

EFFECTS OF PHYSICAL AND VISUAL ACCESS TO PREY ON PATCH SELECTION AND FOOD SEARCH EFFORT IN A SIT-AND-WAIT PREDATOR, THE BLACK PHOEBE

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Abstract. For sit-and-wait predators, a key factor influencing foraging decisions is the ability to detect and track prey, which is expected to vary with the physical and light properties of the environment. We assessed how changes in visual and physical prey availability altered perch selection and visual search activity (head-movement rate and bout length) in the Black Phoebe (*Sayornis nigricans*), a sit-and-wait flycatcher. We used an observational approach by studying individuals in foraging areas that varied in the ecological factors of interest across an urbanized landscape. Black Phoebes selected perches with high levels of tree and grass cover and low light intensity, which could increase access to prey and reduce predation risk. Visual searching for prey decreased as grass cover increased and tree cover decreased, likely because of less physical and visual obstruction. Visual searching increased with light intensity, probably as a result of the effects of glare, but chromatic contrast did not exert a significant influence. We suggest that for Black Phoebes in urbanized areas physical access to prey may be mediated through the availability of an open understory and visual access through illuminance rather than discrimination of prey against the background.

Key words: Black Phoebe, chromatic contrast, flycatcher, food search, foraging, habitat structure, *Sayornis nigricans*, sit-and-wait predator

Efectos del Acceso Físico y Visual a las Presas sobre la Selección de Parches y el Esfuerzo de Búsqueda de Alimento en *Sayornis nigricans*, un Depredador de Tipo Posa y Espera

Resumen. Para los depredadores de tipo posa y espera, un factor clave que influencia las decisiones de forrajeo es la habilidad para detectar y perseguir a las presas, lo cual debería variar con relación a las propiedades físicas y lumínicas del ambiente. Evaluamos como los cambios en la disponibilidad física y visual de las presas alteró la selección de perchas y la búsqueda visual (tasa de movimiento de la cabeza y longitud del ataque) en *Sayornis nigricans*, un depredador de tipo posa y espera. Mediante observaciones, estudiamos individuos en áreas de forrajeo que variaron en los factores ecológicos de interés a lo largo de un ambiente urbanizado. *S. nigricans* seleccionó perchas con alta cobertura de árboles y pastos y con baja intensidad de luz, lo cual podría aumentar el acceso a las presas y reducir el riesgo de depredación. La búsqueda visual de presas disminuyó a medida que la cobertura de pastos aumentó y que la cobertura de árboles disminuyó, probablemente debido a una menor obstrucción física y visual. La búsqueda visual aumentó con la intensidad de luz, probablemente como resultado del efecto del resplandor, pero el contraste cromático no ejerció una influencia significativa. Sugerimos que para *S. nigricans* en áreas urbanizadas, el acceso físico a las presas puede estar regulado por la disponibilidad de sotobosque abierto y de acceso visual con buena iluminación, más que por el contraste de la presa contra el ambiente de fondo.

INTRODUCTION

Sit-and-wait predators gather information about the identity and location of prey from a distance before attacking it at an ambush site (Beachly et al. 1995, Li et al. 2003). Distance to prey is a key factor influencing foraging decisions in sit-and-wait predators (Shafir and Roughgarden 1997, Greef and Whiting 2000) and is expected to depend upon accessibility, which in turn could result from the interaction between the physical and light properties of the environment. Changes

in access to prey may cause predators to choose certain ambush sites and to allocate time to search for prey to enhance detection and tracking opportunities. Little is known, however, about how physical and visual access to prey affects ambush-site selection and food-search effort in avian sit-and-wait predators.

Visual access to prey items can be influenced by the spectral properties of ambient light (Maddocks et al. 2001, Théry 2006), reflectance of the prey item (Uy and Endler 2005), properties of the predator's sensory system (Spaethe

Manuscript received 29 August 2008; accepted 12 December 2008.

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et al. 2001, Håstad et al. 2005, Schaefer et al. 2007a), and even habitat structure (Butler and Gillings 2004). Low light is a limiting factor in the foraging abilities of several taxa (Kacelnik 1979, Richmond et al. 2004, Yamashita et al. 2005) because visual acuity (e.g., the ability to resolve objects in the visual field) is limited by the rate at which light quanta activate photoreceptors (Campbell and Gregory 1960). Extremely intense light, however, can cause glare, which can limit the detection of objects, such as predators (Fernández-Juricic and Tran 2007), although how intense light affects prey detection is unknown. Chromatic contrast (i.e., the relative Euclidean distance between two colors in a multidimensional abstract space) allows individuals to detect large objects (>2 mm for chickens) against different types of backgrounds (Fuentes 1995, Osorio et al., 1999). Achromatic contrast (or brightness) requires fewer photoreceptors than chromatic contrast; it accentuates edges as a result of lateral inhibition and is more relevant when objects are small (Schaefer et al. 2007b).

Physical access to prey can be influenced by habitat structure (Brodmann et al. 1997) but also by predator evasion (Butler et al. 2005). Habitat complexity can restrict active foragers' visual and physical access to prey (Brodmann et al. 1997, Butler and Gillings 2004). Previous studies in non-avian taxa, however, have shown that more complex habitats may increase physical access to prey for sit-and-wait predators by decreasing the ability of both potential prey (Li et al. 2003) and potential predators (Morse 2006, Shepard 2007) to detect the forager.

The purpose of our study was to determine how physical and visual access to prey items affects ambush-site selection and food-search effort in the Black Phoebe (*Sayornis nigricans*). This sit-and-wait predator allocates a discrete period of time to visual food searching before it attacks its prey (Oberlander 1939). We used head movements as a proxy for search activity as they are part of the visual tracking of prey and depth perception in birds (Kral 2003). We used an observational approach to address our goal by conducting three different field studies. We first investigated the effects of light intensity and habitat structure on perch selection (study 1). We then determined how the Black Phoebe's visual search activity (head-movement rate and length of bouts of head movement) was influenced by light intensity and habitat structure (study 2) and by chromatic contrast of prey (study 3). At our study sites, urban parks, Black Phoebes perch on natural and man-made structures and are generally found in areas with moderate levels of tree and grass cover (Wolf 1997). Black Phoebes forage on flying insects by sallying from perches (primarily trees) over open areas of grass, water, or occasionally bare ground (Wolf 1997).

We predicted that Black Phoebes select perches in areas with high grass cover to increase visual and physical access to prey, higher levels of tree cover to provide protection from predators, and relatively lower light intensity to avoid glare.

We also expected Black Phoebes to increase their rate of visual searching for prey in areas with high light intensity that might limit prey detection as a result of glare, high levels of tree cover (and low levels of grass cover) that might obstruct access to prey, and low chromatic contrast that might constrain the birds' ability to resolve prey against the background.

METHODS

STUDY SPECIES

The Black Phoebe is a small sexually monomorphic flycatcher occurring from California and the American Southwest to Central and South America (Wolf 1997). It forages throughout the day by sallying from perches into open areas to hawk insects in flight (Wolf 1991), and it also hovers and gleans insects from vegetation, generally during the early morning and late afternoon (Oberlander 1939). Black Phoebes prey mainly on highly mobile prey such as flies (Diptera) and bees and wasps (Hymenoptera) (Ohlendorf 1976, Wolf 1997). The native habitat of this species is riparian; however, human structures have provided nest sites that facilitated the phoebe's urban expansion in the U.S. (Wolf 1997). Our study sites were in urbanized areas; thus, our conclusions cannot be generalized to individuals inhabiting riparian areas. All the studied parks had similar vegetation structure, with large areas of non-native grasses interspersed with trees.

Black Phoebes are highly territorial, with territories that are smaller in the breeding (0.5–0.8 ha) than in the non-breeding season (9–11 ha, Wolf 1997). We acknowledge that the behavior of the sexes may differ; however, Black Phoebes are sexually monomorphic, so we were unable to distinguish males from females. We did not tag individuals, but their territorial behavior allowed us to minimize the chances of sampling a given individual more than once. We mapped the locations of the sampled individuals in each study area. Small parks (<2 ha) were visited only once for each field study, while large parks or college campuses (>2 ha) were visited more than once, but individuals were sampled at least 500 m away from each other. We increased the distance between sampled individuals during the breeding season because of the seasonal differences in territory size (Wolf 1991). Although we conducted studies in two different seasons, we do not believe that seasonal differences affected our data considerably, because the Black Phoebes we observed executed similar hawking and sallying flights throughout the year and did not noticeably alter their foraging-time budgets over the year, as found by Verbeek (1975). Additionally, because of the relatively low degree of weather variability in southern California, sampled habitats did not vary by season. Gleaning flights (hovering in flight to glean insects from vegetation) did appear to increase during the colder months; however, we did not include these types of foraging flights in this study. We describe each of the three field studies we conducted in different sections.

STUDY 1: EFFECTS OF LIGHT INTENSITY AND HABITAT STRUCTURE ON PERCH SELECTION

This study was conducted during June and early July 2007. Six study areas were selected in Los Angeles and Orange counties. All of the study areas were surrounded by urban matrix, which bounded the suitable habitat for Black Phoebes within the limits of the parks. Habitat structure of all parks was similar.

Through preliminary observations, we established the extent of Black Phoebe foraging areas, which were composed of clusters of trees and open areas where individuals were seen foraging, called plots. At each study area we randomly chose six plots with Black Phoebes (occupied plots) and six without them (random plots) to compare their habitat and light-intensity features. An occupied plot encompassed the first three perches we observed a Black Phoebe using consecutively. A random plot encompassed the three random perches closest to the observer (tree or man-made structure) that Black Phoebes might use. We selected perches in the random plots from objects on which Black Phoebes had been observed perching during our preliminary observations and following Wolf (1997). All of the perches selected in occupied and random plots were within the foraging areas of Black Phoebes.

Following Prodon and Lebreton (1981), we recorded percent grass and tree cover within a 10-m radius around each of the three perches per plot (more than 95% of the observed foraging flights were less than 10 m). We also recorded light intensity (lux) at each of the perches with an Extech Instruments Lux Meter (model 401025, Waltham, MA). Black Phoebes forage throughout the day and thus are subject to large variations in light intensity. We avoided sampling during sunrise and sunset to reduce the chances that light levels lower than the limits of visual resolution affect their foraging behavior. We averaged the habitat structure and light-intensity values of the three perches per sampling plot because a perch could be used from one to three times during consecutive measurements.

STUDY 2: EFFECTS OF LIGHT INTENSITY AND HABITAT STRUCTURE ON VISUAL SEARCHING

This study was conducted from January 2007 to August 2007. We observed a total of 77 Black Phoebes in 24 study areas in Los Angeles and Orange counties.

An individual was observed until it alighted on a perch. Then we began videotaping it with a Canon ZX850 digital camera until it initiated a foraging flight. All the flights recorded for this study were foraging flights, identified by their highly stereotyped path (Verbeek 1975) and visual or auditory confirmation (e.g., bill snapping) of prey capture. We recorded only sallying or hawking flights, which were the most common type of foraging flight. Flights in which Black Phoebes hovered and gleaned insects from vegetation or hopped and took insects from the grass were not included. After a foraging sally was completed, we visually estimated the capture spot (the site where the Black Phoebe attacked the

prey item). We then measured the height of the capture spot by marking the location on the ground below the capture spot and then measuring the height above the ground with a meter tape. Capture height can influence the view of the background against which prey items are detected. Grass and tree cover were measured as described above. We recorded light intensity at both the perch location, because it can alter the ability of the eye to gather information, and the capture location, because it can alter the illumination of the prey object being perceived. We also recorded the temperature at the perch location, because it could confound the effects of light intensity; areas of intense light may be warmer than shaded areas, possibly affecting Black Phoebe metabolism and foraging effort.

Immediately prior to initiating a foraging flight, Black Phoebes moved their heads rapidly ($n = 77$, 17.79 ± 0.22 head movements) over a short period of time ($n = 77$, 18.60 ± 0.21 sec), indicating tracking of prey. We acknowledge that this head movement could have also been caused by anti-predator vigilance (Jones et al. 2007); however, our observations revealed that Black Phoebes initiate foraging flights even in the presence of potential predators (adult predators: Cooper's Hawk, *Accipiter cooperii*; nest predators: American Kestrel, *Falco sparverius*, corvids, *Corvus* spp.). Furthermore, head movements prior to a foraging flight were faster than those when individuals perched but did not attack prey or those before flights to a different perch (Gall and Fernández-Juricic unpubl. data). Thus we considered the high frequency of head movement prior to a foraging flight a proxy for visual searching.

From the video, we measured the length of head-movement bouts and the head-movement rate (number of head movements divided by head-movement-bout length) by using JWatcher 1.0 (Blumstein et al. 2000). We chose these two variables as indicators of frequency and time, respectively, allocated to visually tracking the environment. These variables were not significantly correlated ($r = 0.089$, $P = 0.477$). Our original intent was to analyze capture success; however, 99% of the recorded attacks ended in successful captures.

STUDY 3: EFFECTS OF CHROMATIC CONTRAST OF PREY ON VISUAL SEARCHING

This study was conducted from August 2007 to December 2007. We observed a total of 30 Black Phoebes in five study areas in Los Angeles and Orange counties. Although we were interested in the effects of chromatic contrast of prey, for each individual we also recorded percent tree cover and percent grass cover, as described above, to control for their potential confounding effects. We only included typical sallying flights and measured the rate and bout length of head movements.

In this study, we estimated an indicator of the ability of individuals to perceive a prey object against the background by following Endler and Mielke's (2005) approach, which consists of recording irradiance (the amount of light energy at

each wavelength) and the reflectance of the background (the percent of light transmitted rather than absorbed by an object at each wavelength) after the animal catches a prey item. Chromatic contrast is an important part of target detection, even when objects are moving within the optic field (Dyer and Chittka 2004). In addition, we recorded the reflectance of a model prey item and used parameters of a V-type avian visual system that is characteristic of suboscines like the Black Phoebe (Barker et al. 2001, Hackett et al. 2008). Birds with a V-type visual system have short-wavelength cones with peak sensitivity in the violet wavelengths in addition to cones that absorb light of short, medium, and long wavelengths (reviewed in Hart and Hunt 2007).

We used a Stellarnet EPP2000 portable spectroradiometer (Tampa, FL) to measure reflectance and irradiance. Immediately following a foraging flight, we placed a 1-m² PVC square at the capture location. We recorded reflectance at ground level at 15 randomly selected spots within the square plot every 0.5 nm (range 300–700 nm). We used a micron fiber-optic probe with a Tungsten Krypton light source housed in a black plastic block sheath, which ensured that the light source and distance to the substrate were consistent. The probe was positioned at a 45° angle to prevent glare (Uy and Endler 2004). Prior to each measurement, the probe was calibrated with a flat white standard and a dark current. We recorded irradiance every 0.5 nm (range 400–700 nm) in photons m⁻¹sec⁻¹ at the capture location by means of a cosine-corrected sensor calibrated with a standardized light source. We placed the irradiance probe 15 cm above the substrate and took readings with the probe facing up, north, south, east, and west, representative of the light conditions where objects are being viewed.

Because it was not possible to recover the prey items captured, we used a model insect that Black Phoebes often capture in our study areas (MDG, pers. obs.): the honey bee (*Apis mellifera*). Bees and wasps constitute 31–59% of the Black Phoebe's diet (Beal 1912). Black Phoebes captured honey bees around flowers at ground level. We obtained similar results on the effects of chromatic contrast with other model organisms, such as ants and worms. We took 15 reflectance measurements from the model insect. We used the same micron fiber-optic probe, calibrated as above, but housed it in a round black plastic sheath with an angled tip to facilitate reflectance measurements from small objects.

We averaged the 15 measurements for each component of the radiance spectra (irradiance, substrate reflectance, model prey item's reflectance) for each Black Phoebe recorded. We established the birds' ability to perceive the model by considering the interaction between ambient light (irradiance at the capture site), the spectral properties of the object (reflectance of the background and the prey item), and the properties of both the avian V-type visual systems (e.g., absorbance of the cones' outer segment, transmission spectra of the oil droplets, cross-sectional area of the inner cone segment; see

the appendix of Endler and Mielke 2005 for specific photon-capture values). We calculated the light spectra reaching the individual's eye with the formula $Q(\lambda, X) = I(\lambda)R(\lambda)T(\lambda, X) + V(\lambda)$, where $Q(\lambda, X)$ represents the radiance spectrum of light reaching the eye at distance X , I is the irradiance spectrum (ambient light), R is the reflectance spectrum, $T(\lambda, X)$ is the transmission spectrum at distance X , and V is the veiling light (Endler and Mielke 2005). The transmission spectrum is the amount of light being transmitted at a particular wavelength and distance. Veiling refers to impurities in the air (e.g., fog, particulates) that can scatter light of a particular wavelength. We assumed that $V(\lambda) = 0$ and $T(\lambda, X) = 1$ (Endler and Mielke 2005) because measurements were taken on days without cloud cover and Black Phoebes were within 10 m of the prey when they initiated foraging flights. To determine the total photon capture for each cone type, we used the equation $Q_r(X) = \int_{300}^{700} Q(\lambda, X)C_r$ where $Q_r(X)$ is the total photon capture at distance X of one cone type, $Q(\lambda, X)$ is the total radiance spectrum reaching the eye, C_r is the probability spectrum of photon capture of each cone class. There are no published absorbance spectra for the visual pigments of the Black Phoebe, or any other species of Tyrannidae (Hart and Hunt, 2007), so we used the C_r values reported by Endler and Meikle (2005) with the V-type visual system: cross-sectional area of the cone = 8×10^{-13} m², cone absorption distance = $13\text{--}15 \times 10^{-6}$ m, posterior nodal distance = 8.5×10^{-3} m. C_r values of various species deviate only slightly from those of an average bird with a V-type visual system (Endler and Meikle 2005). We obtained similar results with a U-type visual system.

Little is known about the neural processing involved in avian color discrimination, thus to avoid making assumptions about neural processing and the relative sensitivity of the four cones, we scaled the summed $Q(X)$ for the four avian cone types to one (following Uy and Endler 2004). The values were plotted in a tetrahedral space with a height of one. To determine the chromatic contrast between prey (Q_{rp}) and background (Q_{rb}), we calculated the Euclidean distance between the points in the tetrahedral space as follows:

Contrast =

$$\sqrt{(Q_{1b} - Q_{1p})^2 + (Q_{2b} - Q_{2p})^2 + (Q_{3b} - Q_{3p})^2 + (Q_{4b} - Q_{4p})^2}.$$

STATISTICAL ANALYSES

We checked all data for normality and homoscedasticity and transformed some variables (see below). We used a different dataset for each of the three studies. We analyzed the data with Statistica 8.0. We report mean \pm SE throughout.

Effects of light intensity and habitat structure on perch selection. We used general linear models with park as a random factor and perch (phoebe or random) as a fixed factor to determine whether there were differences in light intensity, grass cover, and tree cover between perches used by Black

Phoebes and random perches. We used a single mean value per sampling plot for the analysis.

Effects of light intensity and habitat structure on visual search activity. We log-transformed head-movement-bout length to meet normality assumptions. Using general linear models, we analyzed the effects of grass cover, tree cover, capture height, and light intensity at the perch and capture sites on head-movement-bout length and head-movement rate. Because of the uneven distribution of capture heights, we entered this variable in the model as categorical (two levels: ground, above ground).

Effects of chromatic contrast on visual searching. We used general linear models to determine the influence of the chromatic contrast of prey on head-movement-bout length and rate. We also included other independent factors as potentially confounding (on the basis of the previous two studies): grass cover and tree cover.

For each study, we present the results of Pearson product-moment correlations between the independent factors, descriptive statistics, and the results of the aforementioned models. We also present the proportion of variability explained by the significant factors with partial η^2 values.

RESULTS

EFFECTS OF LIGHT INTENSITY AND HABITAT STRUCTURE ON PERCH SELECTION

We found significant correlations between the independent factors: tree cover and light intensity were negatively correlated ($r = -0.65$, $P < 0.001$), grass cover and light intensity were negatively correlated ($r = -0.38$, $P = 0.001$), and tree cover and grass cover were positively correlated ($r = 0.25$, $P = 0.037$). Therefore, the effects of each of these factors on perch location cannot be considered independent.

The average height of perches used by Black Phoebes was 1.31 ± 0.11 m. Light intensity at perches used by Black Phoebes (BP) was significantly lower (310.81 ± 39.98 lux) than at random perches (525.41 ± 53.63 lux; partial $\eta^2 = 0.155$; Table 1). Both percent tree cover (BP, $58.47 \pm 5.77\%$; random, $42.56 \pm 6.08\%$; partial $\eta^2 = 0.057$) and percent grass cover (BP, $88.75 \pm 3.29\%$; random, $71.39 \pm 5.45\%$; partial $\eta^2 = 0.120$) were significantly higher at perches used by Black Phoebes than at perches selected at random (Table 1). The effects of park and the interaction between park and perch type were not significant for any of the studied variables (Table 1).

EFFECTS OF LIGHT INTENSITY AND HABITAT STRUCTURE ON VISUAL SEARCHING

There were no significant correlations among the independent factors included in this dataset (grass cover, tree cover, and light intensity at the perch and capture sites; $r < 0.122$; $P > 0.301$), which considers only perches from which a successful hawking/sallying foraging flight was initiated and does not

TABLE 1. Differences in the light intensity, grass cover, and tree cover between perches used by Black Phoebes and random perches. Results from general linear models with one fixed factor (perch type), one random factor (park), and the interaction between perch type and park. Significant effects are marked in bold.

| | <i>F</i> | df | <i>P</i> |
|--------------------------|----------|-------|------------------|
| Light intensity | | | |
| Intercept | 76.80 | 1, 60 | <0.001 |
| Park | 2.68 | 5, 60 | 0.151 |
| Perch type | 13.57 | 1, 60 | 0.014 |
| Park \times perch type | 0.81 | 5, 60 | 0.546 |
| Grass cover | | | |
| Intercept | 300.98 | 1, 60 | <0.001 |
| Park | 2.00 | 5, 60 | 0.232 |
| Perch type | 7.09 | 1, 60 | 0.045 |
| Park \times perch type | 1.16 | 5, 60 | 0.340 |
| Tree cover | | | |
| Intercept | 83.11 | 1, 60 | <0.001 |
| Park | 4.68 | 5, 60 | 0.058 |
| Perch type | 9.65 | 1, 60 | 0.027 |
| Park \times perch type | 0.38 | 5, 60 | 0.862 |

include random perches. Temperature could be a confounding factor related to light intensity, but we found no correlation between these variables at the perch site ($r = 0.122$, $P = 0.306$).

The average head-movement rate was 0.96 ± 0.03 events sec^{-1} with an average bout length of 18.6 ± 1.87 sec. The average distance of hawking/sallying foraging flights was 5.58 ± 0.32 m, the average capture height 0.31 ± 0.10 m.

Head-movement rate was significantly higher when prey items were captured in the air (1.26 ± 0.07 events sec^{-1}) rather than on the ground (1.01 ± 0.043 events sec^{-1} ; partial $\eta^2 = 0.065$). In addition, head-movement rate increased significantly as tree cover (partial $\eta^2 = 0.104$) and light intensity at the capture site increased (partial $\eta^2 = 0.054$; Table 2; Fig 1a, b). Head-movement rate was not significantly associated with light intensity at the perch location or with grass cover (Table 2). Head-movement-bout length decreased significantly as grass cover increased (partial $\eta^2 = 0.074$; Table 2; Fig 1c) but was not significantly affected by light intensity at the perch and capture sites, height at the capture site, and tree cover (Table 2).

EFFECTS OF CHROMATIC CONTRAST ON VISUAL SEARCHING

There were no significant correlations among the independent factors in this dataset (grass cover, tree cover, chromatic contrast of prey; $r < 0.330$, $P > 0.08$). In 23 videos in which we could establish the substrate, the backgrounds over which prey was captured were grass (78.3%), other vegetative ground cover (8.7%), bare earth (4.3%), and concrete (8.7%).

Assuming the V-type visual system, we found that head-movement rate was not significantly affected by chromatic

TABLE 2. Differences in (log) head-movement-bout length and head-movement rate in relation to habitat structure and light intensity. Results from general linear models with five fixed factors (light intensity at the perch site, light intensity at the capture site, grass cover, tree cover, and capture height). Significant effects are marked in bold.

| | <i>F</i> | <i>df</i> | <i>P</i> |
|--|----------|-----------|--------------|
| (log) Head-movement-bout length | | | |
| Intercept | 51.65 | 1, 71 | <0.001 |
| Light intensity at the perch site | 0.80 | 1, 71 | 0.372 |
| Light intensity at the capture site | 1.68 | 1, 71 | 0.199 |
| Percent grass cover | 5.65 | 1, 71 | 0.020 |
| Percent tree cover | 0.04 | 1, 71 | 0.848 |
| Capture height | 0.24 | 1, 71 | 0.627 |
| Head-movement rate | | | |
| Intercept | 29.63 | 1, 71 | <0.001 |
| Light intensity at the perch site | 1.66 | 1, 71 | 0.202 |
| Light intensity at the capture site | 4.06 | 1, 71 | 0.048 |
| Percent grass cover | 3.61 | 1, 71 | 0.061 |
| Percent tree cover | 8.24 | 1, 71 | 0.005 |
| Capture height | 4.95 | 1, 71 | 0.030 |

contrast ($F_{1,26} = 1.92$; $P = 0.177$), controlling for tree cover ($F_{1,26} = 1.14$; $P = 0.296$). Furthermore, head-movement-bout length was not significantly influenced by chromatic contrast ($F_{1,26} = 0.17$; $P = 0.680$), controlling for grass cover ($F_{1,26} = 0.16$; $P = 0.680$).

DISCUSSION

We found that (a) Black Phoebes occupied perches where light intensity was lower and tree and grass cover were higher than at random perches within foraging patches, (b) head-movement-bout length decreased as grass cover increased, (c) head-movement rate increased with increasing tree cover and light intensity at the capture site, and (d) chromatic contrast did not affect visual searching. Using an observational approach, we determined that physical access to prey may be mediated through the availability of an open understory and visual access through illuminance rather than discrimination of prey against the background.

Black Phoebes appear to prefer to perch in locations with high levels of tree cover, even though tree cover can require them to increase visual searching for prey (i.e., increase head-movement rate). However, tree cover may provide Black Phoebes two possible advantages: a reduction in light intensity at the perching site and a reduction in risk of predation. Black Phoebes forage continuously through the day (Wolf 1997) and may experience high light intensity at midday. The average light intensity at the perch sites studied is well above the threshold constraining visual acuity (Dabrowska 1975, Hodos et al. 1976). High light intensity may make resolving prey items more difficult and may also increase heat stress (e.g., Guthery et al. 2005). Furthermore, Black Phoebes are countershaded and forage under trees with a high canopy

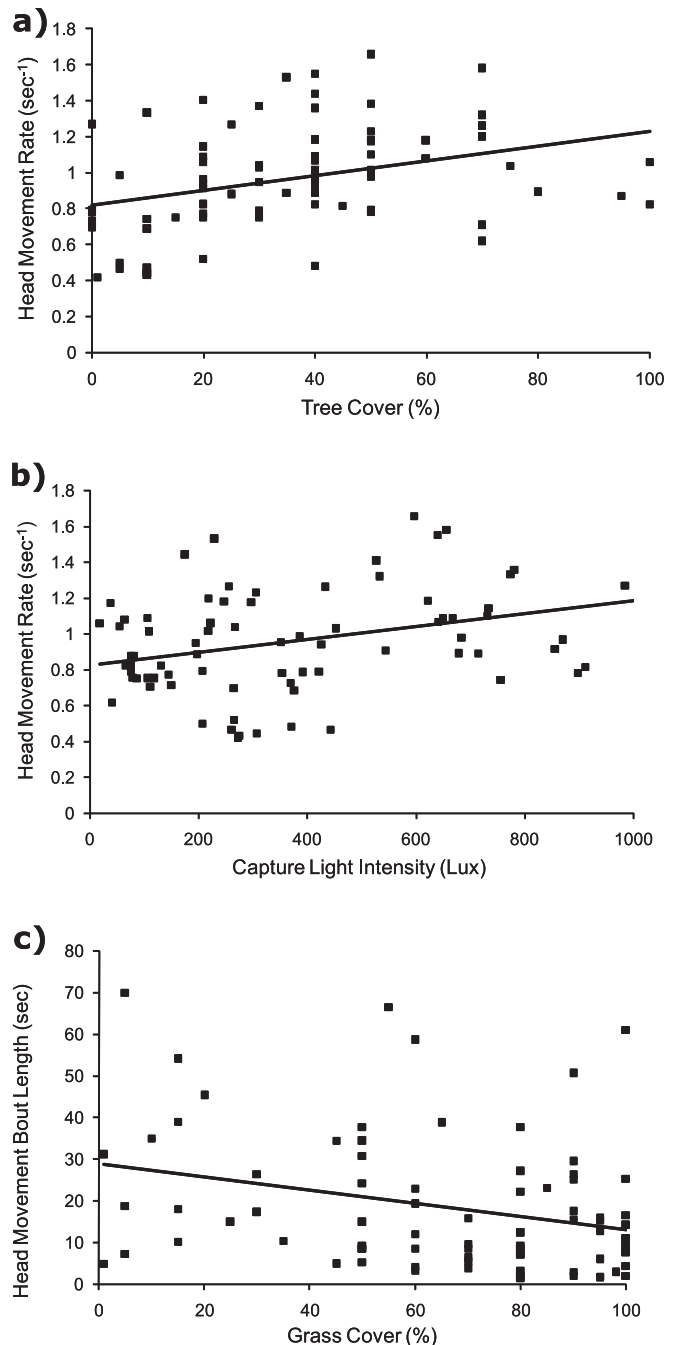


FIGURE 1. Relationships between the Black Phoebe's search effort and factors of habitat structure and light intensity: (a) head-movement rate and tree cover, (b) head-movement rate and light intensity at the capture site, and (c) head-movement-bout length and grass cover.

cover, factors probably concealing them from predators. The sparse distribution of these trees may provide refuge from the Black Phoebe's main predator, the Cooper's Hawk, which prefers habitats with higher tree density (Rosenfield and Bielefeldt 1993).

Black Phoebes are found in areas with high grass cover, which suggests that they avoid shrubby vegetation. An open understory may reduce the need to maneuver and increase the number of potential flight paths that can result in a successful attacks (Verbeek 1975). In urban parks these open areas are watered frequently, creating a higher insect density which also may make them more favorable to phoebes. However, we found that prey density (estimated with Malaise traps) did not affect the Black Phoebe's rate of visual searching (Gall and Fernández-Juricic unpubl. data).

We used head-movement rate as a proxy for rate of visual searching. Black Phoebes increased their head-movement rate with increasing tree cover, which may decrease the ability of individuals to track prey items by obstructing line of sight. Habitat structure that alters visual access has been found to affect search activity in other predators, such as the Water Pipit (*Anthus spinoletta*) (Brodmann et al. 1997) and Northern Lapwing (*Vanellus vanellus*) (Butler and Gillings 2004). Alternatively, increased head movements prior to flight in a patch with high tree cover may also be related to individuals scanning for predators before risking exposure during the foraging flight.

As light intensity increased at the spot in which prey were attacked, Black Phoebes increased their head-movement rate, possibly because of glare (i.e., light scattering in the eye; Campbell and Gregory 1960, Spencer et al. 1995, Fernández-Juricic and Tran 2007). Additionally, where light intensity is high, flying insects may move faster because of higher body temperature (e.g., Brussard and Ehrlich 1970), and these faster-moving insects could also increase the need for Phoebes to track their spatial location. Flying insects move more rapidly and erratically in space than insects on the ground (Dudley 2002). This visual-tracking interpretation is supported by our finding a higher head-movement rate when Black Phoebes captured insects in the air than when they captured them on the ground.

Chromatic contrast is known to affect the conspicuousness of prey (Endler 1984, 1991, Théry and Casas 2002, Håstad et al. 2005) and the selection of prey items (Church et al. 2001, Schaefer et al. 2007a), yet we found little evidence that the chromatic contrast of prey affects the Black Phoebe's visual searching. Grass served as the background against which prey was captured in most of the recorded attacks. Grass has a shallow reflectance spectrum with a peak around 550 nm, which could reduce the chromatic distance between the background and the prey, thereby reducing the role of chromatic contrast in prey detection. Thus visual acuity and motion detection may be more important for detecting and tracking small mobile prey than chromatic contrast is. Future studies should assess whether visual contrast is relevant at the level of perch selection, that is, whether the birds choose perches where the contrast is above a certain threshold).

Our results have implications for habitat-selection mechanisms in this species. The physical structures of the Black

Phoebe's native and urban habitats share some features. Black Phoebes occur in riparian areas with large trees along rivers, where individuals make foraging sallies over open water or occasionally dry riverbeds (Wolf 1997). Similarly, urban phoebes perch in large trees and catch insects over grassy lawns where insects are abundant (Verbeek 1975). We suggest that this type of habitat structure may facilitate access to prey and reduce predation risk, which in concert with a higher availability of nest sites (Wolf 1991), may be important in explaining the expansion of Black Phoebes into urbanized landscapes. Other insectivorous birds, such as the Eastern Bluebird (*Sialis sialis*) across golf courses (Stanback and Seifert 2005), have also expanded into the urban setting.

Our study also has theoretical implications. We found evidence suggesting that physical and visual access to prey influence food-search effort. Such access is key to sit-and-wait predators, as they generally search from a fixed location, which allows them to vary search time without substantially altering energy expenditure (in comparison to active foragers) in order to reduce the costs of an unsuccessful foraging attack. Visual constraints should be taken into consideration when predictions of encounter-at-a-distance models are tested (Shafir and Roughgarden 1997). For instance, in a heterogeneous environment the threshold distance at which a predator may pursue prey is expected to decrease under conditions that reduce visual access to prey (e.g., light-intensity levels that limit visual resolution) irrespective of variation in food density. Future studies should also address how predation risk influences prey-search activity under different light conditions.

ACKNOWLEDGMENTS

We thank C. Lowe, D. Underwood, C. Bosque, and an anonymous reviewer for their useful comments on an earlier version of the draft, and we thank K. Malabanan, M. Weinberger, L. Hough, J. Caprile, and S. Thomas for their assistance in the field. This work was funded by a Sigma Xi Grant-in-Aid of Research.

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