EFFECTS OF TEMPERATURE VARIABILITY ON EGG MASS AND CLUTCH SIZE IN GREAT TITS

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Abstract. Models of climate change generally predict rising mean global temperatures combined with greater variability in some regions. While relationships between mean temperature and several reproductive parameters are well documented, the effect of day-to-day variation in ambient temperature has received little attention. In our study, temperature variation had no significant effects on clutch size in a wild population of Great Tits (*Parus major*). In contrast, egg mass tended to be smaller when ambient temperatures during the week prior to laying were more variable. We suggest that variable temperatures may be disadvantageous to an egg-laying bird. Thermal variability should therefore be considered as a discrete factor, distinct from mean temperature, when assessing the consequences of climate changes for breeding birds.

Key words: egg production, energy expenditure, Great Tits, Parus major*, temperature variability.*

Efectos de la Variabilidad de la Temperatura sobre la Masa del Huevo y el Tamaño de la Nidada en *Parus major*

Resumen. Los modelos de cambio climático generalmente predicen un aumento en la temperatura media global, junto con una mayor variabilidad en algunas regiones. Mientras que la relación entre la temperatura media y varios parámetros reproductivos está bien documentada, el efecto de la variación de la temperatura ambiente de un día a otro ha recibido poca atención. La variación en la temperatura no tuvo efectos significativos en nuestro estudio del tamaño de la nidada en una población silvestre de *Parus major*. En contraste, la masa del huevo tendió a ser menor cuando las temperaturas ambiente durante la semana previa a la puesta fueron más variables. Sugerimos que las temperaturas variables podrían ser desventajosas para un ave que está poniendo huevos. La variación térmica debería por lo tanto ser considerada como un factor discreto, diferente de la temperatura media, cuando se evalúan las consecuencias del cambio climático para las aves reproductivas.

For birds, daily costs of living are greatly influenced by the thermal conditions of the surrounding environment (Kendeigh et al. 1977, Walsberg 1983). Temperature can act on daily energy expenditures by affecting both thermoregulatory costs and foraging behavior. Low temperatures, for example, require increased metabolic heat production by birds at rest (Calder and King 1974, Kendeigh et al. 1977, Walsberg 1983), which is energetically costly (Godfrey and Bryant 2000, Spencer and Bryant 2002).

As a consequence of these metabolic costs and their related effects, temperature can be important, either directly or indirectly, in regulating avian phenology. For many temperate birds, the timing of egg laying is known to be sensitive to temperature, generally advancing under warmer conditions (Lack 1966, van Balen 1973, Meijer et al. 1999, Slater 1999). Low temperatures during the egg-laying period may result in energetic constraints (Perrins 1970, Perrins 1996, Stevenson and Bryant 2000), which can lead to smaller clutch sizes (Lack 1947, Klomp 1970, Cresswell and McCleery 2003) or smaller eggs (Nager and Zandt 1994, Perrins 1996, Stevenson and Bryant 2000). Each of these laying parameters has associated fitness consequences: clutch size determines the upper limit of potential offspring that can be produced in that breeding attempt, and larger egg sizes can improve hatchability and early survival of the offspring (Perrins 1996, Both et al. 1999), especially during poor conditions (Williams 1994, Christians 2002).

With the recent changes in global climate (IPCC 2001) and the correlated effects on plants and animals (such as phenology, reproductive success, and distributions; McCarty 2001, Penuelas and Filella 2001, Parmesan and Yohe 2003), temperature has been shown to play a key role. In many areas, especially in northern latitudes, mean temperature in the last 30 years has risen by up to 3°C and there have also been increases in the range of daily temperatures in some regions (Easterling et al. 1997, IPCC 2001). However, this latter aspect of climate change has received relatively little attention in terms of its possible affects on animals. Studies of captive Japanese Quail (*Cortunix japonica*) have demonstrated that metabolic rates increase with higher daily temperature ranges (Pendlebury et al. 2004) and rapid sinusoidal temperature fluctuations (Prinzinger 1982). Temperature variability is therefore a candidate for affecting energy budgets in wild birds, with possible consequences for reproduc-

tive parameters, such as egg mass (Pendlebury et al. 2004).

The aim of this study was to look at the effects of day-to-day variation in temperature on egg production (egg mass and clutch size), which has not, to our knowledge, been investigated in wild birds. If thermoregulatory costs, particularly those related to temperature variability, trade off against egg-production costs, the resources a bird has available for egg production may alter. Temperature variability may therefore act as a constraint on achieving optimal egg mass or clutch size, and ultimately affect the timing of breeding. Based on observations of elevated costs for captive birds (Pendlebury et al. 2004), we predicted that under variable conditions in the wild, resources would be diverted away from egg production, resulting in reduced egg masses or clutch sizes.

METHODS

STUDY SITE AND POPULATION

We carried out this study in April–June 2001 and 2002 near Stirling, Scotland (56°8′N, 3°54′W), using an established box-nesting population of Great Tits (*Parus major*), breeding in a 2-km^2 area of mixed woodland and parkland. The two study areas were A) Abbey Craig and B) Stirling University campus, Hermitage Wood, and Mine Wood. The woodlands are predominately sycamore (*Acer pseudoplatanus*) and ash (*Fraxinus excelsior*; Shaftow 1992), and the entire study site contained about 200 nestboxes.

TEMPERATURE AND RAINFALL

We placed data loggers (Gemini Data Loggers Ltd, W. Sussex, England) in a shaded site near the center of the study area to record ambient temperature every 5 min. We calculated mean temperatures from these data for the 24-hr period prior to 06:00, the approximate time of egg laying (Perrins 1979, Haftorn 1981), for each day during the egg laying period. We then calculated temperature variability as the variance of 24-hr mean temperatures for the 7-day period prior to the egg being laid. For clutch size analysis, we used the 7-day period prior to clutch initiation.

Data on rainfall were taken from the Parkhead weather station sited on the University campus. The analyses were carried out for rainfall averaged over 1 to 7 days, at 1-day intervals.

EGG LAYING

In April and May, we checked nest boxes for signs of nest building every one to five days. Once the nest-cup was established, we checked nests daily to determine the date of first egg and pattern of laying for each female. We measured the lengths and widths of new eggs with callipers (to 0.1 mm) on the day they were laid, and then numbered them using permanent, non-toxic pens. We calculated egg mass from these measurements, rather than all fresh eggs being weighed, to reduce disturbance to the nests. The following equation was used to estimate egg mass: $W = K_w \times L \times B^2$, where W is the mass of the egg (g), L is the length (cm), B is the width (cm), and K_w is a species-specific constant (Hoyt 1979). K_w for the Stirling Great Tit population was calculated as 0.54 ± 0.001, based on 241
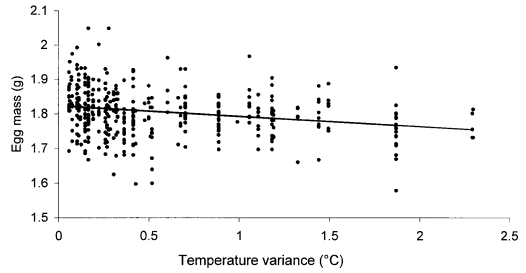

FIGURE 1. Mean egg mass against variance of 24-hr mean temperatures for the 7-day period prior to laying, controlling for mean temperature during the 24-hour period prior to laying, clutch size, laying date, female mass divided by (tarsus)^3, and location. Data from REML output (Table 1).

eggs that were both weighed and measured on the morning of being laid, during 4 different years.

MEASUREMENTS OF FEMALES

Females were caught at the nest three days after clutch completion, rather than during the egg-laying period, so as not to cause nest-desertion or to affect input into egg production. To control for time of day effects, all birds were caught in the afternoon and measured mass to 0.1 g using a Pesola balance. We also measured tarsus length to 0.1 mm using callipers. An index of body condition was derived from the formula mass × (tarsus^3)$^{-1}$. To age females, we used the color of the primary coverts to determine whether a bird was in its first summer, or older (Svensson 1992).

STATISTICAL ANALYSES

We analyzed data using Genstat for Windows (Genstat 5 Committee 2000). We analyzed the variation in egg mass with linear mixed models using restricted maximum likelihood (REML), to account for non independence of eggs from the same clutch and of different clutches laid in the same nestbox, the correlated nature of the temperature variance measures within the same clutch, and the unbalanced structure of the data (Patterson and Thompson 1971). We used generalized linear models to explain variation in clutch size. All data were from first clutches. No females in common between the two years were included in the analyses. Predicted means ± SE from the statistical analyses are presented in the text and tables.

RESULTS

Mean daily temperatures during the egg-laying period varied between 6°C and 16°C. Variance of the 24-hour mean temperatures for the 7-day period varied between 0.05°C and 2.3°C.

Mean egg mass during the 2 years was 1.70 ± 0.03 g (n = 87 clutches). Temperature variability had a negative effect on egg mass (Fig. 1), when controlling for mean ambient temperature during the 24-hr period prior to laying, clutch size, laying date, female body condition, location, and random terms of 'female bird' and 'nestbox' (Table 1). Year, rainfall, female age and po-

TABLE 1. Linear mixed model (REML) of egg mass (g), in relation to variance of 24-hr mean temperatures for the 7-day period prior to laying, mean temperature during the 24-hr period prior to laying, clutch size, laying date, female mass divided by (tarsus)^3, and location. Random terms of 'female bird' and 'nestbox' were used ($\chi^2 = 331.4$; $P < 0.001$) to account for the nonindependence of eggs from the same clutch. The effect size for location B is relative to location A.

Variable	df	Effect size	Wald statistic (χ^2)	P-value
Temperature variance	1	-0.03 ± 0.01	15.0	<0.001
Mean temperature	1	0.010 ± 0.002	19.6	<0.001
Clutch size	1	-0.012 ± 0.005	5.2	<0.01
Laying date	1	0.004 ± 0.001	9.6	<0.01
Female mass (tarsus^3)$^{-1}$	1	241.0 ± 51.5	21.9	<0.001
Location	1	0.10 ± 0.04	7.9	<0.01

sition of egg in the clutch were also considered in the model but were not significant ($P > 0.25$). Temperature variability was found to account for up to 4.1% of variation in egg mass, comparable to up to 4.7% that could be accounted for by mean temperature.

There was a significant difference in mean clutch size between years (2001, 6.4 ± 0.3, $n = 41$; 2002, 7.3 ± 0.4, $n = 47$; $F = 5.3$, $P = 0.02$) and a negative relationship between clutch size and laying date ($F = 25.2$, $P < 0.001$). Mean temperature, temperature variation during the 7-day period prior to clutch initiation, rainfall, female age and body condition were also considered in the model but were not significant ($P > 0.25$).

DISCUSSION

This study has shown an effect of temperature variability (as well as previously known factors) on egg production in a wild population of birds: egg mass tended to be smaller when temperatures over the 7-day period prior to laying were more variable. This suggests there may be a cost associated with more variable temperature conditions that leads to a reduction in resources that are allocated to egg production. There are a number of possible routes by which a cost could arise from more variable temperatures.

First, elevated costs may have a biochemical basis resulting in higher than expected rates of energy expenditure. This could occur due to over-compensation by the feedback system that controls metabolic adjustments to new temperatures (Prinzinger 1982), or during an acclimatization period produced by a thermostatic lag in the transition from cold to warm conditions (MacLeod et al. 1980). The above explanations will result in increased costs of thermoregulation, which could take resources away from egg production (Perrins 1970, Stevenson and Bryant 2000).

A second category of explanations is that more variable conditions may result in increased feeding activity during warmer temperatures. This could occur for various reasons. For example, underlying trade-offs between starvation and predation risks, could lead to more costly but less risky feeding under more favorable conditions (Houston and McNamara 1999). Equally, more feeding activity may compensate for shortfalls in food intake during cold temperatures (due to reduced foraging efficiency because of decreased activity of insects; Avery and Krebs 1984); or it may ensure against future colder temperatures, as more variable conditions are perceived as being more unpredictable. This explanation means that foraging costs are higher than expected during warm conditions, which could divert resources from egg production (Stevenson and Bryant 2000).

Our hypothesis of temperature variability affecting thermoregulatory costs is paralleled by results from laboratory experiments on Japanese Quail. These studies have shown that metabolic rates were increased as a result of higher daily temperature ranges (Pendlebury et al. 2004) and temperature fluctuations (Prinzinger 1982).

Other factors that accounted for variation in egg mass included an index of body condition, laying date, and clutch size. Relationships between egg mass and body condition are common: females in better condition generally invest more into egg production (Christians 2002). An increase in egg mass with laying date is another common trend for passerines (Magrath 1992, Perrins 1996). This may be due to changing temperatures and food conditions altering the levels of available resources; or the observed trend for clutch size to decrease throughout the season (Klomp 1970, Crick et al. 1993). A reduction in clutch size may come about as a strategic response to lower food availability as the season progresses (Lack 1947), and a corresponding need to increase the survival of hatchlings by providing them with more resources than early-laid eggs.

We found no effect of temperature variation on clutch size. This reproductive parameter was more variable between years than egg mass and also declined throughout the season. Clutch size may therefore be more closely linked to seasonal changes in food supply (Lack 1947, Klomp 1970, Dijkstra et al. 1982, Perrins 1991) or other factors that were not controlled for, such as population density (Perrins and McCleery 1989).

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CATTLE GRAZING IN A NATIONAL FOREST GREATLY REDUCES NESTING SUCCESS IN A GROUND-NESTING SPARROW

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Abstract.   Grazing of domestic livestock on public lands in the western United States is a major source of habitat destruction. I quantified nest success of ground-nesting Dark-eyed Juncos (*Junco hyemalis*) breeding in ponderosa pine forests and pine savanna in the Kaibab National Forest of northern Arizona. Comparison of results for areas grazed by cattle to results for immediately adjacent areas protected from grazing revealed that cattle grazing was associated with a dramatic (75%) reduction in nest success. Cattle grazing reduced vegetation cover over nests by an average of 41%, exposing the nest to more extreme climatic conditions as well as possibly making them more conspicuous to predators.

Key words: cattle, grazing, Junco, Junco hyemalis, *nest success.*

El Pastoreo por Ganado Reduce Fuertemente el Éxito de Nidificación de *Junco hyemalis* en un Parque Forestal Nacional

Resumen.   El pastoreo por parte de ganado doméstico en tierras públicas del oeste de los Estados Unidos es una de las principales fuentes de destrucción de hábitat. Cuantifiqué el éxito de nidificación de *Junco hyemalis*, una especie que nidifica en el suelo, en los bosques de pino Ponderosa y las sabanas de pinos en el Bosque Nacional Kaibab, norte de Arizona. La comparación entre los resultados de las áreas pastoreadas por ganado y de las áreas inmediatamente adyacentes que se encuentran protegidas del pastoreo mostró que el pastoreo por ganado se asoció con una reducción dramática (75%) del éxito de nidificación. En promedio el pastoreo por ganado redujo la cobertura vegetal sobre los nidos en un 41%, exponiendo a los nidos a condiciones climáticas más extremas y posiblemente haciéndolos más conspicuos ante los depredadores.

Grazing of domestic livestock on public lands in the United States, such as the U.S. National Forests, is controversial. Although the federal government facilitates and subsidizes such grazing, it is a major source of habitat damage that is produced in exchange for a comparatively small amount of food production (Fleischner 1994, Wuerthner and Matteson 2002, Dobkin and Sauder 2004). I here report consequences of cattle grazing on reproductive success of Dark-eyed Juncos (*Junco hyemalis*). Juncos nest on the ground, constructing an open-cup nest composed largely of grasses (Nolan et al. 2003). In the area studied, nests were always placed at the base of a bunchgrass or a small shrub. These data were collected incidental to a study of the microclimatic consequences of ground nesting in this species.

METHODS

Observations were made in May, June, and July of 2000 and 2001 in open ponderosa pine (*Pinus ponderosa*) forests and pine savanna in the Kaibab National Forest, Coconino County, Arizona, near 35°19′N, 111°56′W. Areas utilized by juncos consisted of a moderately high-altitude community (about 2265 m) dominated by ponderosa pine with an understory composed primarily of a mixture of native grasses. These were largely Arizona fescue (*Festuca arizonica*), mountain muhly (*Muhlenbergia montana*), mutton grass (*Poa fendleriana*), June grass (*Koeleria cristata*), and squirrel-tail (*Sitanion hystrix*).

The area is grazed by substantial populations of native ungulates, the most conspicuous of which are American elk (*Cervus elaphus*). Groups of four to more than 50 elk were seen daily in the study area. Mule deer (*Odocoileus hemionus*) also were seen daily and pronghorn (*Antilocapra americana*) were also present but observed less frequently. Although wire fences (approximately 1 m high) have been constructed to control movement of domestic livestock, these provide no effective barrier to deer and elk, which readily jump over the fences. The entire area is also grazed by privately owned livestock (primarily cattle but occasion-

ally sheep) under permits issued by the U.S. Forest Service. The U.S. Forest Service divides the region into ''pastures,'' with cattle grazing in each pasture restricted to a single five-week period each summer. Average grazing intensity in this allotment was one AUM (animal unit month = one cow + one calf, for one month) per 6.3 ha (USDA Forest Service 2005)

Extensive searching allowed me to locate 38 (16 in 2000, 22 in 2001) junco nests that eventually held complete clutches. Once found, location of the nests was recorded using the combination of a global positioning system and a small-scale map to allow subsequent observations. To reduce the likelihood of drawing nests to the attention of predators, no markers were placed near a nest, nor was a nest approached within 7 m following its initial location until after reproduction was completed or had clearly failed. Refraining from closely approaching a nest also prevented me from confidently counting either the number of eggs or nestlings. Nests were checked daily with binoculars from distances of greater than 7 m and successful fledging was deemed to occur when nestlings were observed in the nest on the morning of their tenth day posthatching. This metric may overestimate fledging success, as juncos can remain in the nest up to 13 days posthatching (Nolan et al. 2003) and some mortality may have occurred during this period.

Cattle were not present on the study site at the start of the field seasons. A few days after the last clutch was completed in the nests under observation, however, cattle were introduced into a pasture comprising one portion of the field area by the grazing permittee and remained in the area for five weeks before being moved to another portion of the National Forest. Fences excluded cattle from the remaining portions of the field area throughout the breeding season, although these areas were immediately adjacent to that grazed by cattle.

Hemispherical photography was used to quantify possible changes in the vegetation cover over nests associated with grazing. Photographs were taken from each nest cup, following the techniques of Walsberg and King (1978) and Walsberg (1981). That is, 180° hemispherical (fisheye) photographs were taken using an Olympus OM-1 camera fitted with a 50-mm lens and a Spiratone™ auxillary hemispherical lens that produced a combined lens with a 7.5-mm focal length. As soon as a nesting attempt had either been completed or clearly failed, the camera was placed in the nest site such that the lens was at the same level as the rim of the nest and the camera axis directed vertically. Photographs thus recorded the mosaic of sky, vegetation, and other features composing the overhead visual environment. The fraction of the upper hemisphere over the nest that was occluded by vegetation was calculated following Walsberg and King (1978).

STATISTICAL ANALYSES

Overall nest success was compared between years using a two-tailed Fisher Exact Test (Zar 1984). The same test was used to compare the frequency of successful nests in areas either grazed or not by cattle. Fractional overhead cover quantified by hemispherical photography was tested using one-way ANOVA. Statistical significance was accepted at $P \le 0.05$. Values are reported as means ± SE.

RESULTS

In 2000, cattle were released on 25 June. This was three days after the last junco clutch was completed. In 2001, cattle were released on 23 June, the day that the last junco clutch was completed. The portion of the field area grazed by cattle contained 17 of the 38 nests. On the day that cattle were released, 13 of these nests contained eggs being incubated and four nests contained nestlings less than 4 days old. On the same dates in the cattle-free area, 16 of the nests contained eggs and six contained nestlings less than 4 days old.

Overall fledging success did not differ between years ($P = 0.49$), and averaged 32% for all nests. Therefore, data for all years were combined to test for effects of cattle grazing.

The area grazed by cattle had a dramatically lower proportion of successful nests compared to the cattle-free area ($P = 0.02$). In the area with cattle, only two of 17 nests (12%) were successful at fledging young. In the cattle-free area, 10 of 21 nests (48%) were successful. That is, the presence of cattle was associated with a 75% (= $1 - [0.12 \times 0.48^{-1}]$) reduction in nest success.

Hemispherical photography revealed that 66% ± 6.3% ($n = 21$) of the upper hemisphere over junco nests was occluded by vegetation in the cattle-free area. Only 39% ± 9.1% ($n = 17$) of the upper hemisphere over nests was occluded by vegetation in areas grazed by cattle, and the differences between the areas with and without cattle was statistically significant ($F = 56$, $P < 0.01$).

DISCUSSION

In areas of cattle grazing, fledging success was reduced by 75%. This very large effect did not simply reflect the presence of grazing herbivores, as elk, deer, and antelope were common in both areas, but rather was specifically associated with the presence of cattle.

There are several possible causes of such nesting failure. The most salient was reduction in vegetation cover over these ground nests as cattle cropped grasses. Such stripping of ground cover by cattle would have exposed nesting birds to more extreme microclimates in terms of increased wind speed, more intense solar radiation during daylight hours, and greater radiative heat loss at night (GEW, unpubl. data). In addition, reduction in overhead cover may well have exposed the birds to increased predation. Visually oriented nest predators, including both Steller's Jays (*Cyanocitta stelleri*) and Common Ravens (*Corvus corax*), were commonly observed in the field area. Other vertebrates that may also prey on junco nests and that were seen in the area included gopher snakes (*Pituophis melanoleucus*) and many mammal species (e.g., coyote [*Canis latrans*], red fox [*Vulpes vulpes*], raccoon, [*Procyon lotor*], striped skunk [*Mephitis mephitis*], long-tailed weasel [*Mustela frenata*], ringtail [*Bassariscus astutus*], black bear [*Euarctos americanus*], bobcat [*Lynx rufus*], gray-collared chipmunks [*Eutamias cinereicollis*], and several squirrels [*Spermophilus lateralis*, *S. variegatus*, *S. spilosoma*, and *Sciurus aberti*]). Attraction of predators to nests may have

been exacerbated by flushing of adults from nests in response to cattle, although this was not observed. Finally, hoof marks over two crushed nests suggest that at least some nests were simply trampled by cattle.

Grazing of domestic livestock has been cited as the most pervasive and important source of habitat destruction in the western United States (Fleischner 1994, Wuerthner and Matteson 2002). In this case, such damage extended even to the extent of essentially preventing reproduction by a small songbird. The damage in the grazed area was so extensive that it seems unlikely that junco populations can be sustained by only a 12% success rate. Although it is not known what the population densities of native birds were prior to the introduction of cattle grazing in these areas, it seems likely that they were substantially higher and that even these smaller populations are maintained only by an influx of birds from areas not exposed to cattle grazing.

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USING THE RISK-DISTURBANCE HYPOTHESIS TO ASSESS THE RELATIVE EFFECTS OF HUMAN DISTURBANCE AND PREDATION RISK ON FORAGING AMERICAN OYSTERCATCHERS

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Abstract. The risk-disturbance hypothesis asserts that animals perceive human disturbance similar to nonlethal predation stimuli, and exhibit comparable responses in the form of optimization tradeoffs. However, few studies have examined how natural predation risk factors interact with human-disturbance stimuli to elicit such responses. We observed American Oystercatcher (*Haematopus palliatus*) vigilance behavior from September–December 2002 on the Cape Romain National Wildlife Refuge, South Carolina. A set of models was constructed based on 340 focal-animal samples and models revealed relationships between vigilance behavior, predator density, and boat activity. Oystercatchers increased vigilance in response to aerial predators, particularly late in the season when predator species composition was dominated by Northern Harriers (*Circus cyaneus*). At a broader temporal scale,

oystercatchers exhibited the highest vigilance rates during simultaneous peaks in boating disturbance and Osprey (*Pandion haliaetus*) activity. Due to this temporal overlap of stimuli, it is difficult to interpret what may have been driving the observed increased in vigilance. Foraging rates appeared to be primarily driven by habitat and tidal stage indicating that time lost to vigilance did not effectively reduce intake. Taken together, these findings provide some support for the risk-disturbance hypothesis, underscore the sensitivity of disturbance studies to temporal scale, and draw attention to the potential confounding effects of natural predation risk.

Key words: American Oystercatcher, boats, disturbance, Haematopus palliatus, *risk-disturbance hypothesis, vigilance.*

Uso de la Hipótesis de Riesgo-Disturbio para Evaluar los Efectos Relativos de los Disturbios Humanos y del Riesgo de Depredación en *Haematopus palliatus*

Resumen. La hipótesis de riesgo-disturbio propone que los animales perciben los disturbios causados por los humanos de un modo similar a como perciben estímulos de depredación no letales, y que exhiben respuestas comparables en términos de compromisos de optimización. Sin embargo, pocos estudios han examinado cómo interactúa el riesgo natural de depredación con los estímulos causados por disturbios humanos para causar dichas respuestas. Observamos el comportamiento de vigilancia del ostrero *Haematopus palliatus* entre septiembre y diciembre de 2002 en el Refugio Nacional de Vida Silverstre Cape Romain, South Carolina. Con base en 340 muestras de animales focales se construyeron una serie de modelos, los cuales mostraron relaciones entre el comportamiento de vigilancia, la densidad de depredadores y la actividad de botes. Los ostreros incrementaron la vigilancia como respuesta a los depredadores aéreos particularmente hacia el final de la temporada, cuando la composición de especies de depredadores estaba dominada por *Circus cyaneus*. A una escala temporal más amplia, los ostreros presentaron las tasas de vigilancia más altas durante picos simultáneos en los disturbios causados por botes y en la actividad de *Pandion haliaetus*. Debido a esta superposición de los estímulos es difícil interpretar cuál de ellos habría estado determinando el incremento en vigilancia observado. Las tasas de forrajeo parecieron estar dadas principalmente por el hábitat y la posición de la marea, lo que indica que el tiempo perdido en vigilancia no redujo la ingestión de alimento efectivamente. En conjunto, estos hallazgos proveen algo de evidencia que apoya la hipótesis de riesgo-disturbio, resaltan la sensibilidad a la escala temporal de los estudios sobre disturbios y enfatizan la necesidad de prestar atención a la posibilidad de que existan efectos enmascarados del riesgo de depredación natural.

Concerns about the possible negative impacts of human disturbance on wildlife populations have led to an expansive literature addressing animal responses to human activity such as recreation, ecotourism, and hunting (reviews in Hill et al. 1997, Frid and Dill 2002). Studies thus far have tended to focus on the direct, immediate effects of human disturbance on animal behavior (Rodgers and Smith 1995, Thomas et al. 2003), or on how disturbance correlates with animal numbers and distributions (Skagen et al. 2001, Quan et al. 2002). However, recent concern has arisen over our lack of understanding of the actual impacts of human disturbance on individual fitness, and how these impacts translate into long-term impacts on population and community health (Hill et al. 1997, Nisbet 2000).

The ''risk-disturbance'' framework, which draws on the rich scientific literature that addresses the impacts of naturally occurring disturbance, in the form of predation risk, on wild populations has recently gained attention as a potential tool for improving our understanding of the effects of human disurbance (Frid and Dill 2002). The risk-disturbance hypothesis contends that animals perceive human disturbance similar to nonlethal predation risk (e.g., risk that does not end in actual predation, but may alter prey species behavior so that they are more difficult to detect, encounter, or capture), and thus will exhibit similar responses in the form of optimization tradeoffs (Lima 1998a, 1998b). These responses will in turn translate into similar overall consequences at the individual, population, and community levels (Lima 1998a, 1998b, Frid and Dill 2002).

The risk-disturbance hypothesis also predicts that individuals will be more vigilant in response to human disturbance when it occurs concurrently with a perceived high-predation risk (Frid and Dill 2002). However to date, few studies have examined how natural predation and human disturbance risk factors interact to influence prey behavior. Vigilance studies, for example, have drawn conclusions about the relationships between vigilance behavior and predation risk (Barnard 1980, Wolff and Van Horn 2003) or vigilance behavior and disturbance (Burger 1994, Fitzpatrick and Bouchez 1998), without considering the potential interactions between the two risk factors. In fact, one common practice in predation risk studies is to use human approaches to simulate predator disturbance (Cooper 1999). If the risk-disturbance hypothesis is correct in its assumptions, ignoring such potential interactions could profoundly affect the interpretations of human-disturbance studies.

The limited number of studies that have addressed predation risk and disturbance simultaneously have focused on individuals' distance from refugia, with the assumption that distance from refuge is positively correlated with perceived predation risk (Ward and Low 1997, Frid 2003). These studies have provided some support for the risk-disturbance hypothesis, with individuals in ''riskier'' foraging patches exhibiting a stronger response to human disturbance (Ward and Low 1997, Ronconi and St. Claire 2002, Frid 2003). However, predator abundance, particularly in migratory species, can also vary quite significantly over time to affect predation risk (Lima 1998a, Lima and Bednekoff 1999, Lima 2002), and human-disturbance pressure often also varies temporally (Burger and

Gochfeld 1998, Fitzpatrick and Bouchez 1998, Lafferty 2001).

We observed vigilance rates in an overwintering population of American Oystercatchers (*Haematopus palliatus*) near Charleston, South Carolina, in relation to fluctuating human disturbance (recreational boats) and predator (diurnal raptors) activity. Our specific objectives were to a) examine the relationships among temporal trends in aerial predator and boat disturbance, b) determine if oystercatcher vigilance and foraging rates changed in relation to increased boat and raptor activity, and c) determine if boat and raptor activity interacted to influence vigilance behavior (i.e., were individuals more likely to increase vigilance in response to boats when predator activity was high?).

METHODS

Our study was conducted on the Cape Romain National Wildlife Refuge (CRNWR), located approximately 30 km north of Charleston, South Carolina. The CRNWR contains nearly 14 000 ha of protected saltmarsh, shallow bays, and barrier islands. Because a significant proportion of the American Oystercatcher population that utilizes the Atlantic flyway has been documented using the refuge (Harrington et al. 1989, Marsh and Wilkinson 1991, Sanders et al. 2004), it has been declared part of the Western Hemisphere Shorebird Reserve Network.

The likelihood that small boat traffic may disturb shorebirds and wading birds has recently become a significant concern, as the region has recently experienced a sharp increase in recreational shrimp-baiting trips. From 1998 until 2002, there has been a 212% increase in the number of shrimp-baiting trips (South Carolina Department of Natural Resources, unpubl. data). The shrimp-baiting fishery is set by law to last 60 days and to coincide with the period when larger white shrimp (*Penaeus setiferu*) are moving seaward. In 2002, the shrimp-baiting season opened on 13 September and closed on 12 November.

DATA COLLECTION

From September to November 2002, we conducted behavioral observations of individual oystercatchers at 18 low-tide foraging areas in the southern region of Cape Romain National Wildlife Refuge. Approximately 1 hr before low tide, we transported an observer to a randomly chosen foraging area who remained at that site until approximately 1 hr after low tide. Within this sampling period, the observer recorded focal-animal observations every 30 min on a randomly chosen bird.

Each focal-animal observation consisted of a 5-min observation period, during which the observer marked the state of the individual as foraging, food handling, preening, resting, agonistic, vigilant (scanning) or other. Vigilance was attributed to individuals who were clearly scanning with their heads above the plane of the body (Bednekoff and Ritter 1994), and did not preclude the probability that birds were also vigilant during other activities, such as preening or foraging (Lima and Bednekoff 1999). We categorized focal birds as mature (3rd year or older) or immature (hatch year to 2nd year) based on bill coloration (Nol and Humphrey 1994, K. Oosterbeek, pers. comm.). Because the majority of focal birds were not marked, there is a possibility that individuals may have been sampled more than once over the study period. We recorded all focal-animal observations using the Spectator Go mobile data acquisition system (Biobserve, Bonn, Germany), installed on a hand-held computer (iPAQ, Hewlett-Packard Company, Palo Alto, California). If a disturbance event occurred during the observation period, we terminated focal-animal sampling. We resumed focal animal sampling 5 min after the flock returned to normal activities, or if a flock flushed and did not return to the sampling area within 5 min, we abandoned observations and moved to a new sampling area.

We completed a standardized strip-transect survey through the study site on each sampling day. We conducted surveys when tidal stages were 3–6 hr from low tide. The route was approximately 21.5-km long and took an average of 61 ± 2 min (SE) to complete in a Boston Whaler at a set motor speed (3000 rpm). Along the route, we recorded the number of diurnal raptors and boats observed within 1000 m of our boat as general indices of disturbance for that day. Raptors were identified to species, and boats were categorized as small (≤ 6 m) or large (>6 m). Although boat activity tends to be slightly higher at CRNWR during lower tides (KAP, unpubl. data), we feel that the middle to high-tide estimates served as a suitable index for daily activity. For instance, the estimates clearly reflected the heavy boat traffic present on the refuge at the onset of the shrimp-baiting season and on weekends. Raptor activity on the refuge is not affected by tidal stage (KAP, unpubl. data). All raptor species were counted, regardless of whether or not they had been recorded in the literature as predators of adult oystercatchers (Nol and Humphrey 1994), as it is not unusual for oystercatcher flocks to flush in response to a passing Osprey (*Pandion haliaetus*), Northern Harrier (*Circus cyaneus*), Bald Eagle (*Haliaeetus leucocephalus*), or Turkey Vulture (*Cathartes aura*; KAP, pers. obs.). Consequently, we regarded most large soaring birds as a perceived predation risk, although actual risk may have been negligible. Osprey, in particular, would be highly unlikely to prey on birds (Poole et al. 2002), whereas Bald Eagles (Buehler 2000) and Northern Harriers (MacWhirter and Bildstein 1996) pose a real threat.

We derived several abiotic parameters associated with each focal-animal sample: minutes past sunrise, moon phase, minutes before or after low tide, and water depth at low tide (Tides and Currents software package, V.2.5, Nobeltec, Portland, Oregon). We based all tidal parameters on estimates for Moore's Landing, South Carolina, which was located on the central western boundary of the study area. We also classified focal observation sites into three general regions of the study area: Bull's Bay, Seewee Bay, and Intracoastal Waterway.

STATISTICAL ANALYSES

We developed two sets of logistic-regression models to estimate the influence of predator, disturbance, and abiotic parameters on oystercatcher behavior. The first set of models explored potential effects on time spent vigilant, and the second set explored potential effects on time spent foraging. Individuals exhibiting vigilant or foraging (foraging + food handling) behavior
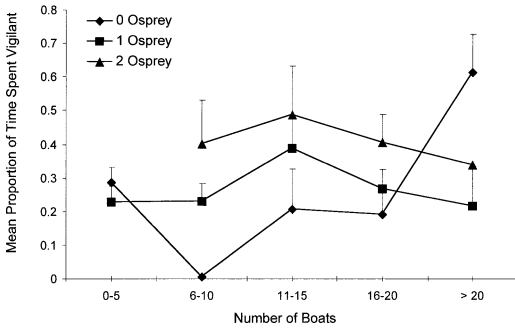
FIGURE 1.   Proportion of time (mean ± SE) American Oystercatchers spent vigilant during 5-min observation periods on Cape Romain National Wildlife Refuge, South Carolina when 0, 1, or 2 Osprey were recorded in the area.

≥50% of a 5-min observation period were coded as "vigilant" or "foraging," respectively. All others were coded as "nonvigilant" or "nonforage". Final models predicted the probability that an individual displayed extensive (≥50% of the time) vigilant or foraging behavior under the conditions as defined by independent parameter estimates at the time that the sample was taken. Independent parameters incorporated in the models included region, day of the year (day 1 = 1 January), minutes past sunrise, minutes before or after low tide, low-tide water level relative to mean, rising or falling tide, number of small boats, number of Northern Harriers, Osprey, and Bald Eagles. Some models also included interactions between the number of boats and each raptor species. Counts of large boats, which were seen only in the Intracoastal Waterway and

were thus spatially removed from foraging oystercatchers, were not included in our analyses.

We used an information-theoretic approach to model selection for each of the two sets of models (Burnham and Anderson 2002). Prior to model construction, we conducted a correlation analysis on all independent variables to assess multicollinearity (e.g., nonorthogonality) among the data. We did not include highly correlated variables ($r \geq 0.50$ or $r \leq -0.50$) in any one model to avoid inflated standard errors of partial regression coefficients (Zar 1998). We defined two sets of *a priori* candidate models, each of which included a global model containing all parameters and interactions considered to have potentially relevant effects on behavior, and five reduced models (Burnham and Anderson 2002). The five reduced candidate models were formulated to specifically address whether oystercatcher vigilance behavior was primarily influenced by abiotic factors, or whether it was driven more by predator density, human disturbance, or by interactions between the two risk factors.

We examined each global model to obtain an overall measure of model fit (Burnham and Anderson 2002). Fit was based on model concordance ratings and by prediction accuracy, as indicated by classification error (SAS Institute 1999). A model response that had a predicted probability greater than or equal to 0.50 was classified as an "event" (e.g., vigilant or foraging) response, in order to assess the prediction accuracy of the model (SAS Institute 1999). Akaike's Information Criterion (AIC) was used to determine the relative strength of support for individual models (Burnham and Anderson 2002). Models within two score points of the highest ranked model were considered to have very strong support (Burnham and Anderson 2002). We present parameter estimates derived from the high-

TABLE 1.   Candidate logistic regression models for predicting extensive vigilance behavior in American Oystercatchers on the Cape Romain National Wildlife Refuge, South Carolina. Models examined the effects of one or more parameters and three interactions ΔAIC_c values reflect the difference in score from the best-performing model.

Model name	Model factors[a]	k[b]	w_i[c]	−2 Log likelihood	ΔAIC_c
RAPTORS, BOATS, and INTERACTIONS	NOHA, OSPR, BAEA, SMBOAT, NOHA-SMBOAT, OSPR-SMBOAT, BAEA-SMBOAT	9	0.43	365.63	0.00
RAPTORS	NOHA, OSPR, BAEA	5	0.27	375.01	0.92
RAPTORS and BOATS	NOHA, OSPR, BAEA, SMBOAT	6	0.16	373.65	1.66
GLOBAL	REGION, NOHA, OSPR, BAEA, MINSUN, MINLOW, LOWCM, RF, SMBOAT, NOHA-SMBOAT, OSPR-SMBOAT, BAEA-SMBOAT	15	0.15	355.75	3.22
BOATS	SMBOAT	3	0.00	393.17	14.91
ENVIROMENTAL	REGION, MINSUN, MINLOW, LOWCM, RF	7	0.00	383.26	15.37

[a] Model parameters: region of the refuge (REGION), minutes past sunrise (MINSUN), minutes past low tide (MINLOW), centimeters above or below mean low tide (LOWCM), rising vs. falling tide (RF), Northern Harrier count (NOHA), Osprey count (OSPR), Bald Eagle count (BAEA), and small boat count (SMBOAT).

[b] Number of estimable parameters, including intercept and error term.
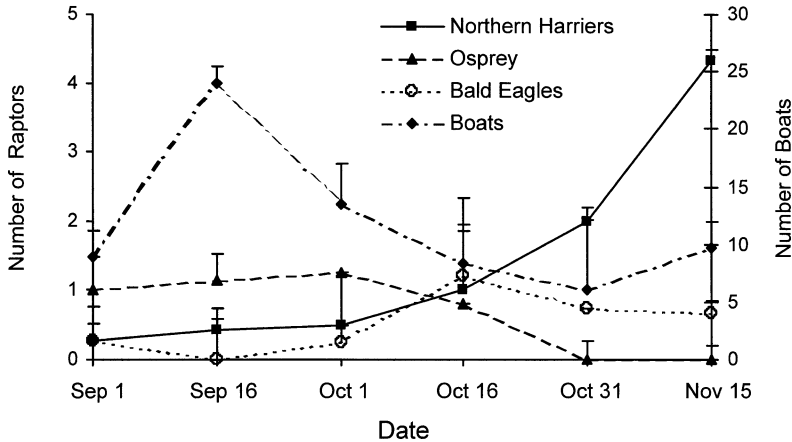
[c] Akaike model weights (Burnham & Anderson 2002).

FIGURE 2. Temporal trends in Northern Harriers, Osprey, Bald Eagles, and boat activity on Cape Romain National Wildlife Refuge, South Carolina, 2002. Data points represent the mean ± SE for each two-week sampling period.

est ranked models as the mean ± SE and accepted significance when $P \le 0.05$. We also provide an estimate of the maximum effect of each parameter (i.e., estimate × maximum value of the parameter), to clarify the magnitude of impact of each independent factor.

RESULTS

We collected 340 low-tide behavioral samples within 34 sample days (3 September to 30 November, 2002). Of the individuals sampled, 91 were classified as "vigilant," and 249 as "nonvigilant." A correlation analysis on the independent variables revealed that Julian date was positively correlated with number of Northern Harriers ($r = 0.68$) and negatively correlated with number of Osprey ($r = -0.64$) and small boats ($r = -0.55$), and was subsequently removed from all candidate models. General fit of the resulting global model was fair (75% correct classification, 64% concordance). Based on AIC_c ranking, the best approximating model for predicting vigilance included the variables small boats, aerial predators, and their interactions (Table 1). According to the model, vigilance increased in relation to the number of boats (Estimate = 0.07 ± 0.02, $P < 0.01$, Maximum Effect = 3.11), Northern Harriers (Estimate = 0.57 ± 0.16, $P < 0.01$, Maximum Effect = 3.96) and Osprey (Estimate = 1.50 ± 0.38, $P = 0.01$, Maximum Effect = 2.99). An interaction between the number of small boats and Osprey was also apparent ($P < 0.01$); contrary to what would be expected by the risk-disturbance hypothesis, oystercatchers appeared to be less sensitive to boats when Osprey activity was high (1 or 2 Osprey present) than when Osprey activity was low (no Osprey present, Fig. 1). This finding, however, was skewed by extremely high vigilance rates observed on one day during which

boat activity was particularly high (44 boats present) and no Osprey were observed. Osprey counts never exceeded two individuals.

A distinctive change in primary raptor composition and boat activity was also recorded during the sample period (Fig. 2). Osprey and boat counts were highest from early September through early October, whereas Northern Harriers tended to increase throughout the season. Bald Eagle counts increased slightly over the survey period, although on only 4 occasions did we record more than one individual. Later in the season, there was a relationship between mean daily vigilance rates and Northern Harrier counts, particularly when harrier activity was very high (Fig. 3, $r^2 = 0.60$). However, on a broader temporal scale, vigilance rates tended to be highest early in the season (4 September to 9 October), when Osprey and boat counts peaked (Fig. 3).

Of the focal animals sampled, 126 were classified as "foraging," and 214 as "nonforaging." General fit of the global model was fair (64% correct classification, 72% concordance). The global model performed better than the reduced models, as evidenced by AIC_c scoring (Table 2). According to the global model, oystercatchers spent less time foraging later in the day (Estimate = 0.004 ± 0.001, $P < 0.01$, Maximum Effect = 2.68), and more time foraging during lower tides (Estimate = 0.024 ± 0.01, $P = 0.04$, Maximum Effect = 1.59). However, increased feeding appeared to occur during the rising and falling tides, rather than at low tide (Estimate = 0.01 ± 0.004, $P < 0.01$, Maximum Effect = 0.86). Furthermore, a strong regional effect was apparent; individuals in Bull's Bay were more likely to spend time foraging than were those in Seewee Bay ($P < 0.001$), although there was no dif-

$\rightarrow$

FIGURE 3. Daily counts of (a) Northern Harriers, (b) Osprey, and (c) boats plotted against the daily mean proportion of 5-min focal periods that oystercatchers spent vigilant.
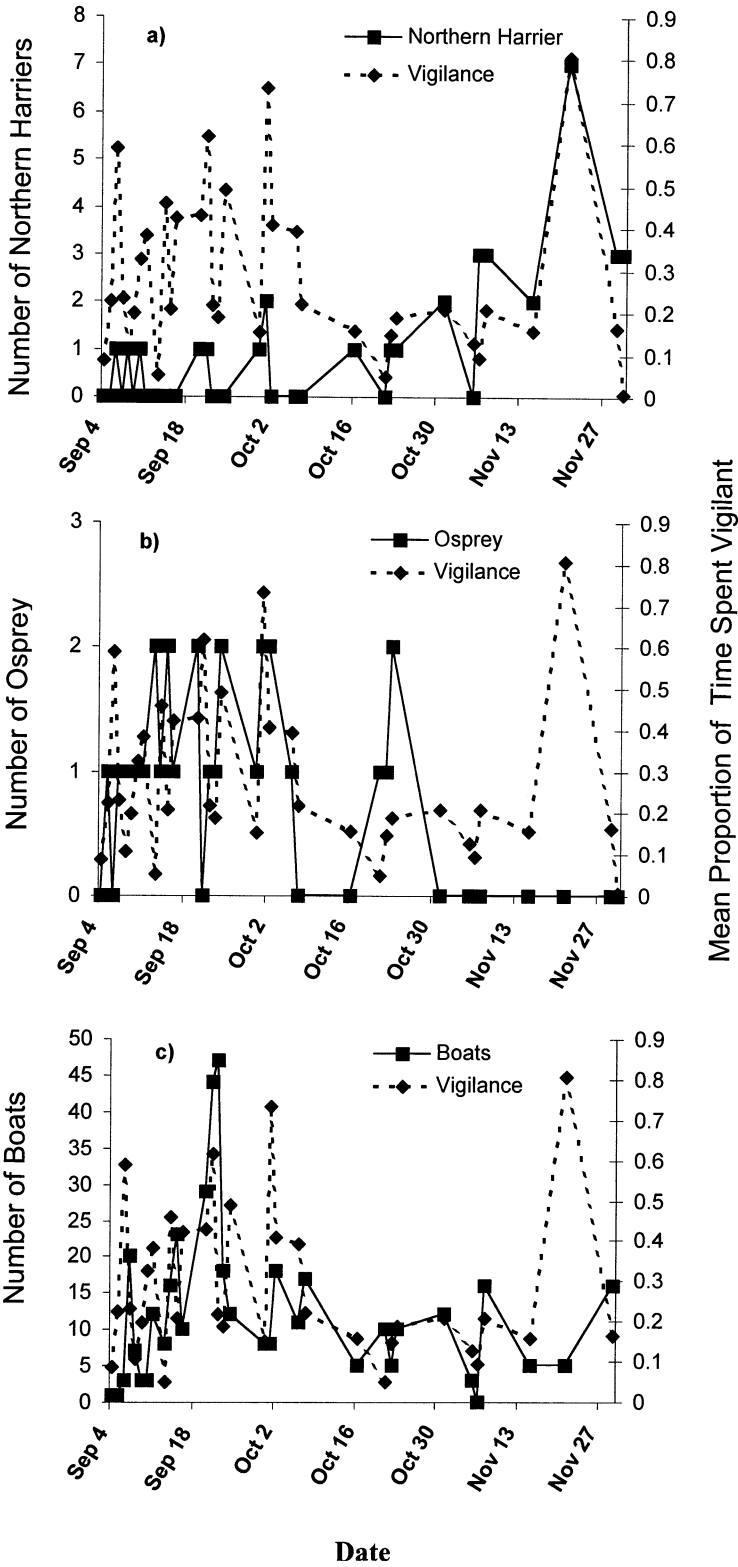
Date

TABLE 2. Candidate logistic regression models for predicting extensive foraging behavior in American Oystercatchers on the Cape Romain National Wildlife Refuge, South Carolina. ΔAIC_c values reflect the difference in score from the best-performing model. Parameter decriptions are provided in Table 1.

Model name	Model factors	k[a]	w_i[b]	-2 Log likelihood	ΔAIC_c
GLOBAL	REGION, NOHA, OSPR, BAEA, MINSUN, MINLOW, LOWCM, RF, SMBOAT, NOHA-SMBOAT, OSPR-SMBOAT, BAEA-SMBOAT	15	0.99	389.36	0.0
ENVIROMENTAL	REGION, MINSUN, MINLOW, LOWCM, RF	7	0.01	413.22	8.5
RAPTORS	NOHA, OSPR, BAEA	5	0.00	435.87	24.9
RAPTORS and BOATS	NOHA, OSPR, BAEA, SMBOAT	6	0.00	434.27	25.4
BOATS	SMBOAT	3	0.00	444.48	29.4
RAPTORS, BOATS, and INTERACTIONS	NOHA, OSPR, BAEA, SMBOAT, NOHA-SMBOAT, OSPR-SMBOAT, BAEA-SMBOAT	9	0.00	432.72	30.3

[a] Number of estimable parameters, including intercept and error term.
[b] Akaike model weights (Burnham & Anderson 2002).

ference in rates between the Intracoastal Waterway and Seewee Bay. Feeding time was significantly reduced when Northern Harrier counts were high (Estimate $=-0.44 \pm 0.18$, $P = 0.02$, Maximum Effect $= -3.07$), but increased when Bald Eagles were recorded in the area (Estimate $= 1.31 \pm 0.43$, $P < 0.01$, Maximum Effect $= 3.91$). There was no relationship between time spent foraging and boat activity ($P = 0.48$), nor were there any significant interactions between the number of Northern Harriers ($P = 0.08$), Osprey ($P = 0.60$), or Bald Eagles ($P = 0.19$), and boat activity.

DISCUSSION

We found that American Oystercatchers tended to increase vigilance behavior in relation to increased boat activity, Northern Harrier activity, and Osprey activity. Late in the season, oystercatcher vigilance rates appeared to track harrier activity on a daily basis. At a broader temporal scale, however, oystercatchers tended to exhibit the highest rates of vigilance during the peak boating period, which also coincided with the period in which peak Osprey counts were recorded. Due to this temporal overlap of Osprey and boat activity, it is difficult to interpret which stimulus may have been driving the increased vigilance that we observed early in the season.

The fact that our findings concerning behavioral response to boats and Osprey were confounded is disconcerting and underscores the importance of taking natural predation risk into account when conducting disturbance studies. Predation risk and disturbance pressures can vary over time, and the temporal scale at which such studies are conducted can greatly affect their outcomes. This is particularly true in a predation-disturbance context, as studies concerning natural disturbance have shown to be sensitive to scale, with reactions driven by a complex interplay of time-dependent factors such as weather, life-history stage, and resource availability (Lima 1998b, Wingfield et al. 1998, McGowan et al. 2002, Stillman and Goss-Custard 2002). For instance, McGowan et al. (2002) found

that Red Knots (*Calidris canutus*) were more likely to flush in response to Peregrine Falcon activity with increased wind speed and temperature, apparently because of detection interference caused by vegetative debris and decreased thermoregulatory costs (Kersten and Piersma 1987), respectively. Redshank (*Tringa totanus*), have also been shown to respond to predation risk at higher temperatures, and to exhibit alarm flights more often when rain and cloud cover may mask approach by aerial predators (Hilton et al. 1999).

Examples from the literature provide some evidence that human disturbance studies are similarly sensitive. Stillman and Goss-Custard (2002) reported that Eurasian Oystercatchers (*H. ostralegus*) were less likely to respond to disturbance later in the winter, when loss of feeding time was especially costly (Kersten and Piersma 1987). Oystercatchers also tend to change primary prey species seasonally, which affects handling time and could potentially make time lost to disturbance more or less damaging (Tucknell and Nol 1997). Ronconi and St. Clair (2002) observed that Black Guillemots (*Cepphus grylle*) foraged further from shore during low tides and were more vulnerable to flushing when further from shore. Therefore, setback recommendations for fast boats varied as much as 2 km between high and low tides. Fernandez-Juricic et al. (2002) observed that several species of passerines were less likely to flush in response to pedestrians when temperatures were high, purportedly due to an increased cost of reacting in the form of heat stress. Physiological responses to disturbance, including elevated gluconeogenesis, may also fluctuate temporally according to different life-history stages and habitats (Wingfield et al. 1998).

The risk-disturbance hypothesis also predicts that prey species are more likely to respond to human disturbance when natural predation risk is high (Frid and Dill 2002). We did not observe such an interaction, as oystercatchers were not more likely to respond to disturbance when raptor activity was high. Furthermore, although we did not see a strong relationship between

raptor activity and human disturbance in our *a priori* correlation analyses, it is important to acknowledge the fact that raptor species themselves often react to disturbance (Richardson and Miller 1997), the occurrence of which would have made any interactions more complex. Prior evidence concerning the potential interaction between predation risk and disturbance is limited. Ward and Low (1997) found that in American Crows (*Corvus brachyrhynchos*) vigilance in response to disturbance increased with distance from protective cover. Black Guillemots were also more vulnerable to flushing from boats when foraging farther from shore.

Finally, some studies have shown that disturbance effectively reduces foraging time in shorebirds (Thomas et al. 2003), and evidence suggests that human disturbance may displace individuals to poorer feeding areas, which could potentially increase mortality (Pfister et al. 1992, 1998, Drilling and Harrington 1996). Although we did not observe a reduction in foraging time in oystercatchers during high disturbance days, it does not preclude the possibility that disturbance plays a more critical role in determining available foraging time later in the winter (Stillman and Goss-Custard 2002).

Frid and Dill (2002) argued that in particular, studies designed to test how factors related to natural predation risk combine with disturbance stimuli would benefit considerably from a predation risk framework. We agree that exploring the testable hypotheses outlined in Frid and Dill's (2002) framework proved valuable and provided insights into the vigilance patterns we observed on Cape Romain National Wildlife Refuge. If the ultimate goal of disturbance studies is to determine if observed effects are significantly adverse to cause negative impacts on populations of concern (Nisbet 2000), our study and others have clearly shown that temporal scaling effects must be taken into consideration. In particular, we suggest that natural predation risk be considered when conducting disturbance studies, and that findings from such studies be taken into account when developing management regimes.

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