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ENVIRONMENTAL CORRELATES OF AFRICAN WOOD-OWL CALLING ACTIVITY IN KIBALE NATIONAL PARK, UGANDA

NATHANIEL E. SEAVY[1]
Department of Zoology, 223 Bartram Hall, P.O. Box 118525, University of Florida, Gainesville, FL 32611 U.S.A. and Klamath Bird Observatory, P.O. Box 758, Ashland, OR 97520 U.S.A.

ABSTRACT.—Over a 1-yr period, I documented the relationship of habitat, season, lunar phase, cloud cover, and wind with patterns of African Wood-Owl (*Strix woodfordii*) calling activity in Kibale National Park, Uganda. During 10-min surveys at 10 locations, five in unlogged and five in selectively-logged tropical forest, I recorded three indices of unsolicited calling activity: whether or not owls were detected at a station, number of individuals detected, and number of vocalizations detected. African Wood-Owls were abundant in the study area and called throughout the year; I detected owls on 232 of 480 (48%) surveys. When measured by number of vocalizations detected, calling activity was greater during full moons and on clear nights, and reduced during new moons and on cloudy nights. Lunar phase and cloud cover did not have a significant effect on whether or not owls were detected or on the number of individuals detected, but nonsignificant trends were consistent using each index. These results demonstrate the importance of considering environmental factors and response variables when designing and interpreting studies that measure calling activity.

KEY WORDS: *African Wood-Owl;* Strix woodfordii; *Uganda; survey; vocalizations; cloud cover; lunar phase.*

CORRELACIONES AMBIENTALES DE LAS VOCALIZACIONES DE *STRIX WOODFORDII* EN EL PARQUE NACIONAL DE KIBALE, UGANDA

RESUMEN.—Durante un periodo de un año, documente la relación de hábitat, estacionalidad, fase lunar, cobertura nubosa y viento con los patrones de vocalización de *Strix woodfordii* en el Parque Nacional de Kibale, Uganda. Durante periodos de 10-minutos en 10 localidades, cinco sin tala y cinco con tala selectiva de bosque tropical, registre tres índices de vocalizaciones espontáneas: presencia/ausencia, numero de individuos y numero de vocalizaciones. Los búhos fueron abundantes en el área de estudio y vocalizaron durante todo el año. Detecte a los Búhos en 232 de los 480 (48%) muestreos. Al medir el numero de vocalizaciones encontré que esta actividad fue mayor durante las lunas llenas, en noches claras y fue menor en las lunas nuevas y noches nubladas. La fase lunar y la cobertura nubosa no tuvieron un efecto significativo para la detección de individuos, aunque las tendencias no significativas fueron consistentes al utilizar cada índice. Estos resultados demuestran la importancia de considerar los factores ambientales y los variables de respuesta cuando se diseña y se interpretan estudios que miden la actividad de vocalización.

[Traducción de César Márquez]

Variation in nighttime-calling activity of owls can be associated with lunar phase (Ganey 1990, Clark and Anderson 1997), cloud cover (Ganey 1990, Clark and Anderson 1997), wind speed (Gerhardt 1991), season (Ritchison et al. 1988, Ganey 1990), and even ecological factors, such as food abundance and mating status (Martin 1974, Lundberg 1980). Understanding these relationships can provide information about the ecological and behavioral significance of owl vocalizations.

Sampling methods used to measure calling activity of owls have varied among studies. Some studies have measured calling activity in response to a broadcast of taped conspecific vocalizations (Gerhardt 1991, Pardieck et al. 1996, Clark and Anderson 1997), whereas others have monitored spontaneous calling activity (Ganey 1990). Furthermore, these studies have used different indices as measures of calling activity. The most commonly used response variable is the number of owls detected during a survey (Clark and Anderson 1997, Pardieck et al. 1996), but other studies have analyzed either the number of calls or calling bouts (Ganey 1990) or whether or not an owl vocaliza-

[1] E-mail address: nseavy@zoo.ufl.edu

tion was detected (Gerhardt 1991). If indices of calling activity are measurably influenced by environmental factors, then apparent variation in the response of owls to environmental conditions may simply reflect differences in methodologies.

The African Wood-Owl (*Strix woodfordii*) is a common resident of forests and dense woodland throughout most of east, central, and southern Africa (Fry et al. 1988). African Wood-Owls can be monitored effectively by acoustical surveys, as demonstrated by the use of sonogram analysis to estimate density and turnover of a population in South Africa (Kemp and Kemp 1989, Delport et al. 2002). Furthermore, the vocal behavior of these owls lends itself to playback experiments that test behavioral hypotheses. However, environmental factors influencing their calling activity have not been studied. Such information is critical for designing and interpreting studies that rely on vocal response to broadcasts of taped vocalizations to estimate owl populations (Forsman 1983, Pardieck et al. 1996) or investigate the behavioral contexts of particular vocalizations (Ritchison et al. 1988).

In 1997–98, I studied African Wood-Owls in Kibale National Park, Uganda to (1) describe the relationship between calling activity and season, lunar phase, cloud cover, and wind speed and (2) compare calling activity using three indices—whether or not owls were detected, number of individuals, and number of vocalizations.

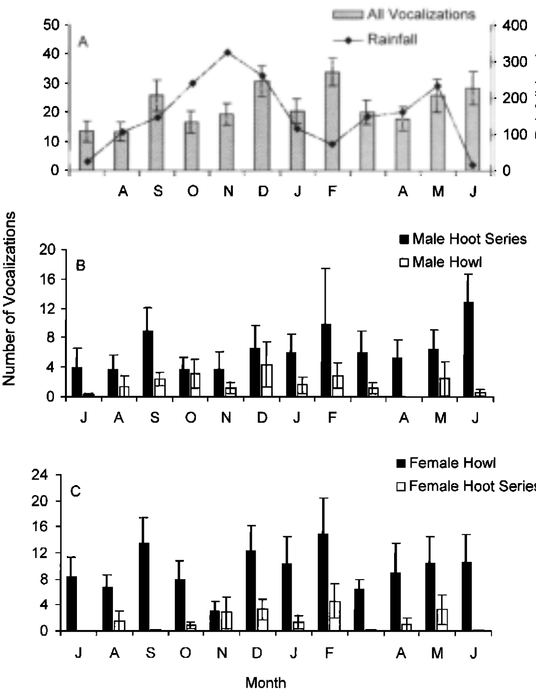

Figure 1. The mean (±SE) number of African Wood-Owl (*Strix woodfordii*) vocalizations detected per station (N = 10) per month between July 1997 and June 1998 and monthly rainfall recorded at Makerere University Biological Field Station, Kibale National Park, Uganda, for the same time period. Panel A is all vocalizations and monthly rainfall, panel B is male vocalizations only, and panel C is female vocalizations only.

STUDY AREA AND METHODS

Kibale National Park (KNP) covers 766 km^2 in western Uganda (0°13′–0°41′N, 30°19′–30°32′E). The topography is characterized by rolling hills and elevation ranges from 920 m above sea level in the south to 1590 m in the north. Yearly rainfall averages 1778 mm and there are two distinct rainy seasons each year (C. Chapman and L. Chapman unpubl. data; Fig. 1). About 58% of the park is covered by moist-evergreen forest, the remainder is secondary forest (19%), grassland (15%), swamp (4%), woodland (4%), and plantations (1%; Chapman and Lambert 2000). The forest is considered moist, evergreen forest, transitional between lowland rainforest and montane forest (Struhsaker 1997); common tree species include *Diospyros abyssinica, Markhamia platycalyx, Celtis durandii, Uvariopsis congensis,* and *Trilepsium phoberos* (Chapman et al. 1997). Canopy height ranges from 25–30 m, with a few trees as tall as 55 m.

I established two transects, one in the unlogged K-30 forestry compartment (282 ha) and the other in the K-14 (405 ha) and K-15 (347 ha) forestry compartments that were selectively logged in 1968 and 1969 (Struhsaker 1997). As a result of harvest and incidental damage, between 50% (K-15) and 25% (K-14) of all trees were destroyed in selectively-logged areas (Chapman et al. 2000) and they now have a dense, brushy understory and a broken canopy when compared to unlogged areas (Chapman and Chapman 1997). Toward one end of both transects there was a short stretch (ca. 250–500 m) with pine plantation on one side of the transect and natural forest on the other.

Each transect had five survey points, located 0.5 km apart (total length = 2 km) along forest tracks that were used infrequently by motor vehicles and never at night when surveys were conducted. The spacing of these points was based on observations of African Wood-Owl densities in South Africa, where territories were located ca. 0.5 km apart along a 23 km stretch of riparian forest (Kemp and Kemp 1989). I surveyed transects from July 1997 through June 1998 generally beginning at 2000 H (ca. 1–1.5 hr after sunset) and finishing ca. 2 hr later. Logged and unlogged transects were sampled on an alternating schedule with one transect sampled per night. The end of the transect at which sampling was initiated was alternated between samples of the same transect. I surveyed transects four times a month, generally once a week, to distribute the sampling effort throughout the lunar cycle. I did not conduct surveys on nights with rain or high winds (ca. 15 kph).

At each point, I recorded five environmental variables. Forest was categorized as either logged or unlogged. Season was defined as either wet or dry, with the six wettest months (October–December, March–May) classified as wet season, and the six driest months (June–September, January–February) classified as dry season. Cloud cover was visually estimated and categorized as 0–25%, 25–50%, 50–75%, or 75–100%. Lunar phase was categorized into four periods centered on the first day of the new moon, first-quarter moon, full moon, and third-quarter moon. Wind speed was classified as one of three levels; no wind, light breeze (1–5 kph), and strong breeze (5–10 kph). After recording the environmental conditions, I recorded all vocalizations and the number of individuals detected during a 10-min listening survey. The number of individuals was a minimum number determined by distinguishing between male and female vocalizations, or, when more than one individual of the same gender was vocalizing, by recording the number of individuals heard calling simultaneously. I differentiated between four vocalization types described by Kemp and Kemp (1989): female hooting calls, female howls, male hooting calls, and male howls. Gender was determined by vocal pitch; female vocalizations are distinctly higher than males (Kemp and Kemp 1989). Single hoots and other vocalizations that did not fit these descriptions, or that could not be identified accurately to gender, were recorded under an "other calls" category.

I used generalized linear models (hereafter GLM; Crawley 1997, Seavy et al. in press) to evaluate if season, habitat, lunar phase, cloud cover, or wind speed were associated with the number of calls detected, number of owls detected, or whether or not an owl was detected (hereafter "presence/absence"). For presence/absence data I used a binomial distribution with a logit link and for the number of calls and number of owls detected I used negative binomial distributions with a log link. I began by considering each 10-min survey as an independent experimental unit. However, because the same stations were surveyed repeatedly during the course of the study, I also analyzed the data with generalized estimating equations (GEE) that adjusted for potential correlation among stations (Horton and Lipsitz 1999). I fit these models using independent, exchangeable, and autoregressive correlation structures and found that the results were not sensitive to the choice of correlation structure.

The GLMs are pseudoreplicated, increasing the risk of Type I error, but the small number of stations limits the power of the GEE approach, increasing the risk of Type II error. I have presented results of both analyses. However, recognizing the increased risk of type I error, I have cautiously discussed only the GLM results. All statistics were performed in SAS (version 9.0) using PROC GENMOD and results were considered significant if $P < 0.05$.

To present the results graphically, I calculated an expected value based on the total survey effort in each category of environmental conditions and then expressed the observed results as a percent deviation from expected.

Table 1. Association of seasonal, forest condition (logged or unlogged), weather, and lunar variables with calling activity of African Wood-Owls (*Strix woodfordii*) as measured by number of vocalizations detected, number of individuals detected, and the presence/absence of owls at survey stations. Comparisons made with generalized linear models, assuming each survey is independent, and generalized estimating equations using an exchangeable correlation structure that accounts for repeated measures of stations. Values in bold are statistically significant.

VARIABLE	GENERALIZED LINEAR MODEL CHI-SQUARE (*P*-VALUE)	GENERALIZED ESTIMATING EQUATION CHI-SQUARE (*P*-VALUE)
Number of vocalizations		
Wind speed	**11.48 (<0.01)**	**7.99 (0.02)**
Percent cloud cover	**11.58 (<0.01)**	6.56 (0.09)
Lunar phase	**8.93 (0.03)**	6.31 (0.10)
Forest: logged/unlogged	1.86 (0.17)	1.92 (0.17)
Season	0.94 (0.33)	0.93 (0.34)
Number of individuals		
Wind speed	**7.90 (0.02)**	4.60 (0.10)
Forest: logged/unlogged	1.82 (0.18)	1.41 (0.24)
Season	1.72 (0.19)	2.60 (0.11)
Lunar phase	3.55 (0.32)	3.70 (0.30)
Percent cloud cover	1.03 (0.79)	0.72 (0.87)
Presence/absence		
Lunar phase	7.61 (0.06)	4.80 (0.19)
Wind speed	4.89 (0.09)	3.02 (0.22)
Forest: logged/unlogged	1.41 (0.24)	0.83 (0.36)
Season	1.14 (0.29)	1.07 (0.30)
Percent cloud cover	2.13 (0.55)	1.89 (0.60)

RESULTS

African Wood-Owls were detected on 232 of 480 (48%) surveys. All detections were aural. Of the 232 surveys during which owls were heard, 56% were of a single owl, 35% were of two owls, and 9% were of 4–6 owls. I heard 2652 vocalizations; 29% were male hooting, 8% male howls, 7% female hooting, 43% female howls, and 13% other calls.

African Wood-Owls were consistently detected calling throughout the year; the greatest numbers of vocalizations were heard during the months of December and February, but there was not a pronounced seasonal pattern of calling activity (Fig. 1). There was no significant difference between wet and dry seasons for any of the response variables (Table 1). The mean number of vocalizations detected per station per month ranged from 13.3–

33.9 (Fig. 1). The absence of seasonal variation of calling activity was consistent for the different vocalizations given by males and females (Fig. 1). During surveys when I detected more than a single owl, males and females often called together in what have been described as "poorly synchronized duets" (Kemp 1987). These duets typically involved the one or two male hoot calls, answered by a female howl, and often continuing in this manner for 5-min or more. The African Wood-Owl was the only species detected; I never detected Red-chested Owlets (*Glaucidium tephronotum*) or Verreaux's Eagle-Owls (*Bubo lacteus*), both of which occur in KNP (Skorupa 1983).

The statistical influence of environmental factors on calling activity varied depending on the index used and whether or not the model accommodated repeated measures (Table 1). For most response variables, the *P*-values for the association with environmental factors were greater when the GEE accounted for repeated measures (Table 1).

The number of vocalizations detected was the index most strongly influenced by environmental factors; the number of vocalizations differed among lunar phases, categories of cloud cover, and wind speeds (Table 1). Owls vocalized more often than expected during full moons and on clear nights, and less frequently during new moons and on cloudy nights (Fig. 2). Fewer calls were detected on nights with stronger winds (Fig. 2). These influences were much less pronounced when measured by the number of owls detected or by the presence/absence of owls (Fig. 2). When the number of individuals was analyzed, only wind speed was significant (Table 1). There was no influence of environmental factors as measured by the presence or absence of owls under different conditions. However, in both cases the nonsignificant trends were again consistent with differences at higher scales; I recorded fewer individuals and fewer detections during new moons and cloudy skies and more individuals and more detections during full moons and clear skies (Fig. 2). There was not a significant difference between the logged and unlogged transects for any of the response variables (Table 1).

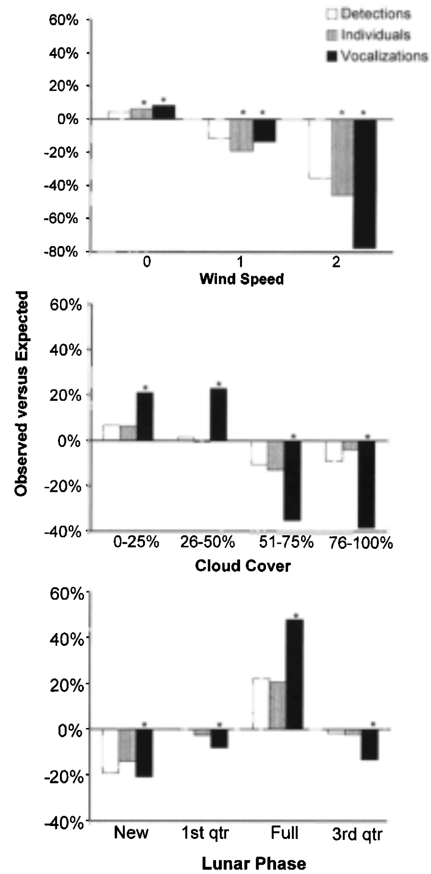

Figure 2. Percent difference between observed and expected [(obs − exp)/exp] number of African Wood-Owl (*Strix woodfordii*) vocalizations, individuals, and detections recorded during different wind speeds, cloud covers, and lunar phases at Kibale National Park, Uganda. * indicate environmental factors with significant relationships to response variables (statistics in Table 1).

DISCUSSION

The number of African Wood-Owl calls was correlated with lunar phase and cloud cover. Owls vocalized more during full moons and on clear nights, and less during new moons and on cloudy nights. Although I did not detect a significant difference in the number of individuals nor in the number of detections, the direction of nonsignificant trends was consistent with the number of calls detected (Fig. 2).

In both temperate and tropical regions, owl calling activity is associated with lunar phase. When lunar phase is a significant factor, it is almost always due to more calling activity during brighter moon phases (Northern Saw-whet Owl [*Aegolius acadicus*], Clark and Anderson 1997; Great Horned Owl [*Bubo virginianus*], Morrell et al. 1991; Mottled Owl [*Ciccaba virgata*], Vermiculated Screech-Owl [*Megascops guatemalae*], Crested Owl [*Lophostrix crista-

ta], Enriquez-Rocha and Rangel-Salazar 2001; and Elf Owl [*Micrathene whitneyi*], Hardy and Morrison 2000). This widespread pattern may result if increased activity (e.g., movement, hunting, and prey deliveries) on well-lit nights leads to a greater number of inter- and intra-pair vocal interactions.

Only Tawny Owls (*Strix aluco*; Hansen 1952) and Spotted Owls (*Strix occidentalis*; Ganey 1990) have been shown to respond negatively to moonlight, calling more on new moons than during brighter lunar phases. However, in not all cases is a positive association with moon phase consistent with a positive association with illumination. For example, of three tropical owls that increased calling activity during full moons, two decreased calling activity on bright nights (Enriquez-Rocha and Rangel-Salazar 2001). They explain these apparently contradictory results by noting that calling often occurred on dark nights with a full moon that was below the horizon or obscured by clouds. Predation risk, especially for small owls, may be a cost that reduces calling activity on moon-lit nights, but there is little evidence to either support or refute this hypothesis.

Calling activity of owls has been measured using a variety of sampling methods and indices of calling activity. This study demonstrated that the choice of index can affect the ability to identify environmental correlates of calling activity. I only detected significant effects of lunar phase and cloud cover based on the number of calls detected. Although calling activity was not significantly influenced when measured by number of individuals or presence/absence, in both cases nonsignificant trends were consistent with differences measured by the number of calls (Fig. 2). Studies that have measured presence/absence of owls may not have detected the influence of cloud cover and lunar phase that would be detected by measuring the number of vocalizations. Recording the number of owl vocalizations per survey may provide greater statistical power to detect relationships between calling activity and environmental factors. Designing studies that record multiple response variables may provide the most insight into these relationships.

African Wood-Owls called consistently throughout the year; I did not detect a difference in calling activity between rainy and dry seasons. In contrast, calling activity of many Nearctic and Palearctic owls that have been studied for an entire year usually show pronounced seasonal variation. Generally, vocal activity of temperate owls peaks either late in the nesting season, when calls accompany frequent prey deliveries to nestlings (Lundberg 1980, but see Ganey 1990), or in late summer or early autumn when young are dispersing and adults may increase calling activity to defend territories (Ritchison et al. 1988, Lundberg 1980). In East Africa, African Wood-Owls have been recorded to lay eggs in January–March and August–November (Fry et al. 1988), suggesting a bimodal breeding season (laying-fledging) during January–April and August–December. However, there was no well-defined peak in calling activity timed within these periods (Fig. 1).

The number of vocalizations, the number of individuals, and the number of points where owls were detected were not significantly different between logged and unlogged areas. However, because the sample size in each habitat was limited ($N = 5$) and statistical power undoubtedly low, these data provide little information about the effects of logging on African Wood-Owl populations.

This study demonstrates that African Wood-Owls are highly vocal and that calling activity of this tropical owl is influenced by environmental factors. The vocal nature of African Wood-Owls, and their strong response to broadcasts of conspecific song (Kemp 1987), suggests that they could be effectively censused using standard playback techniques (Forsman 1983). The use of playbacks may provide such a strong behavioral stimulus that they mask environmental influences of spontaneous calling (Ganey 1990). However, when spontaneous calling is measured, the influence of environmental factors on calling activity should be considered when designing studies and interpreting results. The ability to measure the number of owls calling will be reduced on nights with even light wind (5–10 kph) and survey effort should be standardized to avoid lunar phase and cloud cover biases.

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