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RESEARCH ARTICLE

Minimal changes in heart rate of incubating American Oystercatchers (*Haematopus palliatus*) in response to human activity

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ABSTRACT

An organism's heart rate is commonly used as an indicator of physiological stress due to environmental stimuli. We used heart rate to monitor the physiological response of American Oystercatchers (*Haematopus palliatus*) to human activity in their nesting environment. We placed artificial eggs with embedded microphones in 42 oystercatcher nests to record the heart rate of incubating oystercatchers continuously for up to 27 days. We used continuous video and audio recordings collected simultaneously at the nests to relate physiological response of birds (heart rate) to various types of human activity. We observed military and civilian aircraft, off-road vehicles, and pedestrians around nests. With the exception of high-speed, low-altitude military overflights, we found little evidence that oystercatcher heart rates were influenced by most types of human activity. The low-altitude flights were the only human activity to significantly increase average heart rates of incubating oystercatchers (12% above baseline). Although statistically significant, we do not consider the increase in heart rate during high-speed, low-altitude military overflights to be of biological significance. This noninvasive technique may be appropriate for other studies of stress in nesting birds.

Keywords: American Oystercatcher, heart rate, human activity, artificial egg, physiology, stress, disturbance, habituation

Cambios mínimos en ritmo cardiaco de *Haematopus palliatus* durante incubación en respuesta a la actividad humana

RESUMEN

El ritmo cardiaco de un organismo frecuentemente es utilizado como indicador de estrés fisiológico ante estímulos ambientales. Usamos ritmo cardiaco para monitorear la respuesta fisiológica de *Haematopus palliatus* a las actividades humanas en su ambiente de nidificación. Pusimos huevos artificiales con micrófonos empotrados dentro de 42 nidos de *H. palliatus* para grabar, continuamente por hasta 27 días, el ritmo cardiaco de individuos mientras están incubando. Utilizamos video continuo y grabaciones de audio colectadas simultáneamente en los nidos para relacionar la respuesta fisiológica de las aves (ritmo cardiaco) a varios tipos de actividad humana. Observamos aeronaves militares y civiles, vehículos todoterreno, y peatones alrededor de nidos. Con la excepción de sobre-vuelos militares de alta velocidad y baja altitud, encontramos poca evidencia de un efecto de la mayoría de las actividades humanas sobre ritmos cardiacos de *H. palliatus*. Los vuelos de baja altitud fueron la única actividad humana que causó un aumento significativo en ritmo cardiaco promedio de individuos que están incubando (12% por encima del punto de partida). Aunque fue estadísticamente significativo, no consideramos que el aumento en ritmo cardiaco durante sobrevuelos militares de alta velocidad y baja altitud tenga importancia biológica. Esta técnica no-invasiva podría ser apropiada para otros estudios de estrés en aves que se encuentran anidando.

Palabras clave: Haematopus palliatus, ritmo cardiaco, actividad humana, huevo artificial, fisiología, estrés, disturbio, habituación

INTRODUCTION

The effect of human activity on wildlife populations is a topic of great interest to ecologists, land managers, and policymakers (Boyle and Samson 1985, Sutherland et al. 2006, Sutherland 2007, Fleishman et al. 2011). Although research often focuses on behavioral responses of wildlife to human activity, the lack of a behavioral response does not imply a lack of disturbance (Wilson et al. 1991, Nimon et al. 1996). Human activity can also induce physiological responses, such as stress-induced hormone secretion or inhibition (Fowler 1999, Strasser and Heath 2013) or heart rate increases (de Villiers et al. 2006, Ellenberg et al. 2006, Viblanc et al. 2012), that may reduce the fitness and survival of individual animals (Mullner et al. 2004) or suppress reproduction by reducing parental investment and causing nest abandonment (Strasser and Heath 2013, Thierry et al. 2013). Thus, Nisbet (2000) proposes a definition of human disturbance that includes behavioral or physiological changes in response to human activity.

We examined physiological responses of American Oystercatchers (*Haematopus palliatus*) to human activity by measuring the heart rates of incubating birds. Heart rate monitoring is being used with greater frequency as a measure of disturbance (Hüppop and Hagen 1990, Wilson et al. 1991, Nimon et al. 1995, 1996, Weisenberger et al. 1996, Harms et al. 1997, Giese et al. 1999, de Villiers et al. 2006, Ellenberg et al. 2006, Bisson et al. 2009, Viblanc et al. 2012). Weisenberger et al. (1996) found that simulated aircraft noise caused heart rates to increase in desert ungulates. Nesting Eurasian Oystercatchers (*Haematopus ostralegus*; Hüppop and Hagen 1990) and Hall's Giant-Petrels (*Macronectes halli*; de Villiers et al. 2006) exhibited increased heart rates in response to human disturbance. Although Adelie Penguins (*Pygoscelis adeliae*) showed both behavioral changes and increased heart rates in response to approaching helicopters and humans (Culik et al. 1989, Wilson et al. 1991), the behavioral and heart rate responses of Gentoo Penguins (*Pygoscelis papua*) to approaching humans were minimal (Nimon et al. 1995). Simulated jet noise initially increased the heart rate of Black Ducks (*Anas rubripes*), but the response declined rapidly as exposure continued, with no effect on overall daily heart rate, suggesting no net energetic cost to the ducks (Harms et al. 1997). White-eyed Vireos (*Vireo griseus*) exhibited a similar pattern, initially increasing their heart rate in response to human disturbance, but with little evidence of long-term effects on energy expenditure (Bisson et al. 2009).

Monitoring avian heart rates often requires stressful captures and the use of externally mounted or internally implanted monitoring devices (Culik et al. 1989, Wilson et al. 1991, Harms et al. 1997, Bisson et al. 2009, Viblanc et al. 2012). Instead, we adapted a noninvasive method for recording the heart rates of breeding birds using small microphones mounted in false eggs (Nimon et al. 1996, Arnold et al. 2011). We used this technique to determine heart rates of nesting American Oystercatchers in an area with diverse disturbances, including low-flying military aircraft, civilian aircraft, off-road vehicles, and pedestrians.

METHODS

Study Area

We conducted our field research at North Core Banks, the northern-most island of Cape Lookout National Seashore, located on the central coast of North Carolina, USA (Figure 1). Cape Lookout National Seashore, a unit of the U.S. National Park Service, consists of barrier islands that separate Core Sound to the west from the Atlantic Ocean to the east. North Core Banks is a narrow island just under 37 km (23 mi) in length and is characterized by open beach habitat backed by dunes or sand flats. Sand flats can extend across the width of the island from the ocean to Core Sound or can occur as corridors of bare sand between the outer beach and the primary dunes. Behind the primary dunes, grasses, shrub thickets, and occasional areas of low trees extend to Core Sound.

North Core Banks is accessible only by boat, with public transportation provided by a vehicle-and-pedestrian ferry near the southern end of the island and a pedestrian-only ferry at the northern tip. The full length of the island on the outer beach is open to off-road vehicles; however, vehicle traffic is concentrated on the southern portion of the island and pedestrian activity is heavier on the northern tip. An unpaved road behind the primary dunes that extends from island mile 4 to island mile 6, and again from mile 7 to mile 18.5, provides vehicle access during periods of high water or beach closure. The National Park Service extended this road prior to the 2011 bird breeding season to include a section from island mile 19.3 to mile 20.9. Nevertheless, the island is mostly undeveloped and natural habitats predominate, making it an important breeding location for shorebirds, sea turtles, and other wildlife.

Along with ground-based human activity, aircraft also fly in the vicinity of North Core Banks. Cape Lookout National Seashore lies directly under a military airspace, Core Banks Military Operations Area (Core MOA), which is controlled by the United States Marine Corps. North Core Banks is almost entirely encompassed by the Core MOA. In the past, the minimum altitude for high-speed tactical operations (aircraft flying $>$250 knots) in the Core MOA was 3,048 m (10,000 ft); however, the U.S. Marine Corps requested a reduction in the ceiling to 914.4 m (3,000 ft) during the months of May to July. In 2009, the National Park Service and the U.S. Marine Corps agreed to experimentally lower the altitude to 914.4 m to evaluate the possible effects of high-speed military overflights at low altitudes on shorebirds and colonial waterbirds breeding in the park. Airspaces surrounding the Core MOA have fewer altitude restrictions and are used heavily by all divisions of the U.S. military and by civilian aircraft; we regularly observed aircraft flying rapidly at low altitudes outside of the Core MOA.

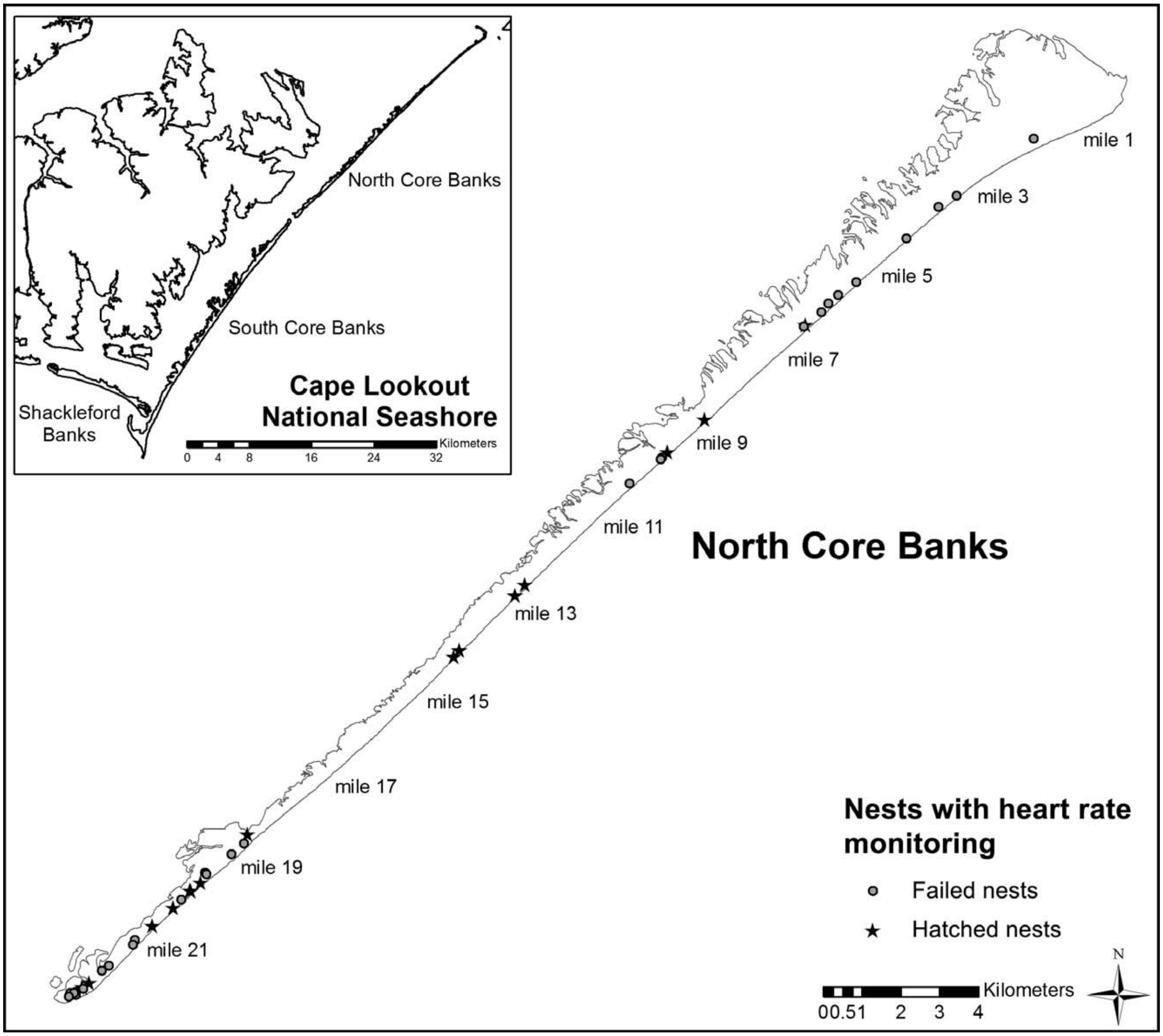

FIGURE 1. North Core Banks, Cape Lookout National Seashore, on the central coast of North Carolina, USA. We conducted heart rate monitoring of incubating American Oystercatchers at 42 nests (38% of 112 total nests) across North Core Banks, of which 15 successfully hatched and 27 failed.

Study Species

American Oystercatchers (*Haematopus palliatus*) are a common breeding shorebird on barrier islands of North Carolina, including Cape Lookout National Seashore. Oystercatchers (Haematopodidae) are found throughout the world, mostly in coastal areas. American Oystercatchers breed throughout eastern North America from Maine to Florida on the Atlantic Coast and along the Gulf of Mexico (American Oystercatcher Working Group et al. 2012). The American Oystercatcher is noted frequently as a species of conservation concern and importance (Brown et al. 2001, U.S. Fish and Wildlife Service 2004, American Oystercatcher Working Group of the National Fish and Wildlife Foundation 2008, North Carolina Wildlife Resources Commission 2008).

North Carolina is an important breeding area for American Oystercatchers, and Cape Lookout National Seashore supports high productivity in the state (T. R. Simons and J. J. Stocking personal communication). Oystercatcher breeding activity at Cape Lookout National Seashore begins in early April. Pairs of oystercatchers establish and defend breeding territories mostly on the open beach or adjacent primary dunes, but may also nest on over-wash flats, sound-side marshes, and dredge-spoil islands. Nests consist of a shallow scrape in the sand or other nesting substrate, in which 1–4 eggs are laid. Both

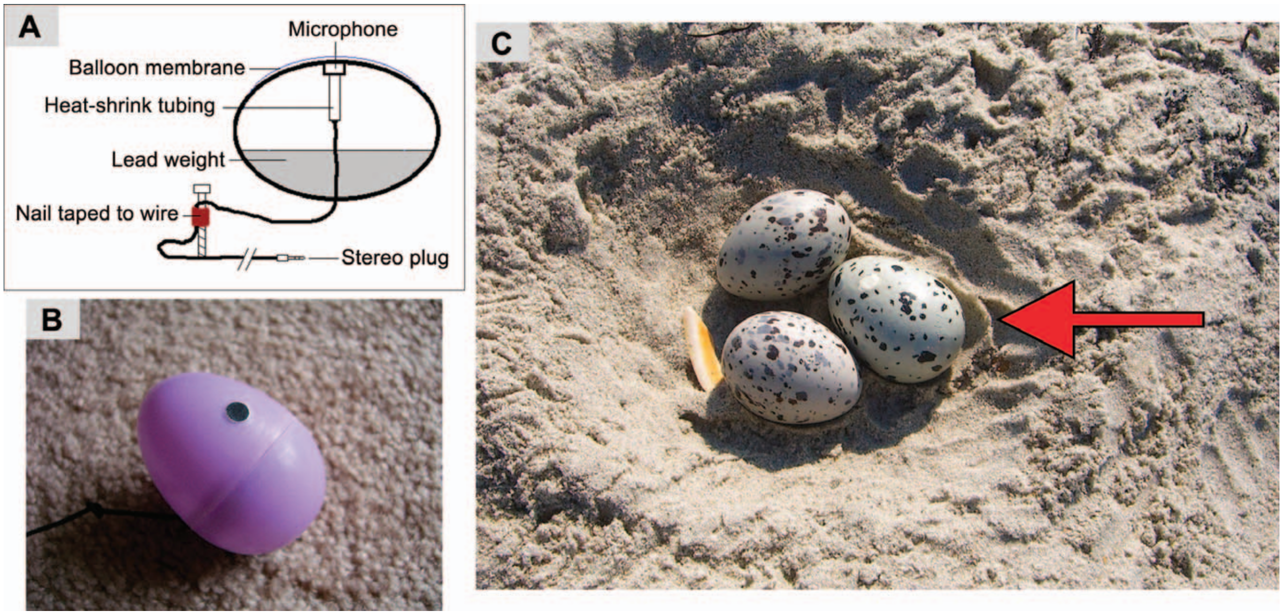

FIGURE 2. To monitor the heart rate of nesting American Oystercatchers, we embedded tiny microphones in plastic eggs (**A** and **B**). Once covered and painted to resemble real American Oystercatcher eggs, the artificial-egg heart-rate monitors were added to active nests (**C**) and recorded the heart rate of incubating American Oystercatchers. The arrow indicates the artificial egg in the nest. The microphone is visible as a white spot on the upper surface of the egg.

adults share incubation duties for 27 days until the eggs hatch. If nests are destroyed before hatching, pairs may renest, attempting multiple clutches in a single breeding season. When nests are successful, the semiprecocial chicks leave the nest within a few hours after hatching.

Nest Monitoring

Anthropogenic activity and behavior monitoring at nests. We monitored incubation behavior of American Oystercatchers and human activity in the vicinity of their nests during the 2010 and 2011 breeding seasons with continuous digital video and audio recording. We were unable to monitor all American Oystercatcher nests with recording equipment and therefore used a stratified sampling scheme in which we selected breeding pairs for monitoring from strata determined by location along the length of the island, location relative to the primary dunes, and vehicle closure status. We recorded selected nests continually for 24 hr per day until the nest either failed or hatched. Video cameras monitored incubating oystercatchers' behavior, as well as the surrounding beach for human activity, while audio recordings provided a record of both natural and anthropogenic sounds in the immediate vicinity of oystercatcher nests. Due to differences in the landscape around nests, the total area surveyed by video recordings varied among nests. Video recordings also provided information about nest predation and interspecific interactions.

We classified nests by habitat as either open sand or dune nests. Open sand habitats included the open beach and sand flats where the terrain was flat and open with minimal vegetation. Dune habitats were areas of elevated, more variable terrain with more vegetation.

Heart rate monitoring at nests. We recorded the heart rates of incubating oystercatchers using miniature microphones (Electret Condenser Microphones, 6.00 mm diameter, sensitivity: –46 dB ± 3 dB, PUI Audio, Dayton, Ohio, USA) implanted in artificial eggs that were added to active nests. This allowed us to collect continuous audio recordings of the incubating adult oystercatcher's heart rate for the duration of the nest incubation period (microphones were neither oriented correctly, nor sensitive enough, to record the heart rate of the chicks in the real eggs). This minimally invasive design has been used previously with terns and gulls (Arnold et al. 2011), but for much shorter monitoring intervals. We constructed our heart rate monitors by drilling a hole in a plastic egg and mounting a small microphone flush with the surface of the shell (Figure 2). A wire lead attached to the microphone allowed us to connect the microphone to an external digital audio recorder. The plastic eggs and microphones were then covered with a balloon to protect and conceal the microphone. The covering was painted to resemble an American Oystercatcher egg. We assembled 20 artificial egg monitors, placing one monitor in each nest selected for heart rate monitoring. Egg monitors were added to clutches of one, two, or three eggs. We did not add an artificial egg to the single nest with a four-egg clutch, because four eggs is the maximum number of eggs that oystercatchers are known to incubate. We placed the audio recorder and a battery in a plastic bucket ~10 m from the nest, burying both the bucket and the wire connecting the microphone and audio recorder. We attached a 15 cm screw to the wire slightly below the artificial egg. The screw was secured in the sand below the nest to maintain the correct orientation of the egg and microphone, which increased the consistency and quality of heart rate recordings. Once we began heart rate monitoring at a nest, we continued monitoring continuously 24 hr per day for the duration of the incubation period until the nest either hatched or failed. Artificial eggs were inspected closely every few days and were periodically replaced as their outer membrane deteriorated; audio recorders and batteries were replaced as needed. On occasion, the artificial egg became separated from the rest of the clutch due to the activity of the incubating adults. When this occurred we moved the artificial egg, usually just a few centimeters, to the location of the other eggs.

Although we were initially concerned that the artificial eggs might disturb incubating birds, we saw little indication of this problem. In fact, on several occasions following destruction of the clutch by a nest predator, adults returned to their nests and continued to incubate the remaining artificial egg until we removed it. Using binoculars from a distance, we checked nests with heart rate monitoring equipment daily to verify that the real eggs had not been depredated.

Analysis of Recordings

We collected approximately 48,000 hr of video and audio recordings and 12,000 hr of heart rate recordings during the 2010 and 2011 breeding seasons. Starting on the day following the deployment of recording equipment at a nest (i.e. the first full 24-hour day of recording), we reviewed all video and audio recording files within a 24 hr period from every fourth day of monitoring. From these subsamples, we noted every occasion when an oystercatcher left or returned to its nest ($n = 6{,}202$), every incident of human activity (heard on the audio recordings, seen on the video recordings, or both; $n = 7{,}285$), and the behavior of the incubating oystercatcher before and during the human activity events ($n = 7{,}248$). A human activity event began at the time when an incident of human activity was first seen or heard on the recordings to the time it was no longer seen or heard. The U.S. Marine Corps provided information on the timing, location, speed, and altitude of military overflights through the Core MOA airspace above Cape Lookout National Seashore. We used this information with the time stamps on the audio and video recordings to identify the Core MOA flights on our recordings and to distinguish these overflights from other aircraft flights. We reviewed all video, audio, and heart rate recordings collected during known Core MOA overflights. We used audio-recording processing software, Audio2NVSPL and Acoustic Monitoring Toolbox (version 1.3877), developed by the Natural Sounds and Night Skies Division of the National Park Service (Joyce 2009), to calculate sound level values (dBA) for all human activity events heard on audio recordings.

Anthropogenic activities recorded in the nesting environment included Core MOA overflights (military aircraft corresponding with reported flights through the Core MOA; $n = 290$), other military fixed-wing aircraft flights (military aircraft not reported as flying through the Core MOA; $n = 1{,}477$), civilian fixed-wing aircraft flights ($n = 492$), rotary-wing aircraft flights (we could not differentiate military from civilian rotary-wing aircraft; $n = 135$), passenger vehicle events ($n = 2{,}109$), all-terrain vehicle events (ATVs, single passenger; $n = 1{,}111$), utility-terrain vehicle events (UTVs, all-terrain vehicles with two passengers side by side; $n = 211$), and pedestrian events ($n = 154$).

If an oystercatcher was on the nest during a human activity event, we reviewed the heart rate recording corresponding to that incident, and calculated heart rate before, during, and after as many human activity events as possible. It was not always possible to calculate heart rates due to poor quality recordings. We used Adobe Audition audio-editing software (Adobe Systems, San Jose, California, USA) to analyze heart rate recordings. We counted the heartbeats as we heard them in the recording, and compared those counts to the number of spikes on 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 we were unable to obtain an unambiguous measure of heart rate, we discarded the sample. We took 10 s samples of heart rate at the peak of human activity events (either the loudest point of the event on the audio recordings or when the human activity stimulus was closest to the nest in the video recordings) and extrapolated those samples to beats per minute by multiplying the sampled heart rate by six. As a baseline control, heart rates were measured in a similar manner exactly 20 min before and 20 min after the peak time of an event. When comparing paired human activity event samples and control samples, we chose 20 min as the time period between the before, during, and after samples to standardize potentially confounding variation by other variables (such as time of day or environmental conditions). From observations of human activity patterns and behavior during fieldwork, we felt that 20 min was a long enough time frame to insure nondisturbance during the control samples.

If necessary, we used Adobe Audition to review video, audio, and heart rate files simultaneously. Concurrent viewing and listening allowed us to align the three recordings with a high degree of temporal accuracy, not achievable by the time stamp on the recordings alone.

Statistical Analysis

All statistical analyses were conducted in R (R Development Core Team 2011), applying a significance level of $P < 0.05$. Values are reported as means $\pm$ SE. We compared hatching success ratios of nests with and without heart rate monitors using a chi-square test. Unfortunately, we could not identify individuals in a pair, as American Oystercatchers are sexually monomorphic. Although some individuals had identifying coded leg bands, the resolution of our video recordings was not high enough to see the leg bands. Therefore, heart rate samples are attributed to a breeding pair, not to individual oystercatchers.

Only samples for which the baseline heart rate measurement (20 min before human activity) was not confounded by other human activity events were used in analyses, assuring to the best of our ability that these samples were resting heart rates. Initially, we pooled heart rate samples from all pairs of oystercatchers for a general analysis of their physiological response to human activity. We compared heart rate samples before and during human activity using paired *t*-tests, hypothesizing that heart rates during human activity would be higher than baseline heart rates 20 min before incidents of human activity. We assessed oystercatcher responses to human activity as a whole, as well as assessing responses to each type of human activity individually. We also compared heart rate samples after human activity to heart rate samples before and during human activity using paired *t*-tests, hypothesizing that heart rates 20 min after human activity events would be lower than heart rates during human activity and the same as baseline heart rates 20 min before human activity. We compared sound levels and oystercatcher heart rates during human activity using simple linear regression.

We also measured the relative change of oystercatcher heart rates (%) from baseline before to during human activity events (((heart rate during human activity − baseline heart rate before human activity) / baseline heart rate before human activity)*100) to standardize the response variable for further analyses.

We postulated that other variables may have been affecting the physiological response of oystercatchers, such as the habitat of the nesting environment, the daily amount of human activity occurring around a nest, clutch size, and the stage of the incubation period in which the event occurred, as well as the potential for variation among the responses of individual breeding pairs of oystercatchers. To assess the relative influence of these additional variables, we conducted an analysis using a linear mixed modeling approach, and contrasted competing models using information-theoretic methods. Linear mixed models were constructed and evaluated using the lme4 and AICcmodavg packages in R, ranking models according to adjusted Akaike's Information Criterion (AIC_c). In these models, we treated human activity type, nesting habitat type, the mean number of human activity events per day, year, clutch size, and the day in the incubation period of the nest as fixed effects, and nest (breeding pair) as a random effect. We included human activity type and mean number of human activity events per day in a multiple variable model. In preliminary analyses, interactions between variables were not significant, so we did not include interactions in our final models.

RESULTS

Heart Rate Monitoring

We monitored 42 nests (38% of 112 total nests; 18 in 2010 and 24 in 2011) of 36 breeding pairs of oystercatchers with heart-rate-monitoring artificial eggs. Of those 42 nests, 15 successfully hatched and 27 failed (Figure 1). The proportion of successfully hatched heart-rate-monitored nests (0.36) was not significantly different from the proportion without heart rate monitors (0.26; $\chi^2_1 = 0.83$, $P = 0.36$).

Physiological Response

We calculated a "resting" heart rate for American Oystercatchers by opportunistically sampling heart rates of incubating oystercatchers with their bills tucked under a wing, a common resting posture in birds, when there was no evidence of human activity on the video and audio recordings. Resting heart rate of incubating oystercatchers ranged from 126 to 288 beats per minute, with an average of 189 $\pm$ 6 beats per minute ($n = 35$ samples from 18 pairs).

Heart rate samples taken before, during, and after human activity came from 28 oystercatcher pairs (recording equipment malfunction or nest failure prevented sampling of all 36 pairs monitored). Baseline heart rate samples 20 min before human activity events ranged from 108 to 342 beats per minute ($n = 501$), while heart rate samples during human activity ranged from 114 to 312 beats per minute ($n = 501$). The average heart rate of incubating oystercatchers during human activity events for all activity types combined (188 $\pm$ 2 beats per minute) was not significantly different from the baseline heart rate of oystercatchers 20 min before the human activity events occurred (189 $\pm$ 2 beats per minute; paired $t = 1.50$, df $= 500$, $P = 0.14$, $n = 501$). Heart rate 20 min after human activity events ranged from 108 to 366 beats per minute ($n = 355$). The average heart rate 20 min after human activity events for all activity types combined (187 $\pm$ 2 beats per

TABLE 1. Incubating American Oystercatcher heart rates (HR, beats per minute [bpm]) before and during different types of human activity in the vicinity of their nests. Core MOA flights were military aircraft corresponding with reported flights through the military operations area (Core MOA) above Cape Lookout National Seashore, North Carolina, USA, while military fixed-wing aircraft were other military aircraft not reported as flying through the Core MOA. ATVs were single-passenger all-terrain vehicles, while UTVs were side-by-side utility-terrain vehicles.

Human activity type	HR before (mean ± SE bpm)	HR during (mean ± SE bpm)	paired *t*	df	*n*	*P*-value
Core MOA flight (low-altitude)	163 ± 6	178 ± 6	−1.74	18	19	0.049*
Core MOA flight (high-altitude)	187 ± 10	176 ± 9	1.29	12	13	0.89
Military fixed-wing aircraft	190 ± 3	186 ± 3	2.04	129	130	0.98
Civilian fixed-wing aircraft	185 ± 4	182 ± 3	0.81	73	74	0.79
Rotary-wing aircraft	176 ± 9	188 ± 14	−1.26	10	11	0.12
Passenger vehicle	192 ± 3	190 ± 3	1.01	184	185	0.84
ATV	192 ± 6	191 ± 5	0.03	40	41	0.51
UTV	208 ± 8	199 ± 8	1.49	17	18	0.92
Pedestrian	190 ± 9	202 ± 9	−1.36	9	10	0.10

* Significant at $P < 0.05$.

minute) did not differ significantly from the baseline 20 min before human activity events (190 ± 2 beats per minute; paired $t = 1.29$, df = 354, $P = 0.20$, $n = 355$) nor from the average during human activity events (187 ± 2 beats per minute; $t = 0.23$, df = 354, $P = 0.82$, $n = 355$). However, the average heart rate of oystercatchers during low-altitude Core MOA flights (178 ± 6 beats per minute) was significantly higher than the baseline heart rate 20 min before the flights (163 ± 6 beats per minute; Table 1, Supplementary Material Appendix A). Average heart rate during all other types of human activity events was not significantly different from the baseline heart rate 20 min before each event (Table 1).

We found an average relative change in oystercatcher heart rate before to during all types of human activity events combined of 0.06 ± 0.67% ($n = 501$). The average relative change in heart rate from before to during each individual human activity type ranged from –4.56 ± 5.26% ($n = 13$) for high-altitude MOA flights to 11.84 ± 5.66% ($n = 19$) for low-altitude MOA flights (Figure 3).

We found that the type of human activity was the most important factor influencing the relative change in oystercatcher heart rate, with an AIC_c model weight (w_i) of 0.56 (Table 2). A combined model with type of activity and number of daily events was also well supported (difference in AIC_c from the top model (ΔAIC_c) = 1.15, w_i = 0.31). Both were more strongly supported than the unconditional model (the model including only the random effect; $\Delta AIC_c = 5.24$; Table 2). Low-altitude Core MOA flights were responsible for the greatest predicted change in average heart rate estimated by the top model, and were the only human activity type with estimated 95% confidence intervals that did not overlap zero, suggesting that these flights significantly influenced a change in heart rate (predicted percentage change in heart rate for low-altitude core MOA flights: 11.86% [95% CI: 5.27, 18.45], high-altitude Core MOA flights: –4.53% (95% CI: –12.48, 3.42), military fixed-wing aircraft flights: –1.82% (95% CI: –4.38, 0.73), civilian fixed-wing aircraft flights: 0.02% (95% CI: –3.34, 3.37), rotary-wing aircraft flights: 7.31% (95% CI: –1.35, 15.97), passenger vehicle events: 0.10% (95% CI: –2.26, 2.06), ATV events: 0.77% (95% CI: –3.72, 5.26), UTV events: –3.59% (95% CI: –10.35, 3.17), and pedestrian events: 7.20% (95% CI: –1.94, 16.34).

We found no relationship between sound levels and oystercatcher heart rates during human activity events ($R^2 = 0.01$, $P = 0.09$), nor did we find a relationship between sound levels and relative change in oystercatcher heart rates before to during human activity events ($R^2 = 0.01$, $P = 0.27$). The noise of rotary-wing aircraft and low-altitude Core MOA flights occasionally drowned out the sound of the heartbeats on the recordings, making it impossible to calculate a heart rate during those events.

DISCUSSION

Physiological changes, such as increased heart rate, often reflect higher stress levels and higher energetic costs, which may be detrimental to reproduction (Wingfield and Sapolsky 2003). Using microphones in eggs and audio- and video-recorders, we were able to monitor both American Oystercatcher heart rates and sources of disturbance for most of the incubation period. Although nesting oystercatchers were subjected to a variety of human activities, including loud low-altitude military overflights, we found minimal effects of human activity on their heart rates.

Our finding that heart rates of incubating oystercatchers were not influenced by most types of human activity may be due to habituation to these activities. Habituation was noted as a potential reason for minimal behavioral responses of several raptor species to low-altitude jet overflights (Ellis et al. 1991, Trimper et al. 1998).

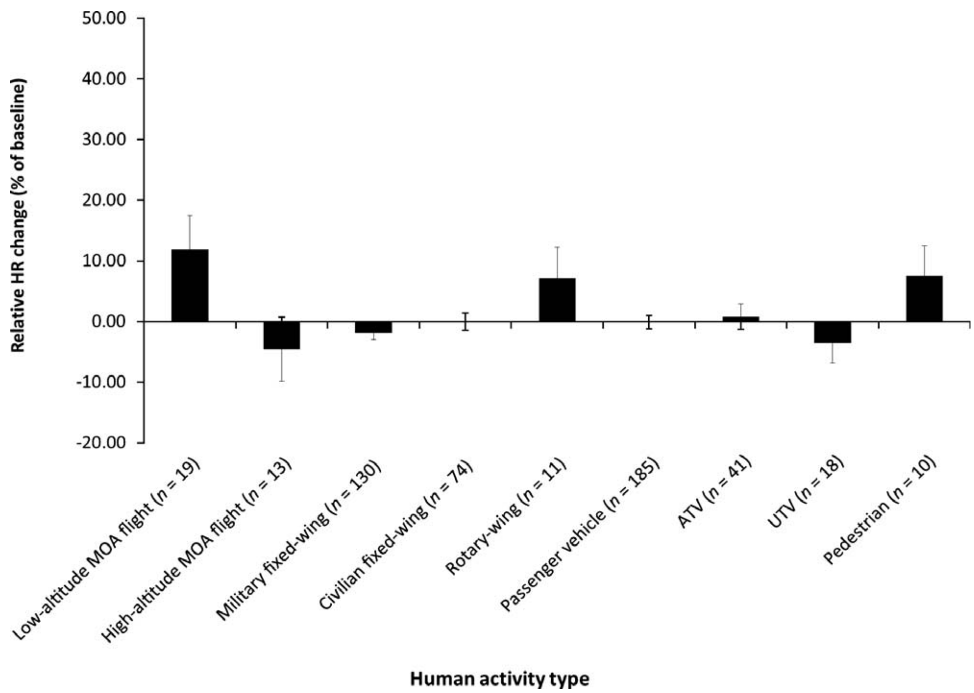

FIGURE 3. Average (± SE) relative change of American Oystercatcher heart rates from baseline before to during human activities. Samples were from 28 oystercatcher pairs monitored for heart rate in 2010 and 2011. MOA flights were military aircraft corresponding with reported flights through the military operations area (Core MOA) above Cape Lookout National Seashore, North Carolina, USA, while military fixed-wing aircraft were other military aircraft not reported as flying through the Core MOA. ATVs were single-passenger all-terrain vehicles, while UTVs were side-by-side utility-terrain vehicles.

Physiological responses may show similar patterns of habituation as well. Harms et al. (1997) suggested habituation as the explanation for declines in heart rate responses of Black Ducks to continued exposure to aircraft noise. King Penguins (*Aptenodytes patagonicus*) also appeared to habituate to chronic human disturbance, as colony members in areas of long-term high disturbance exhibited milder heart rate responses to anthropogenic stressors than birds in low-disturbance areas of the colony (Viblanc et al. 2012).

The recent reduction in the minimum altitude of high-speed Core MOA flights makes these low-altitude flights relatively novel for birds nesting on North Core Banks. The fact that we found evidence that the heart rate of incubating American Oystercatchers increased during high-speed, low-altitude Core MOA flights may indicate that the oystercatchers have not yet habituated to this novel activity. Low-altitude flights may also be perceived as a greater threat by incubating oystercatchers than other forms of human activity because they are louder than other human activities and may be more visible than high-altitude flights. Although our sample sizes were small, we did not see evidence of this in our analysis of rotary-wing aircraft, which also had high sound levels and were observed flying at low altitudes. Unfortunately, the noise

TABLE 2. Model selection results for candidate models describing the relative change in American Oystercatcher heart rates from baseline before to during human activity events at Cape Lookout National Seashore, North Carolina, USA. All models include nest as a random effect. *K* is the number of model parameters, ΔAIC_c is the difference from the top model in Akaike's Information Criterion adjusted for small sample size, AIC_c weight indicates support for each model, and LL is the log-likelihood of each model.

Candidate model	*K*	ΔAIC_c [a]	AIC_c weight	LL
HumanType [b]	11	0.00	0.56	253.83
HumanType + DailyEvents [c]	12	1.15	0.31	254.31
Unconditional [d]	3	5.24	0.04	242.97
DailyEvents	4	6.57	0.02	243.32
ClutchSize	4	6.99	0.02	243.11
Habitat [e]	4	7.04	0.02	243.08
Year	4	7.09	0.02	243.06
IncubationDay [f]	4	7.20	0.02	243.00

[a] The AIC_c value of the top model was –485.13.
[b] Type of human activity.
[c] Mean number of human activity events per day occurring around nests.
[d] The unconditional model includes only nest as a random effect.
[e] Nesting habitat type.
[f] Day in the incubation period of the nest.

of rotary-wing aircraft often obscured the heartbeat of the incubating oystercatchers in our recordings, limiting our ability to obtain a robust sample size for this type of activity. Furthermore, we did not find a relationship between oystercatcher heart rate and the sound level of human activity.

Despite oystercatchers showing evidence of elevated heart rates in response to low-altitude Core MOA flights, they seldom left their nests during these flights (T. E. Borneman personal observation). In contrast, oystercatchers frequently responded to off-road vehicles and pedestrians by leaving their nests, but when they remained on their nests during these types of human activity they did not show elevated heart rates. We suspect that oystercatchers visually detect vehicles and pedestrians at greater distances than aircraft and, as these human activities are ground-based, that oystercatchers often leave their nests in response before their heart rates become elevated. Higher rates of movement to and from a nest may make the nest more vulnerable to predation (Martin et al. 2000), and decreased nest attendance may leave eggs exposed to fluctuating environmental conditions. Oystercatchers that are habituated to vehicles and pedestrians may remain on their nests and not show elevated heart rates.

We did occasionally record very brief increases in heart rate at the beginning of vehicle and pedestrian events. These increases quickly subsided, presumably after the oystercatchers assessed the source of the event. To further evaluate this phenomenon, we subsampled a small number ($n = 93$) of human activity events continuously from 5 min prior to the event to 5 min after the event, taking 20 s samples of heart rate every minute, and we found no indication of bias or inadequacy in our sampling protocol. Nevertheless, we found considerable fluctuation in the baseline heart rate 20 min before human activity, as well as in the resting heart rates of incubating oystercatchers during periods with no evidence of human activity. These variations in our recorded heart rate samples may indicate a response of oystercatchers to activities that were not evident from our video- or audio-monitoring. However, the variations may also reflect the normal range of heart rates for American Oystercatchers. Heart rates may differ among individuals or pairs of oystercatchers, and may be affected by variations in ambient temperature and associated thermoregulatory demands. We were unable to identify unique individuals in a pair, which may have led to pseudoreplication, with one individual potentially being overrepresented in samples from that pair. Because of this limitation, we are unable to draw conclusions specific to heart rates of individual oystercatchers.

Although we did occasionally observe individual cases of elevated heart rate in response to other forms of human activity, low-altitude Core MOA flights were the only type of human activity that significantly increased the heart rate of incubating oystercatchers overall. However, although statistically significant, samples sizes were small, and it is not clear that the increase is biologically significant. We found, on average, that oystercatcher heart rate was 15 beats per minute higher during low-altitude Core MOA flights than baseline rates 20 min before, and the average relative change in heart rate was an increase of only 12% for these flights. A short-term (50 hr) study of a single pair of Eurasian Oystercatchers, a species very similar to American Oystercatchers, found a range of 16 beats per minute difference (152–168 beats per minute) in the baseline heart rate of the pair as they incubated their nest (Hüppop and Hagen 1990). Given that resting heart rates for American Oystercatchers varied over a range of 162 beats per minute difference (126–288 beats per minute), it is unlikely that the increase in heart rate during low-altitude Core MOA flights is biologically significant. Furthermore, the infrequency of these low-altitude flights (24 in 2010 and 35 in 2011 during the 3-month oystercatcher nesting season) suggests that they would have a negligible physiological cost and be of minimal biological significance to nesting oystercatchers.

We believe that the wide range in heart rate that we recorded for American Oystercatchers is attributable to the large number of birds (28 pairs) from which we collected samples and the long duration of time over which samples were gathered (24 hr per day for up to 27 days for each pair). Oystercatchers also nest in a very variable coastal environment. Climatic variables such as wind have been found to affect heart rates of Wandering Albatrosses (*Diomedea exulans*; Weimerskirch et al. 2002) and Adelie Penguins (Culik et al. 1989). The heavily fluctuating nesting environment of oystercatchers may have contributed to the variation in our samples. Our measurements of heart rate for American Oystercatchers were not dissimilar to mean heart rate reported for other nesting coastal birds (Common Terns [*Sterna hirundo*]: 268.6 beats per minute, Caspian Terns [*Hydroprogne caspia*]: 204.2 beats per minute, Ring-billed Gulls [*Larus delawarensis*]: 198.0 beats per minute; Arnold et al. 2011).

American Oystercatchers that remained on their nests during human activity at Cape Lookout National Seashore did not exhibit strong heart rate responses, providing evidence that human activity inflicted minimal physiological disturbance. Mounting evidence suggests that many wildlife species may be more resilient to the activity of humans than has been previously thought (Nimon et al. 1995, Nisbet 2000, Grigg et al. 2012, Rosciano et al. 2013), particularly given time to habituate to nonthreatening disturbances (Conomy et al. 1998, Bisson et al. 2009, Jimenez et al. 2013). Some wildlife species may be able to quickly adapt to changing environmental conditions caused by human activity, both by adjusting behaviors (Jimenez et al. 2013) and by mediating stress (Nimon et al. 1995, Bisson et al. 2009). Wingfield and Sapolsky (2003) argue that chronic stressors may even select for more disturbance-tolerant individuals that can continue to breed under disturbed conditions. Provided that human activity is not lethal and does not render habitat unsuitable, many species of wildlife, including American Oystercatchers, may habituate and adapt to some forms of human disturbance, allowing them to coexist in close proximity to humans.

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