	0.021	0.98
	Trtmt*Island	**1**	**103**	**2.078**	**0.15**
	Time*Island	2	196	0.164	0.85
	Age*Island [†]	1	200	0.550	0.46
	Resid(Trtmt*Time*Age)	2	102	0.278	0.74
	Resid(Trtmt*Time*Island)	2	102	0.038	0.96
	Resid(Trtmt*Age*Island)	1	105	0.351	0.56
	Resid(Time*Age*Island)	2	197	0.344	0.71
	Resid(Trtmt*Time*Age*Island)	2	102	0.557	0.58

[†] Statistically significant effect.
[‡] Responses are logit transformed.

gesting that some of the variance in response variables measured for pairs may have been due to variation in responses between individuals within the pair.

DISCUSSION

Our results from both seasons combined indicated significant changes in the behaviors of incubating American Oystercatchers due to experimental driving treatments. On average, pairs spent less time on their nests during experimental driving treatment periods than they did during control periods. During the time that pairs were incubating or shading their nests, they spent, on average, more time in a "head up" position during experimental driving treatments than they did during control periods. The average rate of nest departures (s^{-1}) increased slightly
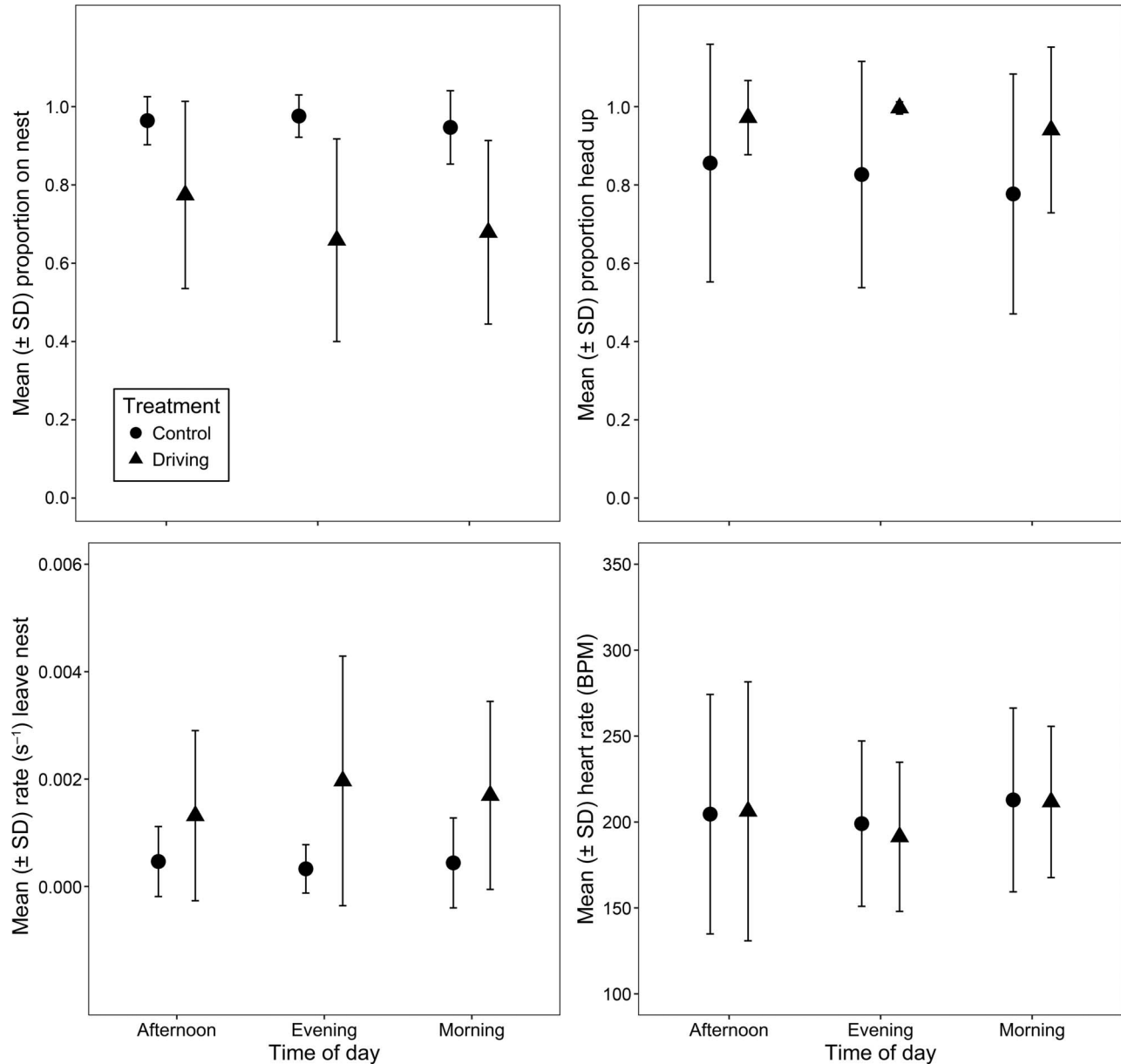
FIGURE 5. Interaction effect of driving treatment with time of day on response behaviors and heart rate of American Oystercatchers in North Carolina, USA, in 2015. "Mean proportion on nest" indicates the proportion of time that pairs remained on the nest, "Mean proportion head up" shows the proportion of time that incubating oystercatchers had their heads up in an alert posture, "Mean rate leave nest" refers to the average number of times (per second) that incubating oystercatchers left their nests, and "Mean heart rate" is the average heart rate (in beats min^{-1}) measured for incubating oystercatchers. Plots illustrate the behavioral and physiological (heart rate) responses of pairs across control and driving treatments; symbols show the mean response, and error bars indicate ±1 SD.

among pairs when confronted with experimental driving. This suggests that, even when pairs were not leaving their nests more frequently in response to driving treatments, they were staying away from their nests for much longer in response to experimental vehicles.

Of particular interest is the unexpected evidence of bradycardia exhibited by several individual oystercatchers

during driving treatments. On average, oystercatcher pairs also exhibited a significant decrease in heart rate during driving periods, though this effect was small in 2015. Although changes in heart rates were statistically significant overall, showing very strong correlation with treatment type for some responses, it is important to note that they were highly variable among pairs and even within
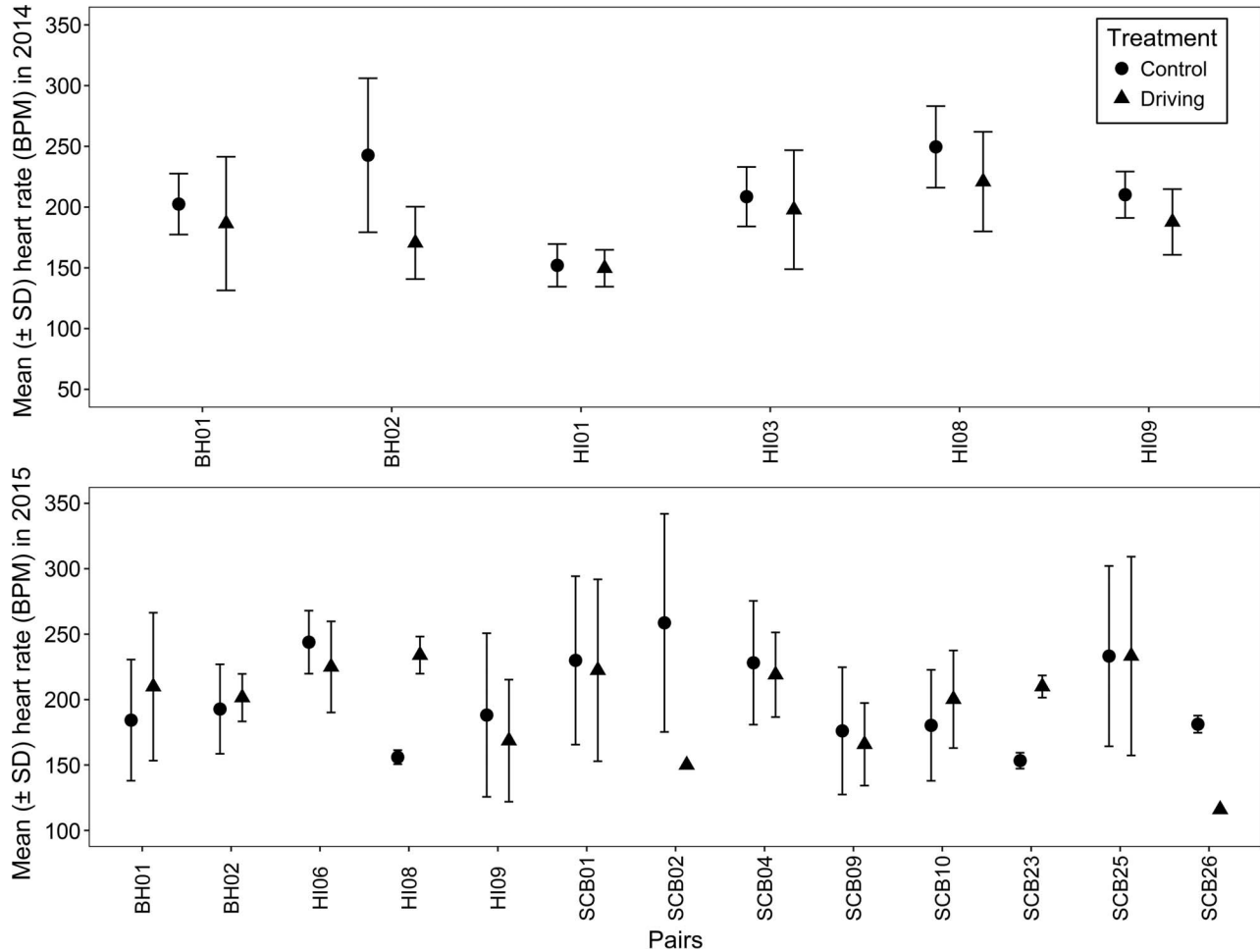
FIGURE 6. Heart rate response paired randomized permutation results for pairs of American Oystercatchers exposed to off-road passenger vehicles (ORVs) during driving experiments in Cape Hatteras and Cape Lookout National Seashores, North Carolina, USA, 2014 and 2015. BH and HI indicate pairs from Hatteras Island, Cape Hatteras; SCB indicates pairs from South Core Banks, Cape Lookout. Plots illustrate the heart rate responses (in beats min^{-1}) of pairs across control and driving treatments; symbols show the mean response, and error bars indicate ±1 SD.

pairs. This could have been due in part to differences in the behavior of individual oystercatchers within a pair. This was demonstrated somewhat by the variation in heart rates between individuals for which identities were verified. Many studies have documented changes in the heart rates of birds and mammals in response to stressors (Weisenberger et al. 1996, Cabanac and Guillemette 2001, de Villiers et al. 2006, Wascher et al. 2011, Viblanc et al. 2012, Derose-Wilson et al. 2015), although they have generally reported increased heart rates as a stress response. In contrast, a study on Willow Ptarmigan (*Lagopus lagopus*) hens found that, while nonincubating individuals exhibited increased heart rates in response to presumed stress-inducing stimuli, hens that were incubating responded to the same stimuli with reduced heart rates, lower respiratory rates, and crouching as part of "freezing" behavior (Steen et al. 1988). The "freezing" behavior described by

Steen et al. (1988) closely resembles the response of American Oystercatchers documented in this study, which suggests that some incubating oystercatchers may respond to driving stimuli with induced bradycardia.

Interaction effects suggested that the response to the experimental driving treatment was slightly reduced during afternoon treatment sessions, when compared with morning or evening treatments (Figure 5), although this was only seen for the proportion of time that pairs spent attending their nests and not for the proportion of time that pairs spent with their heads up nor the rate at which pairs departed their nests. This indicates that incubating adults were similarly responsive to driving treatments at all times of the day, but were quicker to return to their nests during afternoon driving treatments. This may have been to protect their eggs from the sun during the heat of the day.

TABLE 2. ANOVA results from linear mixed model of heart rate responses (in beats min^{-1}) of beach-nesting American Oystercatchers exposed to off-road passenger vehicles (ORVs) experimentally driven in areas closed to public vehicle access in Cape Hatteras and Cape Lookout National Seashores, North Carolina, USA, in 2015. Effects of interest are in bold font.

Effect	Sum of squares	Mean squares	Numerator df	Denominator df	F-value	P-value
Treatment (Trtmt)	**247.9**	**247.9**	**1**	**31**	**0.314**	**0.58**
Time of day (Time)	2,939.6	1,469.8	2	33	1.863	0.17
Nest age (Age)	917.2	917.2	1	41	1.163	0.29
Island	406.7	406.7	1	44	0.515	0.48
Trtmt*Time	**2,398.4**	**1,199.2**	**2**	**608**	**1.520**	**0.22**
Trtmt*Age	**1,221.5**	**1,221.5**	**1**	**601**	**1.550**	**0.21**
Time*Age	1,460.3	730.2	2	40	0.926	0.41
Trtmt*Island	**1,843.7**	**1,843.7**	**1**	**31**	**2.337**	**0.14**
Time*Island	2,319.3	1,159.6	2	33	1.470	0.25
Age*Island	744.4	744.4	1	41	0.944	0.34
Resid(Trtmt*Time*Age)	850.0	425.0	2	602	0.539	0.58
Resid(Trtmt*Time*Island) [†]	20,278.3	10,139.2	2	607	12.852	<<0.001
Resid(Trtmt*Age*Island)	1,641.9	1,641.9	1	601	2.081	0.15
Resid(Time*Age*Island)	3,631.3	1,815.6	2	40	2.301	0.11
Resid(Trtmt*Time*Age*Island) [†]	15,794.5	7,897.2	2	602	10.001	<<0.001

[†] Statistically significant effect.

We note that, while oystercatcher pairs spent more time off their nests and left their nests more frequently during driving treatments than they did during control treatments, these responses diminished slightly as nests approached their expected hatching dates (Table 1). This could have been a result of (1) habituation over time, or (2) decreased willingness to leave the nest unattended as it approached hatching. A similar interaction was not apparent for the head-up or heart rate responses. This provides support for the second explanation, and suggests that oystercatchers continued to respond to driving treatments as nests approached their hatching dates, despite slightly degraded levels of a more obvious flight response.
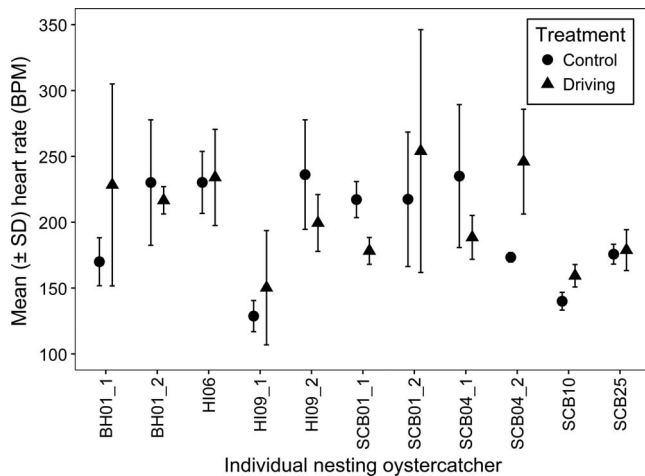
Our experimental approach has provided important insights into the direct effects of ORVs on the physiology and behavior of a beach-nesting shorebird. Despite our inability to randomly select samples, our study design, with explicit hypothesis testing and paired treatment and control samples, has allowed us to draw stronger inferences about the effects of vehicle disturbance than would have been possible from a traditional observational approach (Hill et al. 1997). Our study design allowed us to reduce sources of variation (e.g., weather, tide, distance from disturbance, pedestrian disturbance) that might have confounded results from an observational study. Though the responses that we measured (nest attendance behavior and heart rate) do not directly reflect population-level costs for oystercatchers (Gill et al. 2001), they may reflect fitness consequences. Decreased nest attendance by adults can immediately influence nest survival by exposing nests to predation and overheating (Robert and Ralph 1975, Anderson 2001, Wingfield and Sapolsky 2003). Observational studies have also reported associations between hatching success and vehicle traffic (McGowan and Simons 2006, Schulte and Simons 2015, Borneman et al. 2016).

The amount of vehicle traffic simulated in this experiment (10 passes per experimental day in 2015 or 40 passers per experimental day in 2014) was not

FIGURE 7. Average heart rate of individual American Oystercatchers during experimental driving treatments and control periods in 2015. The pair ID for each oystercatcher is listed along the x-axis. If both individuals of a pair were identified, the pair ID is followed by a "_1" or "_2" suffix. If there is no suffix, then only one individual of the pair could be identified. Prefixes "BH" and "HI" indicate individuals from Hatteras Island, Cape Hatteras National Seashore, and prefix "SCB" indicates individuals from South Core Banks, Cape Lookout National Seashore, North Carolina, USA.

representative of the amount of daily vehicle traffic on open beaches on Hatteras Island. Each nest exposed to experimental driving experienced an average of 5 vehicle passes per day in 2015 and 20 in 2014 from our experimental vehicles. Based on total monthly traffic counts from 2009 to 2016, the most moderate average number of vehicles (including employees) entering the beach on Hatteras Island, Cape Hatteras National Seashore, during the oystercatcher nesting season was during the month of June at Ramp 34. During this month, ~34 vehicles entered the beach each day, on average, through Ramp 34 (National Park Service 2017). Under this scenario, accounting for each vehicle entering and leaving the beach, an oystercatcher nest could be exposed to 68 vehicles passes per day (or 5 passes per hour from 07:00 to 21:00). Compare this with the least moderate estimate, in which 242 vehicles on average enter the beach via Ramps 43 or 44 per day in July. This could equate to 484 vehicle passes per day (or 35 passes per hour) for a nest affected by that ramp's traffic if a drive-through corridor were to be opened (National Park Service 2017). The increased amount of vehicle traffic could potentially exacerbate the results shown here. However, studies on other waterbird species have shown constant low-level disturbance to be less influential on behavior than sporadic sources of disturbance (Hockin et al. 1992). While we did not find evidence of habituation in our study, oystercatchers may be more likely to become habituated to low-intensity vehicle traffic if it were to occur at more regular intervals. However, this could have additional consequences unrelated to oystercatcher incubation behavior (e.g., beach degradation and limited foraging area access).

Although this study did not investigate the consequences of beach driving to oystercatcher populations, there is evidence to suggest that fear responses can have long-term effects on individual health, survival, and reproduction (Elliott et al. 2016). Decreased nest attendance by parents can lower nest survival by increasing the nest's exposure to environmental stressors and predation (Brussee et al. 2016), but fear responses can also have lasting physiological effects that reduce future egg viability and parental body condition (Zanette et al. 2013, Noreikiene et al. 2017). Evidence from this study indicates a negative association between off-road vehicles and oystercatcher nest attendance during incubation. If the management goal is to maximize nest success rates, then evidence suggests that decreasing vehicle presence might increase nest success and parental survival by allowing parents to invest less time and energy into defensive behaviors and more into nest attendance.

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